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AfricanBats NPC

Conserving Africa's Bat diversity

AFRICAN CHIROPTERA REPORT

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Introduction

The purpose of the African Chiroptera Report is to collate published information on, and collate specimen records of, African bats. The advent of the internet provides an opportunity for large amounts of information to be easily and economically updated and accessible, which is particularly important for taxonomic information. The electronic, web-based nature of the information is intended to allow information on African bats to be corrected/updated more frequently than a printed format allows, and to be available to users in an affordable form that can be manipulated to their specific requirements. It is hoped this tool will facilitate research and conservation planning and possibly stimulate interactions across different areas of research. The report is generated from data collated in the African Chiroptera Database that has grown over the past 20 years of development with the addition of new and corrected information.

The incorporation of information other than taxonomic (see the various section headings in the description of the layout below), is still patchy in its execution across the taxa. Information that may answer specific requirements of a user, i.e. more information about the voucher specimens, or specimen collectors, has been drawn from across the database and is presented in separate appendices. Published identification keys for African bat species, have, where necessary, been updated to include current names, and are presented in appendix 5. In appendix 6 images of type specimens are included as they become available.

TAXONOMY

The report is currently most comprehensive in the presentation of information on all known synonyms, for presently accepted taxa of African bat species. Having a high Chiroptera diversity, there are currently 26 families (incl. 5 extinct), 257 genera (26 extinct) and 1500 species (55 extinct) recognized as occurring (or having occurred) in Africa. An overview of the number of genera and species per family occurring in Africa is shown in Figure 1. Usually, the number of species is larger than the number of genera, but there is one exception: in the Megadermatidae, three genera and two species are mentioned. The reason for this is that only extant taxa are included, and although *Megaderma gigas* is an extinct species, the genus itself still has representatives in Asia. The graph further shows that the Vespertilionidae contain the largest number of both genera and species, followed by the Molossidae and Pteropodidae in number of species, and by the Pteropodidae and Molossidae in number of genera.

The report also aims to incorporate information on the whereabouts of type specimens, name combinations, and spelling variations and errors/lapsus calami in names.

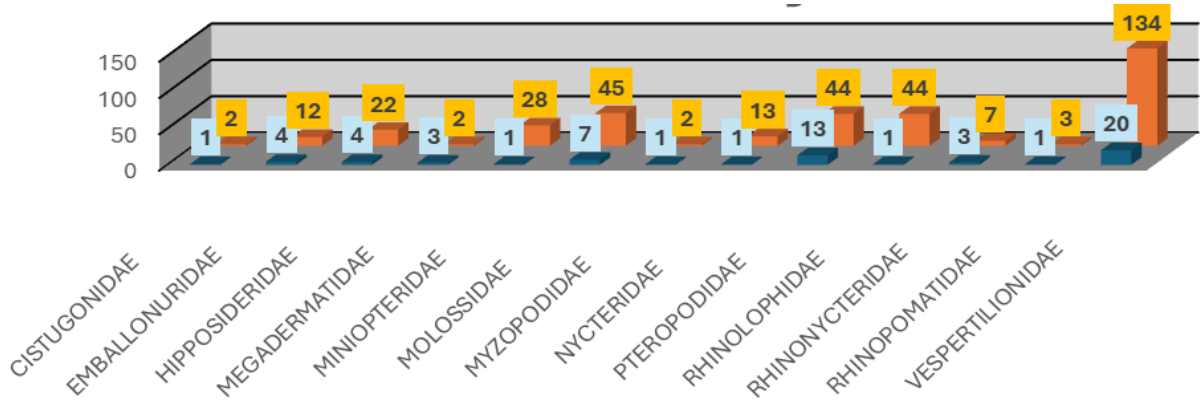

Figure 1. Overview of the number of extant genera (yellow) and species (red) per family occurring in Africa (Modified after Srinivasulu *et al.*, 2010: 1008).

GEOGRAPHIC SCOPE

This report covers the geographic area of the African continent and adjacent regions, including, Madagascar, and other surrounding islands in the Indian and Atlantic oceans (Figure 3). This and previous issues of the report have focused attention mainly on capturing information from the African continent and the associated islands. The taxa from the Arabian Peninsula are included as far as these are shared with the African continent.

SPECIES RICHNESS AND ESTIMATES

Figure 2 shows the number of families, genera and species occurring in the various African countries. The most diverse country in number of genera and species is The Democratic Republic of the Congo, followed by Kenya, Cameroon and Tanzania (all over 100 species) (see Figure 3 and 4).

Species lists per country together with voucher specimens (evidence) can be located in Appendix 2e.

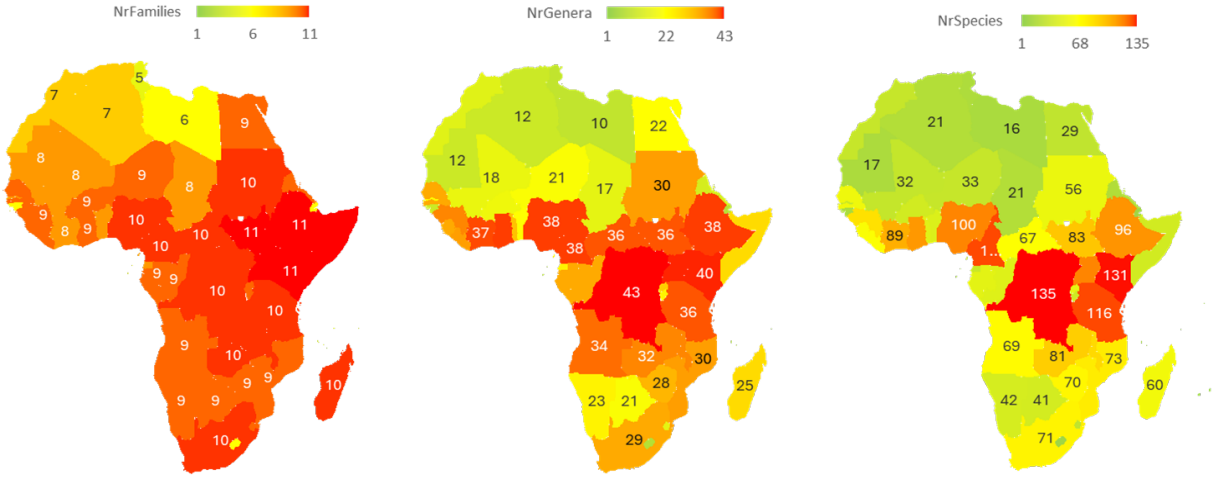

Figure 2. Overview of the number of extant families (blue), genera (yellow) and species (red) occurring in the various countries in Africa (Modified after Srinivasulu *et al.*, 2010: 1008).

Species richness maps for individual countries showing all known records have been mapped at a quarter degree level (0.25) (Appendix 2h).

Examination of the estimated spatial extent of collection coverage (Figure 4) indicates large areas where there is urgent need for surveys. Within southern Africa – southeastern Angola is in desperate need of preliminary survey work, as well as smaller areas in northern Mozambique, Botswana southwestern Zambia and Northern Cape Province of South Africa. In East Africa - Tanzania and Somalia should be prioritized and in Central Africa - The Democratic Republic of the Congo.

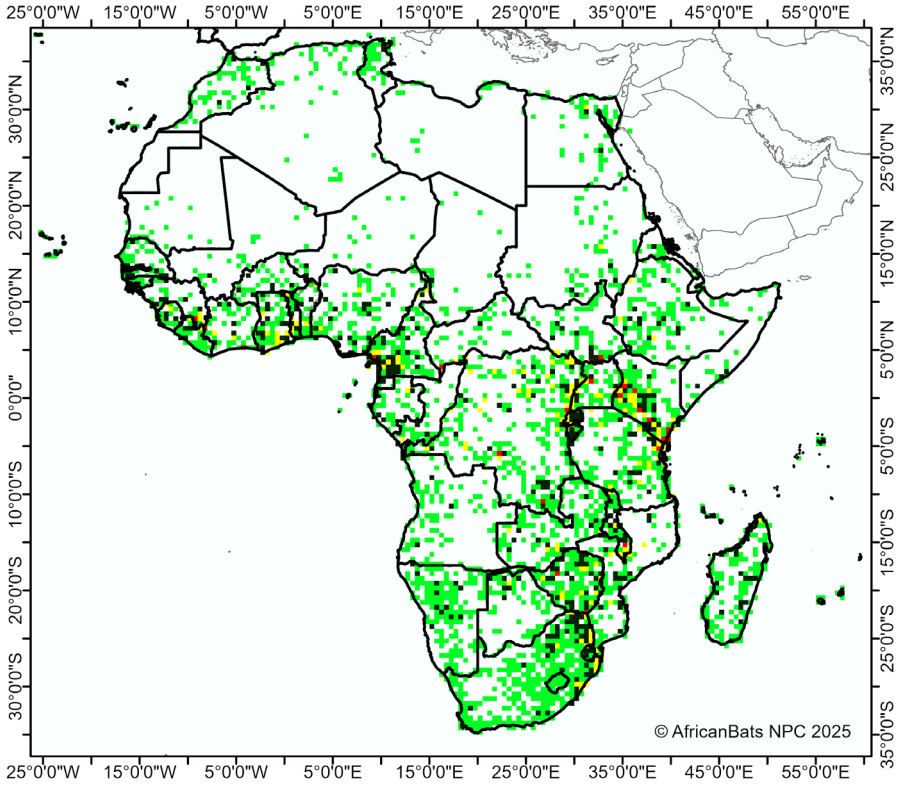

Figure 2. African bat species richness map, calculated in half degree grid (0.5) size from the specimen data in the African Chiroptera Database 2025. Light green = 1- 8 species; dark green / black = 9 – 17 species; yellow = 18 - 25 species; orange = 26 - 34 species; red= 35 - 59 species.

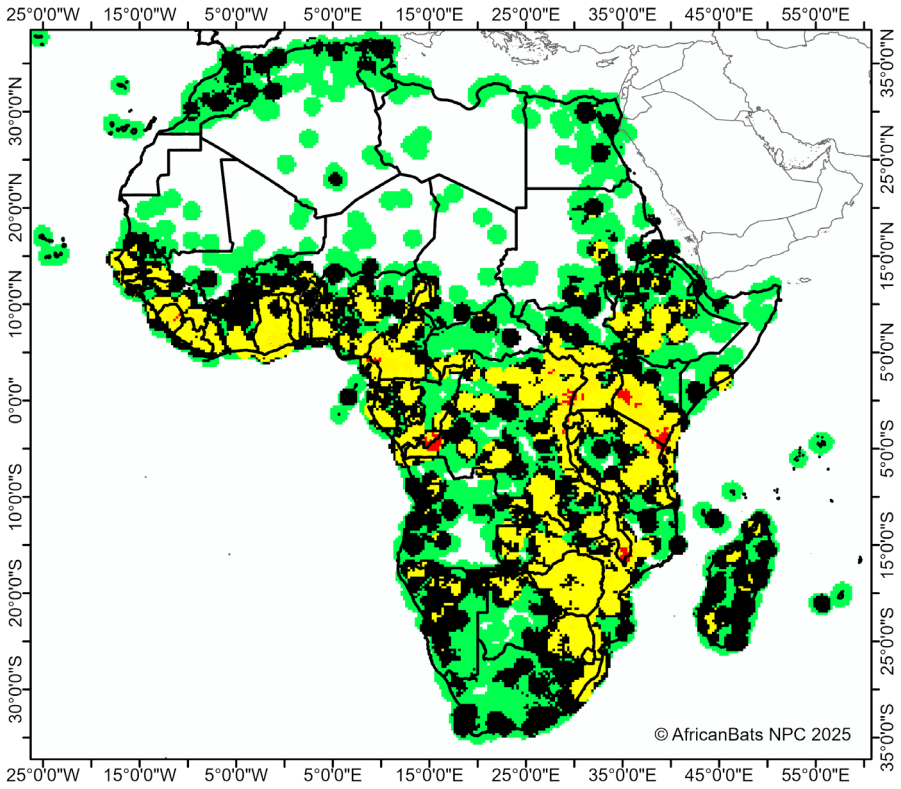

Figure 3. African bat species richness estimator (Chao 2) was used to calculate in quarter degree (0.25) grid size the specimen data in the African Chiroptera Database 2025, using DIVA-GIS 7.4.0.1 (http://www.diva-gis.org) with a nearest neighbour set at 2. Light green = 1 – 10; dark green / black = 11 – 30; yellow = 31 – 65; orange = 66 – 100; red = 101 – 150.

All light green areas in species richness maps should be viewed with some caution as these only represent 1 - 10 species. These areas most likely indicate bat records collected as part of larger

mammal fieldwork or were collected opportunistically. Therefore, areas that are light green require surveys that will focus attention of the bat species found at these sites.

For Sub-Saharan Africa, Monadjem and Schoeman (2013: 104) indicate that the highest species richness is recorded in the Albertine Rift, the northern shores of Lake Victoria in East Africa, and the Upper Guinean forest zone of West Africa. Furthermore, eastern South Africa, southern Mozambique, Zimbabwe, Malawi, coastal Kenya and Tanzania, the Ethiopian rift valley, the Congo basin north of the Congo River and the humid Guinean woodlands north of the rainforest in West Africa have a high species richness. The poorest species richness, they found (not unexpectedly) in the arid zones of south-western Southern Africa, the entire Sahel zone of North Africa, and the Horn of Africa. But the latter might still be the result of (large) collections in various museums, which are still unreported (as was already indicated by Schlitter and Delany, 1985: 47).

SPECIMENS

At the time the 2025 report was generated the African Chiroptera Database contained 151763 specimen records of which 148353 specimens had co-ordinates. This indicates that 97.7 % of the available records could be plotted.

The species distribution maps created in this report probably indicate biases in relation to the collections from which data has currently been obtained. In previous issues of the ACR, it was estimated that about 100,000 to 150,000 specimen records were available for African Chiroptera in collections around the world. This is now believed to be a serious underestimate of potentially available specimens (many European, African and Asian museum collections have not been captured as yet). We currently suspect that a more realistic number of records is possibly between 200,000 – 300,000. Using these revised estimates, we assume that between 50.5 - 75.8 % of available records have been captured in the ACD, for 2025.

LAYOUT OF ACCOUNTS

The taxa are presented in alphabetical order, top down (Order, Suborder, Infraorder…etc.).

In the synonyms list, an asterisk (*) in front of the year indicates that the synonym represents the original name for the taxon. This also reveals instances where it is not necessarily the oldest name that has taken precedence. The use of colours denotes the following: red - first name used; blue - name currently in use; green - valid synonyms; black - name combinations, spelling variations and errors/lapsus calami. A question mark (?) in the position of the year indicates that the first use of a particular name combination has not yet been determined.

Information relating to the following section headings, or citations to relevant publications, may also be presented in an account, if information relating to these sections has been published or communicated (e.g. "*pers. comm.*" or "unpublished report"), and has been entered in the database. Sections marked as "unknown" indicate that literature data explicitly mention that this information is "not known" (contrary to not having found any information on the topic).

Taxonomy:
Provides a brief history of previous studies in systematics, giving a summary of different conclusions arising from different methodologies and the resulting taxonomic debates. Much of this information has been taken from Simmons (2005).

Common names:
Common names used, in a variety of different languages, and found in various sources: e.g. Afrikaans (Roberts, 1951),Chinese (Musila *et al.*, 2018a), Czech (Benda, 2010), Dutch (Dietz and Kiefer, 2017), English (Roberts, 1951; Wilson and Cole, 2000), French (http://www.planet-mammiferes.org; Stéphane Aulagnier, pers. comm.), German (Rudi Hasslauer, pers. comm.), Greek, Albanian and Macedonian (Papadatou *et al.*, 2011), Italian: (Lanza *et al.*, 2015), Maltese (http://www.geocities.com/RainForest/3096/bats.html), Spanish (UNEP-WCMC, 2003; Fa, 1991), Arabian and Hebrew (Ferguson, 2002), Tamil (Kamalakannan and Nameer, 2019). Lina (2017) provided an overview of common names of Europan bats in every possible European language. As a large number of these bats also occur in (northern) Africa, these vernacular names are included too.

Etymology of name:
Information about the origin/meaning of the name.

Similar species:
Information about other taxa, with which there has been a recorded mistake in identification.

Palaeontological / archaeological records:
Any records identified from palaeontological or archaeological sites.

Conservation status:
This section is split into two categories: Global - provides information on past and present Red data assessments of the global populations of a species and; Regional - provides information on past and present Red data assessments of regional or country specific assessments of a species.

General distribution:
Distribution of the taxa in Africa, and extra-limital to Africa. Much of this information also comes from Simmons (2005). Additional records are indicated by a reference to their source.

Biogeography:
Information about the evolutionary processes that have driven speciation of the taxa and also its possible historical distributions in association with sister taxa.

Geographic variation:
Any known variation within a taxon across its distribution.

General description of external morphology:
Information about the outward appearance that may distinguish a taxon.

General description of cranial and dental morphology:
Information about the skull, mandible and teeth that may be distinguishing characters of a taxon.

Detailed morphology:
More detailed description of some structure of a taxon, i.e. for the baculum, tragus, hyoid, or wingshape.

Functional morphology:
Information on any work that has related morphological structure to function.

Sexual dimorphism:
Any known variation within a taxon between males and females.

Echolocation:
Information about the echolocation call of a taxon.

Molecular biology:
Information in this section is currently divided into three categories for information on DNA, Karyotype, and Protein/allozyme. The following abbreviations are used in the description of the karyotype: **2n -** diploid number, **FN -** fundamental number of autosomal chromosome arms, **BA -** total number of biarmed autosomal chromosomes, **X -** female sex chromosome, and **Y -** male sex chromosome.

Habitat:
Information about the environment in which a taxon has been recorded.

Behaviour:
Information about the timing and actions of a taxon.

Roost:
Indicates where a taxon settles during the day and at night.

Migration:
Any records of period movement from one geographic area to another.

Feeding/diet:
Records of behaviour in relation to feeding, and what is eaten.

Predators:
Records of other species know to eat the taxon in question.

Population:
Information in this section is separated into two categories: structure - in relation to any organization between individuals, and density - in relation to the number of individuals.

Lifespan:
Records relating to how long individuals of a taxon are known to live for.

Reproduction and ontogeny:
Information relating to the biology associated with producing further members of a species, and the growth/development over the course of a lifespan.

Mating:
Information relating to the behaviour associated with producing further members of a species.

Post-natal development:
Information relating to changes that occur after birth.

Parasites:
Information relating to both ectoparasites (parasites living outside the body), and endoparasites (parasites living within the body).

Viruses:
Any known viruses carried by a taxon. The taxonomy followed is that by the ICTV (International Committee on Taxonomy of Viruses - http://www.ictvonline.org/index.asp).

Utilization/significance:
Information about how a taxon may be used or viewed by people.

Distribution map:
The species distribution maps should still be viewed with some caution, since these are based on voucher specimen records currently included in the African Chiroptera Database. Hence, the actual distribution of the taxon might be more extensive than indicated on the maps, and the voucher specimen classification/identification may not be accurate. On the other hand, it might also be possible that the actual distribution is more restricted than indicated on the maps. This might be due to the inclusion of historical data, which indicate localities where the animals might have occurred a 100 (or less) years ago, when the habitat was favourable for the animals, but which currently is no longer the case (e.g. increased desertification, destruction of rain forest…). Additionally, it needs to be pointed out that due to variety of reasons not all voucher specimen localities have been plotted, i.e. no X, Y co-ordinates could be found, or these co-ordinates fall outside the country where this locality is supposed to be located. Voucher specimen localities that were not plotted are, however, indicated in the Appendices dealing with voucher specimens. Similarly, the position of the point within a country does not necessarily confirm its presence at that spot on the map, as data has currently only been screened to fall within its associated country of representation. Appendix 2g contains a larger version of the maps displayed in the taxa accounts.

Distribution based on voucher specimens:
This is a calculated paragraph, where information is derived from information in the African Chiroptera Database and provides a list of countries from which there are voucher specimens. A note of caution in viewing this data is that it is based on voucher specimen information currently in the African Chiroptera Database, hence there may be voucher specimen records that have not yet been included in the database, and voucher specimen classification/identification may not be accurate. Again, if you

have any knowledge of omissions or errors in relation to voucher specimens, please send this information to the managing editors of the database (ACD@africanbats.org) for inclusion in the next revision.

An additional, calculated query indicates through the use of colour in the country name, the period of time when voucher specimens were last collected from a country. Green indicates that voucher specimens have been collected within the past 20 years, blue within the past 20-50 years, orange within the past 50-100 years, and red if the last voucher specimens were collected more than 100 years ago. Country names in black represent countries for which voucher specimens currently have no associated date of collection. The purpose of this ranking is to assist researchers and conservation planners to focus attention on species and areas where further collecting needs to be done to ascertain data on current presence in an area.

References

In the references section of the report, the author names are colour coded to indicate in which part of the report the reference was mentioned: blue indicates that the reference is used in the main report, green that it is found in the appendices, and red is used for references occurring in both the main report and the appendices. References without colour code have not been used in the main report nor in the appendices (volume 2), but are included to provide an overview of all publications pertaining to African bats.

Future of the report

The current managing editors felt this project may have a better chance of being a successful tool for some time into the future, by encouraging contributions of data and information from interested individuals and organizations. It is hoped the African Chiroptera Report will continue to grow and develop with many more contributions of new and corrected information, i.e. verification of specimens, and specimen voucher records to the database from interested individuals and organizations. Not assigning individual names to authorship/editorship of the report has also been an intentional decision, to try and develop "ownership" of the project among all individuals and organizations who contribute to the database. It is envisaged that each release of the report, being built on the foundation of the previous report, will retain the information of whom and in what capacity they contributed to the project in a particular cycle.

Future funding is being sought for the continued support and development of the African Chiroptera Project and the development of additional tools and resources. Some of the tools and resources being explored are contracting in of additional technical skills to develop web access, GIS integration for spatial queries and information dissemination. The saying goes 'Garbage in garbage out', the African Chiroptera Project will continue to refine, verify and interrogate information contained in the database. This will be achieved through the development of teams who will verify and check all information contained in the database – verification of identifications, spatial accuracy of collection sites, and the entering in of recent and historical information from published sources.

Any mistakes, misrepresentation of data, or omitted publications can be reported to the managing editors of the database (ACD@africanbats.org). This will allow corrections and updates to be made in the next report (2026).

Taxa profiles

ORDER CHIROPTERA Blumenbach, 1779

1767. *Vespertiliones* Pallas, Vespertiliones in genre. pp. 1–35, in Spicilegia Zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur. Tomus 1. Fascicle Tertius. G. A. Lange, Berolini, Germany, 3. - Comments: Jackson and Groves (2015: 227) consider this as a synonym of Chiroptera. Originally, the name was proposed without rank, and included the genus *Vespertilio* Linnaeus, 1758.

*1779. *CHIROPTERA* Blumenbach, Handbuch der Naturgeschichte, 58. - Etymology: Neuter plural scientific Latin substantive made up of the Greek substantives, respectively feminine and neuter "*χείρ*" (kheír) [genitive "*χειρός*" (kheirós)] meaning "hand" and "*πτερόν*" (pterón) meaning "wing", or combined: "with the hand serving as a wing" or "with the hand changed into a wing" (see Lanza *et al.*, 2015: 13). - ZooBank: 06148AD8-596C-45A5-8756-74BCF5758557.

1806. *Chiropteren* Duméril, Zoologie Analytique, 5, 11. - Comments: Jackson and Groves (2015: 227) indicate that Duméril introduced this "family" name to include the genera: *Galeopithecus* Pallas, 1780 [Order Dermoptera]; *Pteropus* Brisson, 1762; *Noctilio* Linnaeus, 1766; *Vespertilio* Linnaeus, 1758; *Rhinolophen* [= *Rhinolophus* Lacépède, 1799]; and *Phyllostomen* [= *Phyllostomus* Lacépède, 1799].

1815. *Chiropteria* Rafinesque, Analyse de la Nature, 51, 54. - Comments: Jackson and Groves (2015: 227) indicate that the name originally included the families Galeopia Rafinesque, 1815 [= Galeopithecidae Gray, 1821] and Vespertilia Rafinesque, 1815 [= Vespertilionidae J. Gray, 1821], and is an unjustified emendation of Chiroptera Blumenbach, 1779. (Lapsus).

1816. *Cheiroptères* G. Cuvier, xxx, 121. - Comments: Originally proposed as family name and included the genera *Vespertilio* Linnaeus, 1758; *Pteropus* Brisson, 1762; *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797]; *Dysopes* Illiger, 1811: 122 [= *Molossus* É. Geoffroy, 1805]; *Noctilio* Linnaeus, 1766; *Phyllostoma* G. Cuvier, 1800 [= *Phyllostomus* Lacépède, 1799]; Les Megadermes [= *Megaderma* É. Geoffroy, 1810]; *Rhinolophus* Lacépède, 1799; *Nycteris* É. Geoffroy & G. Cuvier, 1795; *Thaphozous* [= *Taphozous* É. Geoffroy, 1818]; and *Plecotus* É. Geoffroy, 1818 (see Jackson and Groves, 2015: 227).

1821. *CHEIROPTERA* J. E. Gray, 299. - Comments: Proposed as a class, and originally included the orders Fructivorae J. Gray, 1821) [= Pteropodidae J. Gray, 1821] and Insectivorae J. Gray, 1821 [= Yangochiroptera Koopman, 1985 part] (see Jackson and Groves, 2015: 227). Synonymized with Chiroptera by McKenna and Bell (1997: 295).

1822. *CHEIROPTERA* Fleming, The Philosophy of Zoology, xxxii, 175. - Comments: Originally proposed as order and included the genera *Galeopithecus* Pallas, 1780 [Order Dermoptera (Illiger, 1811)]; *Pteropus* Brisson, 1762; *Cephalotes* É. Geoffroy, 1810b [= *Nyctimene* Borkhausen, 1797]; *Noctilio* Linnaeus, 1766; *Phyllostoma* G. Cuvier, 1800 [= *Phyllostomus* Lacépède, 1799]; *Molossus* É. Geoffroy, 1805; *Stenoderma* É. Geoffroy, 1818; *Rhinopoma* É. Geoffroy, 1818; *Rhinolophus* Lacépède, 1799; *Nycteris* É. Geoffroy and G. Cuvier, 1795; *Megaderma* É. Geoffroy, 1810; *Thaphozus* [sic = *Thaphozous*] Bowdich, 1821 [= *Taphozous* É. Geoffroy, 1818; *Vespertilio* Linnaeus, 1758; and *Plecotus* É. Geoffroy, 1818 (see Jackson and Groves, 2015: 227) . Synonymized with Chiroptera by McKenna and Bell (1997: 295).

1866. *Nycterides* Haeckel, Generelle Morphologie der Organismen, 2: clx. - Comments: *Nomen oblitum*. Jackson and Groves (2015: 227) indicated that this name was proposed as suborder for the "families" Gymnorrhina [= Gymnorhina Giebel, 1855] [= Yangochiroptera Koopman, 1985 part] (including the genera *Vespertilio, Dysopes, Noctilio*) and Histiorrhina [= Histiorhina Van der Hoeven, 1855] [= Rhinolophidae J. Gray, 1825] (including the genera *Rhinolophus, Megaderma, Phyllostoma*). McKenna and Bell (1997: 301) synonymized the name with Chiroptera.

1872. *ANIMALIVORA* Gill, Smiths. Misc. Coll., 11 (1): 16. - Comments: Proposed as a suborder, which originally included the following families: Desmodidae Bonaparte, 1845, Phyllostomidae J. Gray, 1825, Mormopidae [= Mormoopidae de Saussure, 1860], Rhinolophidae J. Gray, 1825, Megadermidae Gill, 1872 [= Megadermatidae H. Allen, 1864], Vespertilionidae J. Gray, 1821, Molossidae Gervais, 1855 and Noctilionidae J. Gray, 1821 (see Jackson and Groves, 2015: 228). Generally synonymized with the Microchiroptera.

1875. *MICROCHIROPTERA* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (95): 346. - Comments: Originally included the families Rhinolophidae J. Gray, 1825, Nycteridae Van der Hoeven, 1855, Vespertilionidae J. Gray, 1821, Emballonuridae Gervais, 1855, and Phyllostomidae J. Gray, 1825 (Jackson and Groves (2015: 228). - Etymology: From neuter plural scientific Latin substantive made up of the Greek adjective "*μικρός*" (mikrós) meaning "small" and chiroptera, in opposition to Megachiroptera ("big Chiroptera") (see Lanza *et al.*, 2015: 18).

1883. *Chiropteri* de Rochebrune, Act. Soc. Linn. Bordeaux, 37: 87. - Comments: Unjustified emendation of Chiroptera Blumenbach, 1779. Originally included the families Pteropidae [= Pteropodidae J. Gray, 1821], Megadermidae Gill, 1872 [= Megadermatidae H. Allen, 1864], Nycteridae Van der Hoeven, 1855, Rhinolophidae J. Gray, 1825, Phyllorhinidae de Rochebrune, 1883 [= Hipposideridae Flower & Lydekker, 1891], Taphozoidae Jerdon, 1867 [= Emballonuridae Gervais, 1855b], Molossidae Gervais, 1855, and Vespertilionidae J. Gray, 1821 (see Jackson and Groves, 2015: 228).

1889. *Ptética* Ameghino, Actas Acad. Nac. Cien. Rep. Arg. Cór., 6: xxi, 44, 348. - Comments: Proposed as "Grand Seccion" and included the orders Prochiroptera Ameghino, 1889 and Chiroptera Blumenbach (see Jackson and Groves, 2015: 228). McKenna and Bell (1997: 295) synonymized the name with Chiroptera. Pre-occupied by *Ptetica* Saussure, 1884 (Orthoptera: Acrididae).

1985. *Yinochiroptera* Koopman, Bat Res. News, 25 (3/4): 26 (for 1984). - Comments: Proposed as infraorder and originally included the superfamilies Emballonuroidea Gervais, 1855 and Rhinolophoidea J. Gray, 1825 (Jackson and Groves, 2015: 228).

1994. *Chiropteriformes* Kinman, The Kinman System, 37. - Comments: Proposed as order. McKenna and Bell (1997: 295) synonymized this name with Chiroptera (Jackson and Groves, 2015: 228).

2014. *Vespertilioniformes* Zagorodniuk, Proc. Theriol. School, 12: 8.
330 BC. *DERMAPTERA* Aristotle. - Comments: ca. 330 B.C. Non-Linnean but noted here for the sake of interest.

TAXONOMY:
Higher classification of the Chiroptera follows Alonso-Zarazaga (2005), Eick *et al.* (2005), Hutcheon and Kirsch (2006), and Teeling *et al.* (2005).

The chiropteran monophyly/diphyly debate that raged over the last decade or so has been quelled by recent molecular studies (Stanhope *et al.*, 1992; Van Den Bussche *et al.*, 1998; Allard *et al.*, 1999; Miyamoto *et al.*, 2000; Murphy *et al.*, 2001a, 2001b; Liu *et al.*, 2001; Butler *et al.*, 2010; Amador *et al.*, 2016; Jebb *et al.*, 2020) that have unequivocally demonstrated bat monophyly, and thereby dispelled the "flying primate" hypothesis (e.g., Pettigrew, 1986). Molecular analyses reject any close relationship among bats, flying lemurs and tree shrews (once grouped in the cohort Archonta), and instead support a sister-taxon relationship between Chiroptera and Eulipotyphla (Murphy *et al.*, 2001a, 2001b), which together are the sister-group of the Fereuungulata clade (Nikaido *et al.*, 2001, Van Valen, 1979, Feijoo and Parada, 2017: 79), in the supercohort Laurasiatheria (also represented by carnivores, pangolins, cetartiodactyls and perissodactyls) (Murphy *et al.*, 2001a, 2001b; Madsen *et al.*, 2001; Eizirik *et al.*, 2001; Scalley *et al.*, 2001; Nikaido *et al.*, 2001; Springer *et al.*, 2001; Nery *et al.*, 2012; Tsagkogeorga *et al.*, 2013; Foley *et al.*, 2016). On of the most recent reviews (Chen *et al.*, 2017: 1998) suggests a close relationship between Chiroptera and Perissodactyla. The relationship between these two is mentioned as "plausible" by Esselstyn *et al.* (2017: 2308). However, based on neural findings on 38 mammalian species and 82 characters, Dell *et al.* (2010: 177) still suggest a diphyletic origin of Chiroptera with Megachiropterans being a sister-group of the primates.

Jackson and Groves (2015) present the following higher order subdivision for the Chiroptera:
Class Mammalia Linnaeus, 1758
Subclass Theria Parker and Haswell, 1897
Superlegion Trenchnotheria McKenna, 1975
Legion Yangotheria Chow and Rich, 1982
Sublegion Cladotheria McKenna, 1975
Infralegion Zatheria McKenna, 1975
Infraclass Tribosphenida McKenna, 1975
Supercohort Placentalia Bonaparte, 1838
Cohort Laurasiatheria Waddell et al., 1999
Subcohort Scrotifera Waddell et al., 1999
Order Chiroptera Blumenbach, 1779

They also provide an impressive historical overview of the content and synonyms of these divisions.

Studies using molecular techniques to investigate higher level relationships within Chiroptera have challenged the monophyly of Microchiroptera, as supported by morphological characters associated with laryngeal echolocation (see list of references in Simmons, 1994), and altered the traditional subordinal division of bats as Megachiroptera and Microchiroptera. Recent analyses of nuclear and mtDNA gene sequences (Teeling *et al.*, 2000; Springer *et al.*, 2001; Van Den Bussche *et al.*, 2002; Teeling *et al.*, 2002; 2003; Hoofer *et al.*, 2003; Hutcheon and Kirsch, 2004b; Teeling *et al.*, 2005; Eick *et al.*, 2005; Teeling *et al.*, 2000; Hahn and Nakhleh, 2015; Khwanmunee *et al.*, 2015; Amador *et al.*, 2016; Feijoo and Parada, 2017; Hawkins *et al.*, 2019) now strongly support an alliance of megachiropterans and rhinolophoids (excluding Nycteridae) in one suborder, and all other microbats and nycteriids in the other suborder. Although these independent studies identified similar subordinal groups, Teeling *et al.* (2002; 2003; 2005), Springer *et al.* (2001), Amrine-Madsen *et al.* (2003) and Tsagkogeorga *et al.* (2013: 2263) named the two rearranged Chiropteran suborders as: “Yinpterochiroptera” (including Pteropodidae, Rhinolophidae - includes Hipposideridae, Megadermatidae, Craseonycteridae and Rhinopomatidae) [Springer *et al.*, 2001, also include Nycteridae in the Yinpterochiroptera] and “Yangochiroptera” (including Emballonuridae, Nycteridae, Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Vespertilionidae, Mysctacinidae, and Molossidae), whereas Hutcheon and Kirsch (2004b; 2006) and Eick *et al.* (2005: 1876), following the Principal of Typification (International Code of Zoological Nomenclature, 1999), named the two Chiropteran suborders as: "Pteropodiformes" (including the Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, and Rhinopomatidae) and "Vespertilioniformes" (including Emballonuridae, Nycteridae, Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Vespertilionidae, Mystacinidae, Miniopteridae and Molossidae). These studies showing microbat paraphyly indicate that the complex suite of morphological innovations for nasal emission of laryngeal echolocation pulses found in rhinolophoid bats either evolved independently at least twice, or once with the

subsequent loss in Pteropodidae (Simmons and Geisler, 1998; Springer *et al.*, 2001). This also has implications for the evolution of flight, where many features of flight and ventilation are either directly related or functionally correlated with echolocation (Teeling *et al.*, 2000). Hence, morphological characters previously suggested as synapomorphies of microchiropterans (e.g., features of the inner ear and post-cranial skeleton) have probably also evolved independently, together with the evolution of laryngeal echolocation (Teeling *et al.*, 2000).

Based on the structure of the scutellar cartilages in the ear, Pedersen *et al.* (2024: 13) conclude that these do not support the Yinpterochiroptera suborder, but rather the more traditional Yangochiroptera, Yinochiroptera and Pteropodidae subdivision.

Based on transcriptome RNA-seq data, Lei and Dong (2016: 1) estimate the split between Yinpterochiroptera and Yangochiroptera at around 63 MYA.

Teeling *et al.* (2000: 190) suggest two additional considerations that support the hypothesis that rhinolophids and megabats are more closely related: First, a sister-group relationship between these two rather than between megabats and all other chiropterans, reduces the duration of the implied ghost lineage for megabats from the early Eocene to the late Eocene. Second, both groups have distributions that are restricted to the Old World.

The subdivision into suborders "Pteropodiformes" and "Vespertilioniformes" is also supported by cytogenetic data (Volleth *et al.*, 2011: 518), as the order of sub-segments in the HSA 4 homologous segment differs between members of both suborders.

Contrary to an earlier suggestion that included Furipteridae, Natalidae, Thyropteridae, and Myzopodidae in the Rhinolophoidea clade (Simmons and Geisler, 1998), the recent molecular studies have confirmed an expanded superfamily, Noctilionoidea, which includes the families Noctilionidae, Furipteridae, Phyllostomidae, Mormoopidae, Mystacinidae, and Thyropteridae (Teeling *et al.*, 2002; Hoofer *et al.*, 2003; Van Den Bussche and Hoofer, 2004b; Teeling *et al.*, 2005; Eick *et al.*, 2005). However, placement of some families is still controversial, since the results of Teeling *et al.* (2005) showed good support for the basal position of Myzopodidae within Noctilionoidae, while those of (Hoofer *et al.* (2003) did not placed Myzopoda within the Noctilionoidae, but rather in a basal position to all other “yangochiropterans” (Emballonuridae (or EMBALLONUROIDEA?), Vespertilionoidea, Noctilionoidea). While Eick *et al.* (2005) also indicated Myzopodidae to be basal to the Vespertilionoidea, Noctilionoidea and Emballonuroidea (see figure 1 in Eick *et al.*, 2005: 1874), their finding apparently had no significant nodal support and alternative topologies could not be rejected by the data (Eick *et al.*, 2005).

The other superfamilies recognised by the molecular studies are the Rhinolophoidea (including the families Rhinolophidae, Megadermatidae, Craseonycteridae, and Rhinopomatidae), Emballonuroidea (including the families Emballonuridae and Nycteridae), and Vespertilionoidea (including the families Vespertilionidae, Molossidae, Natalidae, and Miniopteridae) (Eick *et al.*, 2005; Teeling *et al.*, 2005 [although no miniopterids were included in this study], Springer *et al.*, 2001; Hoofer *et al.*, 2003 [although no miniopterids were included in this study]). Springer *et al.* (2001) also recognised the superfamily Pteropodoidea.

Both Eick *et al.* (2005) and Teeling *et al.* (2005) also found similar sister taxa groups between the families, with Furipteridae and Noctilionidae (probably what was meant by Noctilionoidae in Eick *et al.* (2005)), and Nycteridae and Emballonuridae being sister taxa.

Many families can be diagnosed by unique morphological apomorphies and/or combinations of plesiomorphic and apomorphic features that strongly suggest monophyly (Miller, 1897; 1907; Hill, 1974a; Van Valen, 1979; Koopman, 1984c; 1994; Griffiths and Smith, 1991; Corbet and Hill, 1992; Griffiths *et al.*, 1992; Griffiths, 1994). The principal exception is Vespertilionidae, a diverse group that comprises between five and eight subfamilies in different classifications: Kerivoulinae, Miniopterinae, Murininae, Tomopeatinae, Vespertilioninae, Nyctophilinae (included within Vespertilioninae by Koopman (1994) and Volleth and Heller (1994)), Antrozoinae (named as a subfamily by Miller (1897) but subsequently included either within Nyctophilinae (e.g., Hill and Smith, 1984) or Vespertilioninae (e.g., Koopman, 1993a; 1994), and Myotinae (usually included as a tribe within Vespertilioninae (Koopman, 1994) but here raised to subfamily rank following the suggestion of Volleth and Heller (1994). The molecular work of Hoofer and Van Den Bussche (2003) suggested four subfamilies in the family Vespertilionidae: Vespertilioninae, Myotinae, Kerivoulinae and Murininae, with the subfamily Miniopterinae being elevated to family level, Miniopteridae. However, the intron results of Eick *et al.* (2005) were not

able to reject or support alternative hypotheses that Miniopteridae was the sister taxa of Molossidae, and not the sister taxa of Vespertilionidae.

Based on upper molar morphology, Fracasso *et al.* (2011: 422) propose the following tree structure: The Icaronycteridae is positioned at the base, followed by three clades: Yinochiroptera, Noctilionoidea, Yangochiroptera. Within the Yinochiroptera, the Emballonuridae form the basal node, followed by Rhinopomatidae, Nycteridae, Megadermatidae, Rhinolophidae, and Hipposideridae. The Yangochiroptera have a basic split-up between the Nataloidea (including the Myzopodidae [at the base], Thyropteridae, and Furipteridae) and the group formed by the Antrozoinae, Mystacinidae, Molossidae (including Molossinae and Tomopeatinae), and Vespertilionidae (as a poorly supported monophyletic group, including Myotinae, Miniopterinae, Kerivoulinae, and Murininae).

If the suggestion to follow the format proposed for standardization of nomenclature of higher taxa by Alonso-Zarazaga (2005) is accepted for renaming of the suborders, then the suggested typified name for the order would be, VESPERTILIONIFORMES, from the oldest generic name of *Vespertilio* Linnaeus 1758.

Zagorodniuk (2014: 8) uses an alternative hierarchy, which starts with the Superorder Chiroptera, which contains the order Vespertilioniformes (Chiroptera auct.), which itself contains two suborders: Vespertilionimorpha (Yangochiroptera) and Pteropodimorpha (Yingochiroptera).

Known Chiroptera families:
† **Aegyptonycteridae** Simmons, Seiffert and Gunnell, 2016
† **Necromantidae** Sigé, 2011
† **Philisidae** Sigé, 1985
† Icaronycteridae Jepsen, 1966
† Archaeonycteridae Revilliod, 1917
† Onychonycteridae Simmons, Seymour, Habersetzer and Gunnell, 2008
† Palaeochiropterygidae Revilliod, 1917
† Hassianycteridae Habersetzer and Storch, 1987
† Mixopterygidae Maitre, 2008
† **Tanzanycteridida**e Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003
Pteropodidae Gray, 1821
Hipposideridae Lydekker, 1891
Megadermatidae H. Allen, 1864
Rhinolophidae Gray, 1825
Rhinonycteridae J. E. Gray, 1866
Craseonycteridae Hill, 1974
Rhinopomatidae Dobson, 1872
Emballonuridae Gervais, 1855
Nycteridae Van der Hoeven, 1855
Myzopodidae Thomas, 1904
Mystacinidae Dobson, 1875
Phyllostomidae Gray, 1825
Mormoopidae Saussure, 1860
Noctilionidae Gray, 1821
Furipteridae Gray, 1866
Thyropteridae Miller, 1907
Natalidae Gray, 1866
Molossidae Gervais, 1856
Cistugonidae Lack, Roehrs, Stanley, Ruedi and Van den Bussche, 2010
Miniopteridae Dobson, 1875
Vespertilionidae Gray, 1821

Worldwide, six of the extant families (Pteropodidae, Rhinolophidae, Hipposideridae, Phyllostomatidae, Molossidae and Vespertilionidae) contain about 75 % of all species (see Shi and Rabosky, 2015: 1529).

COMMON NAMES:
Arabian: Bouchaara, Boujlida, خفاش الوطواط. Castilian (Spain): Murcielagos. Czech: letouni či netopýři, letaunowé, ptákossavci, upírové, letouni lysoblaní. Dutch: Vleermuizen. English: Bats. French: Chauves-souris. German: Fledermäuse. Italian: Chiròtreri, Pipistrèlli. isiXhosa: ilulwane, idludaka. Kabyle (Algeria): Imtchaghyeye. Portuguese: Morcegos. Somalian: Fidmer, Fidmair, Auo-rnèr, Kibille, Kibillei, Kibil, Fid Mer, Sodan silli, Sod silli (see Lanza *et al.*, 2015: 13). Swahili: Popo. Tanoboase (Ghana): ampane (singular), mmpane (plural) (see Ohemeng *et al.*, 2017: 184). Turkish: Yarasalar. Twi (Ghana): apan (singular), mmpan (plural).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The paleontological record of the Chiroptera in Africa, as in the world, is generally incomplete (Butler, 1978), which is especially the case in Africa (see discussion in Pretorius, 2024).

The first bats appeared somewhere in the Mid- to Late Cretaceous (about 88.7 million years ago), and the diversification began at about 74.9 to 63 MYA (Bininda-Emonds *et al.*, 2007: 509; Lovegrove, 2011: 152). However, dos Reis *et al.* (2012: 3494) situate the origin of the Chiroptera at 59.1 MYA, hence: after the Cretaceous-Paleogene event. Yu *et al.* (2014: 2204) suggest that the Chiroptera have an Asian origin and that there was rapid adaptive radiation from the emergence of crown bats until the Early Eocene Climatic Optimum. This was followed by a decreased diversification between 49 and 35

MYA, and another period of high diversification between 35 and 25 MYA.

Gunnell *et al.* (2017: 18) indicate that the earliest known bat fossils came from Europe, India, North Africa and Australia (around 53 - 54 MYA), but they all represent archaic bat groups that have no clear phylogenetic connections with modern taxa. Modern families of bats began to appear in the late early to middle Eocene of Europe and North Africa. They also pointed out (p. 1) that only 13 placental mammal genera first occurred in the middle to late Paleogene, of which six represented bats, including some extant genera belonging to both Yangochiroptera and Yinpterochiroptera.

The rapid diversification at the Palaeocene-Eocene thermal maximum might have been the result of the large increase in insect abundance during that period (Eriksson, 2014: 175).

Springer *et al.* (2011: 2493) mention that the oldest bat fossils are from the Early Eocene of North America, and that further Early Eocene bats are also known from Europe, Africa and Australia. Most researchers seem to agree that bats originated in Laurasia, but some see Gondwana as the cradle for the Chiroptera. Teeling *et al.* (2005) [in Springer *et al.* (2011: 2493)] suggested North America or Laurasia as the ancestral area for bats, and Asia, Europe or Laurasia as the ancestral area for both Pteropodiformi (Yinpterochiroptera) and Vespertilioniformi (Yangochiroptera).

The oldest fossil bat described from Africa is: *Vampyravus* (= *Provampyrus*) *orientalis*, from the Oligocene of the Fayum (Egypt). However, in their abstract on an upper molar and two fragments of lower molars from El Kohol (Algeria), Ravel *et al.* (2010: 149) mention these belong to a member of the "Eochiroptera" (sensu Van Valen, 1979), dating back to the Early Eocene. Ravel *et al.* (2016: 359) indicate that these "Eochiroptera" cover six families (Onychonycteridae Simmons, Seymour, Habersetzer and Gunnell, 2008, Icaronycteridae Jepsen, 1966, Archaeonycteridae Revilliod, 1917, Hassianycteridae Habersetzer and Storch, 1987, Palaeochiropterygidae Revilliod, 1917, and Tanzanycteridae Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003), none of which are related to the current day families. The oldest of the current day families start to appear in the lower Eocene of Africa, whereas on the other continents they only appeared in the middle Eocene (and even in the upper Eocene of Australia). This points to the great importance of Africa during the first phase of the development of modern bats (Ravel *et al.*, 2016: 359).

Hildebrand *et al.* (2010: 268, 281) recorded unknown bat species from the Kumali and Koka sites in southern Ethiopia.

CONSERVATION STATUS:
Worldwide, Amori *et al.* (2013: 98) state that 177 out of 1,116 bat species reported by Wilson and Reeder (2005) or 15.39 % have an IUCN status of CR, E, or VU. González-Gutiérrez *et al.* (2025: 23) pointed out that the IUCN categories are irregularly updated and therefore might not respresent the most recent trends.

Wieringa (2022: 529) [referring to various other studies] indicated that a small geographic range and low wing aspect ratio are indicators of a higher extinction risk.

MAJOR THREATS:
Sherwin *et al.* (2012: 173) [referring to Ciechanowski *et al.*, 2007] indicate that aerial-hawking species are probably more sensitive to climatic changes as they are dependent of a food supply that is extremely variable in time as well as in space. This is less the case for species foraging above water surfaces, as they rely on stable and spatially concentrated food resources. "Water Stress" will become an important climatic change risk factor for species living in arid regions, as they depend on permanent water resources close to roosts (see Adams and Hayes, 2008 [in Sherwin *et al.* (2012: 173)]).

For southern Africa, Pio *et al.* (2014: 1543) predict that high concentrations of phylogenetic diversity (PD) will contract considerably by 2080, but that climate change will not result in higher nor lower PD losses, on average, compared to random extinction simulations. They also indicated (p. 1546) that the Kalahari will become very barren in terms of future surviving bat PD.

For the Mediterranean area, Maiorano *et al.* (2011: Table S2) predict that none of the presently occurring species will be extinct by the end of the century, but up to five of the Vespertilionid species might encounter a projected range loss of over 80 %. Between two and fifteen species will probably see a loss between 50 and 80 %, which will also be the case for four of the Rhinolophid species. Between four and eleven of the Vespertilionid species will encounter a loss of between 30 and 50 % of their range, which will also be the case for up to two of the Rhinolophid species. All bat families will contain species which will have a range loss of up to 30 %. One of the Hipposiderid species, one or

both of the Rhinopomatid species, and one or two of the Vespertilionid species, however, will gain from the changing.

O'Shea *et al.* (2016) reviewed multiple mortality events in bats and identified nineteen events for Africa: Intentional killing (n = 11), Biotic (n = 5), Accidental (n = 1), Wind Turbines (n = 1), Viral or bacterial disease (n = 1).

Some bat populations are killed to prevent them spreading viral diseases. However; Plowright *et al.* (2016: 16) mention that "culling bats may decrease spillover risk if transmission of the virus increases as population size increases (SIR [Susceptible-Infectious-Recovered] dynamics), whereas culling may increase spillover risk if pulses are driven by viral reactivation after stress (SILI [Susceptible-Infectious-Latent-Infectious] dynamics)."

Another threat is the bushmeat trade (see Dougnon *et al.*, 2012; Friant *et al.*, 2015; Jenkins and Racey, 2008; Kamins *et al.*, 2010, 2011a, 2011b; Kaswera Kyamakya *et al.*, 2019; Mickleburgh *et al.*, 2009; Musaba Akawa *et al.*, 2017; Waylen, 2004), although this might be (temporarily) reduced as a result of zoonotic outbreaks: e.g., Duonamou *et al.* (2020) found that 78.3 % of their respondents consumed bat meat prior to the 2013-2016 Ebola outbreak in Guinea, but only 31.9 % consumed it during the outbreak. In Nigeria, Funk *et al.* (2021: 2, 3) found that fruit bats (and monkeys) nearly disappeared on the wild meat markets. These low numbers did not recover during the post Ebola period (January 2016 to December 2019), whereas this was the case for bush pigs, carnivores, rodents and ungulates.

Although there is little evidence of it being a major threat, Aldebsawi *et al.* (2021) investigated the "bating process" in the Middle East (including Egypt, where it is in use since the days of the Pharaohs) during which bat blood is applied on infant girls' skin to reduce body hair growth. Of the 120 people they interviewed, 97 % had heard about this procedure and 71 % had it experienced on themselves.

Chaber *et al.* (2021) investigated the e-commerce trade in bats and found - between 11 and 25 May 2020 - 237 bat products (covering a total of 4,476 bat specimens) listed by 25 sellers worldwide. 1,873 referred to taxidermy specimens (41.9 %) and included six *Eidolon helvum*, seven *Hypsignathus monstrosus*, one *Micropteropus pusillus* and one *Nanonycteris veldkampii* from Cameroon and Ghana. Aggrey *et al.* (2024: 6) also indicate that, in Tanzania, bats form an important part of e-commerce as they are turned into souvenirs sold to tourists, a business that "appears to be illegal".

Worldwide, at least 19 % of all bat species are threatened by hunting (Tanalgo *et al.*, 2023: 1), especially the large-bodied species living in tropical regions. In the Afrotropics, 22 % of the bat species are hunted (Tanalgo *et al.*, 2023: 5). Two African countries make it in the list of top 15 countries ranked in terms of hunted species and their corresponding rank in terms of threatened and endemic: Madagascar (position 14, with 14 hunted species, 10 threatened and 5 endemics) and Tanzania (position 15, with 14 hunted species, 21 threatened and 14 endemics).

In their study on the potential of online data sources on bat exploitation, Hunter *et al.* (2024: 7) pointed out that eight African countries (Algeria, Central African Republic, Egypt, Rwanda, Senegal, Somalia, South Sudan, and Zimbabwe) were only covered by online sources and not in systematic (academic) literature search. However, they also show (p. 10, 11) that Africa is the only continent where there are more academic studies than online records, but this might be the result of low number of internet users (or the author's use of English language queries for online searches).

Nkrumah *et al.* (2021: 8) indicated that habitat loss, climate change, mining, agriculture, groundwater overexploitation and contamination are critical factors threatening cave ecosystems in Ghana. Additionally, cave tourism, easy accessibility, cave lighting, cave camping and cleaning by religious groups, and drumming and dancing, force bats to leave these caves (especially in the Mframabuom cave).

Oedin *et al.* (2021) discuss the role (and effects) of cats (*Felis catus*) as bat predators, and they suggest (p. 11) that IUCN conservation accounts should consider including predation by cats as a threat and enhanced management of cats needs to be included as a priority conservation response.

Clements *et al.* (2024) developed the bii4africa dataset of faunal and floral population intactness estimates across Africa's major land uses, which also gives special attention to bats.

Fatalities near wind energy facilities in the RSA between 2011 and 2022 were estimated by Aronson (2022: 181) to be 12,601 or 2.8 bat fatality/MW/year. He also estimated that between 2013 and 2050 a minimum of 996,974 bats may be killed at South African wind energy facilities.

In their overview paper on ecological and evolutionary traps (EETs), Tanalgo *et al.* (2025: 4) indicate that studies dealing with these are extremely limited for the African continent, and restricted to Egypt, Togo, Nigeria, Cameroon, Mozambique, Zimbabwe, RSA and Madagascar.

CONSERVATION ACTIONS:
Racey (2013: 523) stated "Africa is largely a void so far as bat conservation is concerned and that is a matter of great concern in view of the large-scale human consumption of fruit bats, mainly in West and Central Africa, and their role as vectors of Ebola haemorrhagic fever also in Central Africa." (The link with Ebola is still not confirmed - see Viruses section below.)

Lisón *et al.* (2019: 11) pointed out that bat conservation in semi-arid and arid landscapes is receiving little research interest, and that studies in these areas are especially under-represented in Africa and Australia (p. 1).

Based on the results of their study into African megaherbivore conservation and its effect on bat diversity in the Namib Desert, Laverty and Berger (2021: 1) suggest that community game guard programs, water-point protection near human settlements, and ecotourism might indirectly promote bat conservation as well.

In their review of bats and wetlands, Mas *et al.* (2021: 6) pointed out that only 5 % of the studies were carried out in Africa. This results in an enormous gap in our knowledge. They also indicate (p. 11) that in Congo and Chad (where rates of wetland loss are the highest); research efforts in wetland areas should be prioritized.

Another review by Tuneu-Corral *et al.* (2023: 1) into ecoservices delivered by insectivorous bats, indicates that the most frequent recommendations include increasing habitat heterogeneity, providing additional roosts, and implementing laws to protect bats and reduce agrochemical use.

Based on a study of Ghanaian bats, Meyer *et al.* (2024: 1) indicate that biodiversity conservation may be the most proactive measure to prevent the spread of pathogens with zoonotic potential.

Although in general the presence of bats (and birds) is considered to be advantageous on plantations, this doesn't seem to be the case under all circumstances. Ferreira *et al.* (2022c: 1) found that in cacao plantations with heavy shaded trees, these trees had 3.9 times fewer flowers and 3.2 times fewer large pods in areas where bats and birds were excluded (leading to an average loss of 478 USD/ha/year. However, if the trees provided less shade, the situation was completely different as these trees had 5.2 times more flowers and 3.7 times more large pods (leading to an average saving of 796 USD/ha/year). Ferreira *et al.* (2024b: 2) suggest three conceptual designs to manage cacao landscapes: one for insectivores (with high cover of natural habitats), one for frugivores/nectarivores (with natural habitats and nearby anthropogenic habitats - with potentially more flowering and fruiting trees) and a third design that maximises the trade-offs between these three guilds.

Xavier *et al.* (2023: 11) did a literature study (309 papers) on the relation between bats and agricultural systems and recommend that the Indo-Malayan and Afrotropical regions needs more priority (especially the non-forest biomes and habitats).as they are underrepresented and are critical for bat conservation.

GENERAL DISTRIBUTION:
Marsh *et al.* (2022: 12) provide a link to online distribution maps (https://mol.org/species), which also cover African bats.

Monadjem *et al.* (2023a: 5) reported that bats show an extreme decline with elevation, and are absent at elevations higher than 3,500 m. The mean species richness remains constant up to 500 m at about 18 species. Upwards of this, it declines to three species above 3,000 m..

BIOGEOGRAPHY:
Maas *et al.* (2015: 1086) indicate that the Afrotropics (roughly Africa south of the Sahara) is certainly not the most specious zoogeographical region (the Neotropics has 100 species more), but it has with 211 out of 237 species the highest percentage of endemics (89 %), versus 75 % in the second region (Neotropics).

Tanshi *et al.* (2022b: 1213) point out that hard-to-catch bats were generally missed in inventories, resulting in the conclusion that the Afrotropical bat fauna was considered to be "depauperate". However, the use of appropriate sampling techniques especially harp trap, ground and canopy mist nets, as well as acoustic surveys/libraries could/would confirm the presence of these bats.

GEOGRAPHIC VARIATION:
Based on a literature study of bats worldwide, Molinari (2023: 10) concluded that even if size divergence is similar in populations on islands and nearby mainland, populations in these two

areas are more likely to be considered different (sub)species as compared with populations living on different islands or in different areas on the mainland. As such, island biogeography and taxonomy potentially influenced each other for a very long time.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Lucati and López-Baucells (2016: 117) provided a summary of chromatic disorders reported in bats and found that this character is underreported for Africa: Albinism (All-white hairs, pale skin and red eyes) is reported from five localities on the African continent and one in Réunion and Piedbaldism (All-white fur/skin patches, eyes always normally coloured) from two on the continent. Other disorders, such as Melanism (Increase in black or brown pigmentation on the whole body), Partial melanism (Increase in black or brown pigmentation on a part of the body), Leucism (All-white or whitish hairs, pale skin, eyes always normally coloured.) and Hypomelanism (Beige, golden, yellowish or reddish fur and skin, eyes always normally coloured) weren't reported from Africa at all.

Delmore *et al.* (2018: 127) studied the pigmentation of the tissues surrounding the testes and suggest that scrotal melanin may protect mature sperm from UV damage, and from oxidative damage in species with male sperm storage.

Harris *et al.* (2022; 8) microscopically examined the hair structure of 33 South African bat species. Within the species they found differences in hair scales from the three sampled body regions (dorsal, ventral and neck). Hairs from the same body area were distinctively different in Molossidae as compared with other families, and multivariate analyses also showed differences between Pteropodidae, Rhinolophidae and Vespertilionidae.

DETAILED MORPHOLOGY:
Bahlman *et al.* (2016: 118) provide a schematic overview of the wing joints and musculature of the various bat families.

In their study of the caudal auricular muscles of the Asiatic *Cynopterus sphinx* Chi *et al.* (2023: 571) reported that the number of cervicoauricularis muscles and their innervation pattern in pteropodids is very similar to that of the yangochiropterans and non-bat mammals as they all have three cervicoauricularis muscles. The rhinolophid bats, however, were reported to have a derived condition with four muscles.

FUNCTIONAL MORPHOLOGY:
Adams and Carter (2017) studied the climbing and walking locomotion of a number of Pteropodids and Vespertilionids and found fundamental differences. The Pteropodids had a far greater ability to climb in a head-up posture than the Vespertilionids, whereas the situation was quite the inverse when walking on the ground was compared. The Pteropodids behaved much more like other arboreal mammals (e.g., two-toed sloths - *Choloepus hoffmanni* Peters, 1858).

Stanchak *et al.* (2019: 1591) compared evolutionary models of calcar length and the corresponding disparity-through-time. They found that these indicate that the calcar diversified early in the evolutionary history of Chiroptera, as the variation in calcar length and its relative proportion to tibia and forearm length is of functional relevance to flight-related behaviours, leading to a large phylogenetic diversification.

Cosentino *et al.* (2023a) developed the AfroBaT database (https://doi.org/10.6084/m9.figshare.c.6272838.v1) which compiles trait data on 320 African bats. The 86 traits covered deal with morphology, reproduction, life-history, trophic ecology, and species distributions.

For data on wing morphology, see Crane *et al.* (2021: Suppl.).

ECHOLOCATION:
Fenton (1994: 28) states "Echolocation profoundly affects the biology of bats, their behaviour and ecology and may have been central to their evolution".

MOLECULAR BIOLOGY:
Genetics
The following statement has been made by Dell *et al.* (2013: 65): "So DNA sequence results in bats may have to be accepted with caution in view of the possibility that DNA is perhaps as susceptible to convergent evolution as morphological systems.", indicating that the results of these state-of-the-art techniques need to be interpreted with caution.

Dool *et al.* (2016a: 196) furthermore suggest: "We caution against the indiscriminate use of mtDNA in phylogenetic studies and advocate for pilot studies to select nuclear introns. The selection of marker type and number is a crucial step that is best based on critical examination of preliminary or previously published data. Based on our findings and previous publications, we

recommend the following markers to recover phylogenetic relationships between recently diverged taxa (< 20 My) in bats and other mammals: ACOX2, COPS7A, BGN, ROGDI and STAT5A."

See also Kruskop and Artyushin (2021) for a deeper discussion on this subject.

HABITAT:
Reardon and Schoeman (2017: 273) investigated the taxonomic and functional diversity of the assemblage structure of insectivorous bat communities along the Mount Nimba elevational gradient in view of rising global temperatures. They found that there was a taxonomic shift along the gradient, but that functionally, the assemblage remained largely intact.

In their study on the bat fauna of the southern African arid region, Monadjem *et al.* (2017a: 5) found that at a regional scale, landscape features might be more relevant for bats living in arid regions, as opposed to aridity gradients. They also found that open air foragers are restricted in the southern African arid region, although they could not determine the factor behind this. Furthermore, they were unable to determine the ecosystem services provided by bats in arid environment (as opposed to limiting pest insects in agro-ecosystems).

In Tanzania, Katunzi *et al.* (2020: 1) found that bat activity was higher in lowland habitats (such as rice paddy, riverine and sisal estates) than in upland habitats (forest and banana-coffee plantations). Insectivorous species were primarily found in riverine and rice paddy habitats, whereas fruit-eating bats preferred riverine and banana–coffee habitats.

Marsden *et al.* (2023: 3) investigated the urban tolerance of African bats. The categorized these bats in three groups: urban exploiters, adapters or avoiders. Bats belonging to the first group are open-air bats, having high wing loading and aspect ratios and their roost habits are highly flexible (including the use of anthropogenic resources). Urban adapters cover narrow-edge space bats with intermediate wing loading and aspect ratios. They still have fairly flexible roosting habits. The urban avoiders are narrow-space bats with restricted roosting requirements (e.g., obligate cave roosters). Marsden *et al.* (2023: 6) specifically studied 54 bat species of which 23 (43 %) were classified as urban avoiders, 19 (35 %) as adapters and 12 (22 %) as exploiters.

A literature study by Martínez-Fonseca *et al.* (2024: 5) revealed that only 1.7 % of the landscape analysis studies relating to bats were done in the Afrotropical region.

ROOST:
Of the 574 houses assessed by Nsengimana *et al.* (2023: 2) in eastern Rwanda, 42 % were inhabited by (insectivorous) bats.

DIET:
Webala *et al.* (2019a: 260-261, 266) divide the equatorial African bat fauna into four groups: frugivores, forest-interior insectivores, forest-edge insectivores and open-space insectivores. They suggest that forest-interior insectivores are strongly associated with the interior of the larger, more intact forests, and are more vulnerable to habitat fragmentation and degradation. The three other groups are more strongly associated with edges and smaller, more degraded forest fragments.

Every night, insectivorous bats consume approximately 1/4 to 2/3 of their body mass (Lacher *et al.*, 2019: 948). A large proportion of their prey consists of pest insects, e.g., stink bugs. Taylor *et al.* (2017a: 376) indicated that the percentage of Hemiptera in the diet of bats (at Levubu, RSA) varied between 6-20 % in *Nycteris thebaica* to 50 % in *Pipistrellus hesperidus*. They also calculated (p. 378) that the South African macadamia industry (covering about 25,000 ha) avoided a yearly cost between 56.81 and 138.91 USD/hectare as a result of this. Linden *et al.* (2019: 2069) performed exclusion experiments in macademia orchards in South Africa and found that the benefits of allowing birds and bats access to the trees economically well outweighed the disadvantages caused by crop raiding by monkeys (approximately +5 000 USD per ha/year versus -1 600 USD per ha/year).

Boyles *et al.* (2013: 511) pointed out that in many parts of Africa sustenance farmers have no access to modern pesticides, and therefore bats may act as a primary suppressor of crop pests. Nsanzimana *et al.* (2025: 1) indicate that protecting bats in and around Madagascan protected areas may offer a cost-effective means to augment agricultural productivity and enhance public health.

However, in Guinea-Bissau, Sottomayor *et al.* (2024: 1) found that exclusion of birds and bats had only marginal effects on rice damage and no detectable effect on yield.

PREDATORS:
Black *et al.* (1979: 19) reported that the prey of a bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) observed in Zambia most likely consisted of *Cloeotis percivali, Rhinolophus simulator, Hipposideros caffer*, and *Nycteris thebaica*.

Mikula *et al.* (2016: Supplemental data) mention the following birds preying on unspecified bats: Frances's sparrowhawk (*Accipiter francesiae* A. Smith, 1834), Rufous-breasted sparrowhawk (*Accipiter rufiventris* A. Smith, 1830), Ovambo sparrowhawk (*Accipiter ovampensis* Gurney, 1875) [on large bat], Tawny eagle (*Aquila rapax* (Temminck, 1828)), Mountain buzzard (*Buteo oreophilus* Hartert and Neumann, 1914), African marsh harrier (*Circus ranivorus* (Daudin, 1800)), Sooty falcon (*Falco concolor* Temminck, 1825) [on insectivorous bats], African hobby (*Falco cuvierii* A. Smith, 1830), Dickinson's kestrel (*Falco dickinsoni* Sclater, 1864) [on small insectivorous bat], Taita falcon (*Falco fasciinucha* Reichenow and Neumann, 1895); Lilac-breasted roller (*Coracias caudatus* Linnaeus, 1766) [on insectivorous bat], Brown-hooded kingfisher (*Halcyon albiventris* (Scopoli, 1786)) [on insectivorous bat], Woodland kingfisher (*Halcyon senegalensis* (Linnaeus, 1766)), Southern grey shrike (*Lanius meridionalis* (Temminck, 1820)), Gabar goshawk (*Micronisus gabar* (Daudin, 1800)), Green wood hoopoe (*Phoeniculus purpureus* (J.F. Miller, 1784)), Long-tailed hawk (*Urotriorchis macrourus* (Hartlaub, 1855)).

Stanton (2016: 318) mentioned that the capture success on emerging bats was 41.4 % for Wahlberg's eagles (*Hieraaetus wahlbergi* (Sundevall, 1850)) in 49.3 % for bat hawks (*Macheiramphus alcinus* Bonaparte, 1850), 50 % for Eurasian hobbies (*Falco subbuteo* Linnaeus, 1758) and even 75 % for African goshawks (*Accipiter tachiro* (Daudin, 1800)).

Tapanes *et al.* (2016: 405, 406) indicate that several primates prey on bats: *Pan paniscus* Schwarz, 1929 (Bonobo); *Papio anubis* (Lesson, 1827) (olive baboon, Anubis baboon); *Perodicticus potto* (Statius Müller, 1766) (Potto); *Cercopithecus mitis* Wolf, 1822 (Blue monkey) and a *C. mitis* x *C. ascanius* hybrid. These observations suggest an alternative pathway for bat-*Cercopithecus* disease transmission that has implications for zoonotic disease transmission to humans. Of the 13 bat predations they observed, three were on Pteropodidae and one on Molossidae. In four additional events, the bats were small (13 - 18 cm body length) and one large (ca. 50 cm wingspan).

Szentivanyi *et al.* (2023: 3) point to an iNaturalist project 'Bat (Chiroptera) predation by domestic cats (*Felis catus*)': [https://www.inaturalist.org/projects/bat-chiroptera-predation-by-domestic-cats-felis-catus], which currently [May 2024] contains records of *Laephotis capensis*, *Miniopterus* sp., *Mops (Chaerephon) pumilus*, *Nycteris hispida*, *Nycteris thebaica*, *Scotophilus* sp., *Scotophilus dinganii*, and *Tadarida aegyptiaca*.

Labadie *et al.* (2024: 1) filmed a rusty-spotted genet (*Genetta maculata* (Linnaeus, 1758)) capturing and eating undefined bats in or in front of the Boundou Cave (Republic of Congo).

LIFESPAN:
Wilkinson and Adams (2019: 1) found at least four lineages of bats (*Rhinolophus, Plecotus, Desmodus* and some *Myotis* groups) that have a lifespan that is more than four times longer than similar-sized placental mammals. The longevity could be predicted from their body mass and hibernation. In hibernating bats, the median latitude of the species range and cave use are the best predictive factors, whereas in non-hibernating bats these factors are cave use and the lack of sexual dimorphism.

ACTIVITY AND BEHAVIOUR:
Schoeman (2015: 122, 125) classified South African insectivorous bats in three functional urban groups (based on wing and echolocation characteristics and foraging and/or roosting characteristics):

1) **urban avoiders** - slow-flying bats that typically hunt prey in forests or dense vegetation and have specific roosting requirements such as obligate cave roosters (e.g., *Nycteris thebaica, Rhinolophus simulator*);

2) **urban adapters** - bats that forage mainly along forest edges and adjacent open areas, and readily utilize favourable conditions provided by humans, for example, forage at wastewater treatment plants and/or roost in man-made structures or plants in gardens (e.g., *Miniopterus natalensis, Neoromicia capensis, Neoromicia nana, Pipistrellus hesperidus/Hypsugo anchietai, Taphozous mauritianus*).

3) **urban exploiters** - fast-flying, open-air bats often recorded in urbanized landscapes that depend to a certain degree on urban resources such as houses that provide suitable roosting sites and can sustain large bat colonies (e.g., *Chaerephon pumilus, Mops condylurus, Otomops martiensseni, Scotophilus dinganii, Tadarida aegyptiaca*).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: 676) report that the modal litter size in most bats is one (monotocy). Only some of the Vespertilionidae have litter sizes with more than one young (polytocy).

PARASITES:
BACTERIA
Lutz *et al.* (2019a: 3) investigated the microbial richness of the bat's skin, oral cavity and gut and found that the skin contained a significant higher richness than the two other areas. They also found that the geographical location was more important than the taxonomical relationship to explain the microbial variation. In decreasing order, they found the following groups of bacteria in the gut: Proteobacteria (Enterobacteriaceae) and Firmicutes (Clostridiaceae and Streptococcaceae). In the oral cavity, they found Proteobacteria (Pasteurellaceae and Neisseriaceae) and Firmicutes (Streptococcaceae and Gemellaceae). No specific bacterial phylum was found overabundant in the skin swaps, but Proetobacteria (Enterobacteriaceae), Actinobacteria (Mycobacteriaceae, Pseudonocardiaceae, Nocardiaceae), Bacteroidetes (Moraxellaceae) and Euryarchaeota (Halobacteriaceae) were most present.

FUNGI
Wu *et al.* (2024: 1) discuss the vulnerability of southern hemisphere bats to White-Nose syndrome (WNS), and indicate that this might be an important threat to naïve bat populations, also in Africa.

HEMOSPORIDIA
Perkins and Schaer (2016: 776) provide an overview of the malaria parasites of bats, which include nine genera, of which the most important ones are: *Hepatocystis, Polychromophilus, Nycteria*, and *Plasmodium* (the others are: *Bioccala*, Biguetiella*, Sprattiella*, Johnsprentia**, and *Dionisia* - *: not in Africa).

Killick-Kendrick (1973: 647) mentions *Plasmodium (Vinckea) voltaicum* Van Der Kaay, 1964 from a non-specified bat. Makanga *et al.* (2017: Suppl.) refers to an *Anopheles marshalli* infected with *Polychromophilus melanipherus*, which it could only have received from sucking blood of a bat.

Rudoler *et al.* (2018: 392) found four species of *Plasmodium* in pools of blood from various Ugandan bats: *P. bergei* Vincke and Lips, 1948, *P. falciparum* Welch, 1897, *P. yoelii* Landau, Michel and Adam, 1968 and *P. chabaudi* Landau, 1965.

TREMATODA
Richard (1966: 416) described *Acanthatrium (Acaisthatrium) houini* from and unidentified bat from Ranomafana (Madagascar).

HEMIPTERA
Cimicidae
Loxaspis miranda Rothschild, 1912 from Gogrial, Sudan, but no host given (Haeselbarth *et al.*, 1966: 10). *Cacodmus ignotus* Rothschild, 1912 described from a single female without locality data, and a subsequent collection is reported from Uganda (Haeselbarth *et al.*, 1966: 10). In the British Museum there are also specimens of *Cacodmus sparsilis* Rothschild, 1914 from Pietermaritzburg, South Africa, without host records (Haeselbarth *et al.*, 1966: 10): *Aphrania barys* Jordan and Rothschild, 1912 described from Maseru, Lesotho, host is not known (Haeselbarth *et al.*, 1966: 11). *Aphrania recta* Ferris and Usinger, 1957 described from Mutir, Uganda, and another record from Mabal, Congo, but hosts unknown (Haeselbarth *et al.*, 1966: 11-12). *Leptocimex boueti* (Brumpt, 1910) has been recorded from a few places in Guinea, the northern Gold Coast [=Ghana], Upper Volta [=Burkinan Faso], Dahomey [=Benin] and the former French Sudan [=Mali], where it was found biting humans, the hosts are bats but no definite species (Haeselbarth *et al.*, 1966: 13). *Stricticimex antennatus* Ferris and Usinger, 1957, found in the Cape Province, South Africa in caves at Bredasdorp and Sister's Rocks, the host-bat not recorded (Haeselbarth *et al.*, 1966: 14). *Stricticimex brevispinosus* Usinger, 1959, found in a cave near Lake Victoria, Urundi [=Burundi] associated with an unidentified bat (Haeselbarth *et al.*, 1966: 14). *Stricticimex intermedius* Ferris and Usinger, 1959, was recorded from a cave near Mombasa, Kenya, the host not recorded (Haeselbarth *et al.*, 1966: 14). *Stricticimex transverses* Ferris and Usinger, 1957 was originally described from an unknown bat from Bloemfontein, South Africa (Haeselbarth *et al.*, 1966: 14).

Polyctenidae
Eoctenes intermedius (Speiser, 1904) found on an unidentified bat in the Sudan (Haeselbarth *et al.*, 1966: 16). *Androctenes horvathi* Jordan, 1912 described form an unidentified bat in Somalia (Haeselbarth *et al.*, 1966: 17).

DIPTERA
Streblidae
Raymondia huberi Frauenfeld, 1856 from unidentified bat in the Rukwa Valley, Tanzania

(Haeselbarth *et al.*, 1966: 102). *Raymondia setosa* Jobling, 1930 collected from a "broad-eared bat" at Aden (Haeselbarth *et al.*, 1966: 104). *Raymondiodes leleupi* Jobling, 1954 described form a poorly identified bat (*Hipposideros caffer* or *Miniopterus* sp.) from Thysville, Congo (Haeselbarth *et al.*, 1966: 104).

Shapiro *et al.* (2016: 255) indicates that Kessel (1925: 24) mentions *Raymondia lobulata* Speiser, 1900 "off *Megaderma lyra* from Ceylon, from bats in Madras and British Somaliland".

Nycteribiidae

Nycteribia hoogstraali Theodor 1957 from the Congo and Tanzania host unidentified (Haeselbarth *et al.*, 1966: 109). *Basilia meridionalis* Theodor 1956 host and exact locality not recorded from South Africa (Haeselbarth *et al.*, 1966: 111). *Basilia bouvieri* (Falcoz, 1924) originally described without exact locality (West Africa) or host (Haeselbarth *et al.*, 1966: 111). *Basilia glabra* Theodor, 1957 from Aruwimi province in the Congo, but no host is given (Haeselbarth *et al.*, 1966: 112). *Dipseliopoda arcuata* Theodor, 1955, collected from an unknown bat at Addis Ababa, Ethiopia (Haeselbarth *et al.*, 1966: 115).

When studying the Nycteribiid abundance on fruit bats and insectivorous bats, Luguterah and Lawer (2015: 4) found that fruit bats were much more infested than insectivorous bats. This could be the result of fruit bats being poorer in nitrogen, which leads to a lack of protein, which in turn inhibits the proper functioning of the immune system. Another explanation might be that insectivorous bats capture their prey on the wing and as such minimize contact with contaminated surfaces.

Szentivanyi *et al.* (2017: 182) found that bat fly species showed a higher diversity towards the equator, and also that bat species assigned to the IUCN LC category hosted a larger number of bat fly specimens than bats assigned to the VU category.

SIPHONAPTERA

Pulicidae

Echidnophaga aethiops Jordan and Rothschild, 1906 host recorded as unidentified Chiroptera and locality not mentioned (Haeselbarth *et al.*, 1966: 135).

Ischnopsyllidae

Dampfia grahami equatoris Smit, 1954 found on a 'small insectivorous bat' in the Kivu district of the Congo (Haeselbarth *et al.*, 1966: 187).

ARACHNIDA

Argasidae

Morel and Mouchet (1965: 492) report the presence of *Carios vespertilionis* Latreille, 1796 and *Carios boueti* Roubaud and Colas-Belcour, 1933 on non-specified bats in Cameroun.

ACARI

Trombiculidae

Stekolnikov (2018a: 33) reported *Schoengastiella vattierae* (Tauffleib, 1964) from unidentified bats from the Central African Republic. He also indicated (p. 116) that *Trisetica aethiopica* (Hirst, 1926) was described from a non-specified bat, and that he found (p. 157) *Microtrombicula machadoi* Tauffleib, 1965. Zajkowska *et al.* (2018: 134) [referring to Tauffleib (1965)] mentions *Schoutedenichia cordiformis* Vercammen-Grandjean, 1958 from an unidentified bat.

VIRUSES:

Worldwide, over 4,100 distinct viruses have been associated with bats (Liu *et al.*, 2023: 206).

In their review of potentially zoonotic viruses, Kohl *et al.* (2021: 1) indicated that on 31 March 2021 the NCBI Genbank and DBatVir databases contained sequences of 12,476 bat-associated viruses, of which 2,728 originated from Africa (second only to Asia with 5,225 sequences). More than 100 of these were identified as important for "emerging and re-emerging human infections", but for a major part of these viruses, it is not certain that bats are the reservoir species (Weinberg and Yovel (2022: 2).

A study by Afelt *et al.* (2018: 115) showed that Africa is the third most intensively studied continent as far as virus research is concerned (after Asia and North America). They also reported (p. 119) that worldwide, 33 % of virus-related publications deal with Rhabdoviridae, 31 % with Coronaviridae, 10 % with Paramyxoviridae, 6 % with Astroviridae, 3 % with Reoviridae and Adenoviridae, 2 % with Circoviridae, Herpesviridae and Flaviviridae, and 1 % with Parvoviridae, Picornaviridae, Polyomaviridae, Papilliomaviridae and Filoviridae.

Luis *et al.* (2013, 2015) and O'Shea *et al.* (2014: 741) indicate that bats are more likely to be infected with more zoonotic viruses per host species than were rodents, and therefore adding weight to the suggestion that bats might in some way be unique as sources of emerging zoonoses. Luis *et al.* (2015) found that gregarious bats are more likely to share more viruses and regionally migrating bats are important for spreading viruses through the "viral sharing network". O'Shea *et al.* (2014: 742) also indicate that body temperatures

of flying bats are elevated (in the range of typical fever temperatures), and they suggest that these daily high temperatures might arm bats against some pathogens during the early stages of infection. This hypothesis, however, was rejected by Schountz *et al.* (2017: 2) as fever response to a virus infection is much more complex than simply raising the body temperature. These authors also point to the "allways on" IFN (interferon) system and the immunoglobulin repertoires of bats. However, see Schoen *et al.* (2023).

Reusken and Heyman (2013: 99) [referring to Weiss *et al.* (2012b)] indicate that bats might be the primordial reservoir for the majority of viruses pathogenic to humans. Brierley *et al.* (2016: "5") report that - based on viral richness alone - the risk of bat-human virus sharing showed prominent hotspots in Central/South America, sub-Saharan Africa, and parts of Southeast Asia. Yinda *et al.* (2019) analysed the gut virome of Cameroonians and found a genetic relatedness between orthoreovirus, picobirnavirus and smacovirus found in humans and those of bats and/or other animals.

Crowley *et al.* (2020: 7) point out that the main predictor of (filo)virus evidence of infection is sampling effort, which is currently too heavily focused on pteropodid bats, and that wider sampling is necessary. Additionally, Thompson *et al.* (2021: 1) highlight the lack of host voucher specimens being collected during host-pathogen studies, which might prevent verification/confirmation of the host's identity.

Guy *et al.* (2020: 5748) found that bat species with longer life spans, broad geographic distributions in the eastern hemisphere, and large group sizes carry more viruses overall. Life span was also an important predictor for DNA viruses, whereas group size and family were more important for predicting the harbouring of RNA virus.

The accounts below represent only viruses where the host (e.g., bat) is unknown. For further information see taxa accounts where the virus is associated with a particular taxon. Also see Chen *et al.* (2014: 1) for an online database on bat-associated viruses. Furthermore, Moratelli and Calisher (2015: suppl. Table II) provide an overview of bat host genera and their associated virus genera, and Young and Olival (2016: suppl. Table S2) provide details on species level for both bat hosts and viruses. See also http://www.mgc.ac.cn/DBatVir/ for more details on bats and viruses (Nieto-Rabiela *et al.*, 2019: 657).

Cheetham and Markotter (2021: 314, 316) report that at least 27 families of viruses have been associated with bats. Of these, Coronaviridae (36 % of GenBank entries) and Rhabdoviridae (24 %) are the most commonly found. 45 % of all the viruses are found in the Vespertilionidae, followed by the Pteropodidae (21 %), and the Rhinolophidae (15 %). No viral sequences have been found in the Mystacinidae, Rhinopomatidae, Megadermatidae, Natalidae or Nycteridae (however, see *Nycteris thebaica* account). 23 % of the viruses were reported from Africa.

Guy *et al.* (2020: Suppl. Fig. 5A) found that worldwide about 125 bat species were reported to carry Coronaviruses, followed by about 80 bat species carrying Rhabdoviruses and 70 carrying Paramixoviruses. About 45 bat species carried Herpesviridae and some 40 Astroviridae. All other virus families were identified from less than 30 bat species.

Méndez-Rodríguez *et al.* (2024: 9) indicate that high prevalences of adenoviruses and herpesviruses reported in various publications are based on infections of animals which were generally collected in the same locality (or nearby) and at the same time. As such, this doesn't represent the real prevalence across a population or species.

For a more detailed overview of viral zoonoses (linked with bats and other mammals), see Ahmed *et al.* (2025).

Brüssow (2025a: 1) claims that "The excretion of viruses that are highly pathogenic for other mammalian orders could be used as biological weapons to defend their habitat against intrusion by mammalian competitors, including humans. This hypothesis might explain the increasing involvement of bat viruses in emerging infectious diseases observed in recent decades and expected in the future."

Jagadesh *et al.* (2025: 2) indicate that 59,902 km^2 in Africa can be classified as high-risk area for bat-borne diseases, with the DRC accounting for the largest high-risk area (19,864 km^2 = 33 %). The highest mean probability for bat-borne diseases in Africa are found in Equatorial Guinea (76 %) and Gabon (56 %).

Astroviridae

From a study on 962 bats (*Hipposideros* cf. *ruber, Hipposideros gigas, Coleura afra, Miniopterus inflatus*, and *Rousettus aegyptiacus*) from Gabon, Rougeron *et al.* (2016: 386) found that bat astroviruses form a group that is genetically distinct from astroviruses infecting other

mammals (including humans). These viruses also showed an important genetic diversity and low host restriction in bat species.

Bunyaviridae
Hantavirus
Gu *et al.* (2014: 1904) argue that primordial hantaviruses may have emerged in an early common ancestor for all bats as bat species hosting these viruses belong to both currently accepted suborders of the Chiroptera (Pteropodiformi [Hipposideridae + Rhinolophidae] and Vespertilioniformi [Nycteridae + Vespertilionidae]). This led Yanagihara *et al.* (2014: 9) to suggest that primordial hantaviruses may have infected an early common ancestor of bats. Yanagihara *et al.* (2014: 9) also indicate that the five known bat hantaviruses are among the most genetically diverse described to date.

Coronaviridae - Coronaviruses
Severe Acute Respiratory Syndrome-associated coronavirus (SARS-CoV or hu-SARS-CoV)
Balboni *et al.* (2012: 8) indicate that SARS-like CoVs have possibly originated in Africa as the viruses themselves has been found in several species of the genera *Hipposideros* and *Chaerephon*, and antibodies against SARS-CoV antigens have been found in *Hypsignathus, Lyssonycteris, Miniopterus, Mops, Myonycteris, Rhinolophus* and *Rousettus* species.

Specifically for Coronaviruses worldwide, Anthony *et al.* (2017b: 7) found that a large number of bat host species were not infected by these viruses, but they also remarked that none of these species were sampled extensively. They found that all species with sample sizes >110 individuals were positive for one or more CoVs, suggesting that CoVs may be detected in some of the negative species if sampling effort were increased. They also calculated (p. 9) that with 154 host individuals, an average of one CoV would be detected, and with 397 individuals, up to five CoVs would be detected. As they did not find any bat species with more than five viral sequence clusters, sampling 397 bats should capture all of the CoVs in a specific bat species.

In their study on bats from the two Congos, Kumakamba *et al.* (2021: 6-7) found 10 % of the bats they examined during the wet season and 6.6 % of the bats examined during the dry season were coronavirus RNA positive animals. This was particularly true for Pteropodidae and Rhinolophidae. For Hipposideridae, Miniopteridae, Molossidae, and Vespertilionidae this was rather the inverse. Bats that were collected for bushmeat were 25.4 % positive whereas only 5 % of the bats sampled during other human-animal interactions were positive. Additionally, there seemed to be a bias for male bats being carriers for these viruses. Their data also indicated that 109 out of the 119 coronavirus positive bats were collected with at least one other positive bat and confirmed that coronaviruses are shared among the bats in a given area, even with other species.

For Cameroon, Ntumvi *et al.* (2022: 1, 22) slightly lower percentages of positive bats: 8.2 % during the wet season and 4.5 % during the dry season. In their study, 175 of 2581 bats (6.8 %) tested positive for CoV RNA, covering 17 genetic clusters, of which eight seem to represent new CoV species.

An overview of coronavirus surveillance in Africa is given in Geldenhuys *et al.* (2021: 9). They found that eleven African bat families were tested (Myzopodidae and Cistugonidae were not sampled), and only from two of them no coronaviruses were reported (Rhinopomatidae- with only one animal tested, and Emballonuridae - with about 678 bats tested, belonging to *Coleura afra, Taphozous perforatus, Taphozous mauritianus*, and *Taphozous hildegardeae*)

Warmuth *et al.* (2023: Fig 1) reported an overall prevalence in African wild bats of 8.64 %.

VanAcker *et al.* (2025: 3) mentioned that within the Betacoronavirus genus, the four subgenera are hosted by specific bat families: *Sarbecovirus* (Rhinolophidae), *Merbecovirus* (Vespertilionidae), *Nobecovirus* (Pteropodidae) and *Hibecovirus* (Hipposideridae). The subgenus *Embecovirus* is primarily found in rodents and bovids, but was also found in some bats.

Filoviridae - Filo viruses
Han *et al.* (2016) reported on traits that discriminate host and non-host (= filovirus-positive) bat species, and they provide a list of bat species most likely to be filovirus-positive on the basis of intrinsic trait similarity with known filovirus-positive bats (See also Sylla *et al.*, 2015).

In their study, Schuh *et al.* (2017c) point to the accumulating number of links between filovirus haemorrhagic fever (FHF) index cases and prior exposure to environments inhabited by bats.

Becker *et al.* (2019: 4) point out that strong temporal dynamics exist in both Marburg and Ebola virus outbreaks, which may be linked to bat reproduction or food availability.

Marburgvirus

Peterson and Holder (2012: 1831) analysed fifteen Marburg virus sequences from bats, and found no indication from the topology of the tree or the branch lengths that the bat-derived filoviruses represent a population distinct from viruses collected from human outbreaks. They suggest that bat sequences do not form a monophyletic group, nor are they associated with long or “deep” branches in the tree. This situation could indicate that the bats are the reservoir population, or that high gene flow exists between virus populations in bats and those in some other taxon (see Towner *et al.*, 2009). Given the short sequence lengths obtained from bat filovirus (about 302 nucleotides of the VP35 gene for most samples), it is also possible that Peterson and Holder, 2012: 1831) lacked the power to detect subtle evidence for population structuring. Thus, firm conclusions about gene flow between the "bat" filovirus populations and the true source of human infections will require more data.

Ebola virus

Most papers related to Ebola (e.g., Alexander *et al.*, 2015) do not provide any details on the bat species involved ("fruit bats", "possibly fruit bats") or refer to the "usual suspects" (*Myonycteris torquata, Hypsignathus monstrosus, Eidolon helvum*". Murray (2015: 802) indicates that the transmission of Ebola virus from bats to humans must be uncommon because the potential reservoir of Ebola virus is huge. Buceta and Johnson (2017) provide a model of the Ebola zoonotic dynamics suggesting a bidirectional coupling between the available resources and the dynamics of the bat population, and indicating that environmental pressure is the main driving force for bats' migration. Based on the fact that the human sero-positive zone is wider than the distribution area of *M. torquata, H. monstrosus* and *E. franqueti*, Formella and Gatherer (2016: 3125) suggest that *E. helvum*, which has a wider distribution, may be involved. They also point out that some (early) Ebola outbreaks, which lie beyond the distribution range of the fruit bats, may have been overlooked.

An extensive survey of Ebola viruses in 4,022 bats from Guinea, Cameroon and the DRC by De Nys *et al.* (2018) showed antibodies in *Mops* sp., *Eidolon helvum*, *Epomophorus* sp., *Hypsignathus monstrosus, Lissonycteris angolensis, Micropteropus pusillus* and *Rousettus aegyptiacus*. No antibodies were found in *Hipposideros* sp., *Miniopterus* sp., *Chaerephon* sp., *Nycteris* sp., *Rhinolophus* sp., *Glauconycteris* sp., *Kerivoula* sp., *Myotis bocagii*, *Neoromicia* sp., *Scotophilus* sp., *Epomops* sp., *Megaloglossus woermanni*, *Myonycteris torquata* or *Scotonycteris zenkeri*.

Koch *et al.* (2020: 2) mention that antibodies against different Ebola species were found in at least 14 bat species, of which nine had antibodies against ZEBOV using serology methods: *Eidolon helvum, Epomophorus gambianus, Lissonycteris angolensis, Micropteropus pusillus, Mops condylurus, Rousettus aegyptiacus, Epomops franqueti, Hypsignathus monstrosus*, and *Myonycteris torquata*. PCR methods could only detect antibodies in *Epomops franqueti, Hypsignathus monstrosus* and *Myonycteris torquata*. PCR evidences for *Rousettus aegyptiacus* have been ambiguous and inconsistent. They also point out (p. 5) that all of the investigated species show a strong association with artificial surfaces and associated areas

A phylogenetic analysis, combined with phylogeographical data led Hassanin *et al.* (2016: 518) to conclude that only three bat species are able to disperse directly ZEBOV (Zaire Ebola) from the Congo Basin to Upper Guinea: *E. helvum*, *H. monstrosus*, and *R. aegyptiacus*.

de La Vega *et al.* (2015: 6) [referring to Biek *et al.* (2006)] indicate that the L gene of bat-derived EBOV showed that it could have recently experienced a genetic bottleneck-type event. Biek *et al.* (2006) proposed a number of scenario's, of which the first suggests that the bat population (around 1999 when the most recent common ancestor to all currently known Ebola viruses existed) decreased significantly, causing a reduction in the viral population size. A second scenario suggested that infected bats could have introduced EBOV in the region near Congo and Gabon circa 1999, and a final scenario is that the fruit bat species identified by Leroy *et al.* (2005) is not the primary reservoir, and that EBOV was possibly introduced by another (bat) species.

Analysing the outbreak data and the distribution area of the various bat species, made Pigott *et al.* (2016: 2) select four species of bats as explaining more of the variation than the rest: *Hypsignathus monstrosus, Epomops franqueti* (from both of which Ebolavirus RNA has been isolated), *Otomops martiensseni* and *Epomophorus labiatus* (both identified through trait-based machine learning approaches as being similar to species already reporting filoviral infection, as suggested by Han *et al.* (2016)).

However, Leendertz (2016: 1) finds it questionable whether these viruses are circulating regularly in bat populations as both

fruit and insectivorous bats have a long lifespan and can fly over large distances, which means that seropositive specimens could be sampled for a long period of time and at large distances from the place where they could have been exposed to the Ebolavirus. Furthermore, the various types of Ebola seem to be linked with different river basins, which do not form barriers for fruit bats. She furthermore suggests to look at insects (e.g., mayflies) as possible vectors. Additionally, Spengler *et al.* (2016: 958) point out that EBOV has yet to be isolated in nature from any bat species (or non-human primates). Furthermore, EFSA AHAW Panel (EFSA Panel on Animal Health and W (2017: 6) remark that natural shedding of the virus has not been reported and that the suspected links between bats and human outbreaks have not been confirmed and further research is necessary to confirm or identify reservoir species. A similar conclusion is drawn by Holmes *et al.* (2016: 198), who indicate that it is likely that other host species exist, which may have a major bearing on epidemiological dynamics. Schmidt *et al.* (2019: 1) indicated that provisional results suggest that some insectivorous bat genera, Old World monkeys and forest antelopes should receive priority in Ebolavirus survey efforts. The extensive survey by Ayouba *et al.* (2019), however, supports the reservoir role of bats (see also Hayman (2019) for a further discussion).

Hranac *et al.* (2019: "1") indicate that no full *Ebolavirus* RNA has been isolated in bats yet, but RNA viral fragments have been found in fruit bats (*Epomops franqueti, Hypsignathus monstrosus* and *Myonycteris torquata*) and in *Miniopterus inflatus*. They (p. "8") were able to find some statistical support for a correlation between the time of births in fruit bats and the outbreaks of Ebola Virus Disease.

Kinganda-Lusamaki *et al.* (2024: e110) confirmed that no Ebolavirus species have been definitely identified in bat hosts, but that bats seropositive for Ebolavirus have been found in the Nord Kivu and Equateur provinces of the DRC and in the Republic of Congo.

Gale (2017: 1678) argues that although previous studies failed to detect the presence of EBOV in arthropods, these studies might not have included the correct arthropod species: "This is because filoviruses are not 'arboviruses' in the sense that arboviruses are transmitted in a defined cycle which alternates between the vertebrate host and the arthropod vector. Instead, filovirus transmission pathways appear to be more random in terms of host species. Indeed, if these arthropod species were the reservoir for EBOV, then EBOV would be an arbovirus with a vertebrate host defined by the host preference of the arthropod." If an arthropod is the intermediate host, then an insectivorous bat would rather be the host than any of the Pteropodids. Gale (2017: 1678) also indicates that the higher body temperature of the bat (40°C in *Mops condylurus*, compared to that of an arthropod, which is the ambient temperature) would activate the virus reproduction in the bat, and hence, its increased probability to infect humans. However, the bats will still need to ingest a large quantity of the virus to start off with, but this could happen during an ephemeral mass emergence of mayflies.

Li *et al.* (2016: 127) also pointed out that as large quantities of bat meat are consumed every year, the virus must be very rare in its reservoir, otherwise more frequent outbreaks of the virus would be observed, which led them to the suggestion that strict restrictions on bushmeat are not recommended for local citizens, especially as interviews done by Tijani *et al.* (2021: 1962) revealed that 76.6 % (315 out of 411) of hunters in Kwara State, Nigeria believed that consumption of bush meat isn't linked with the transmission of Ebola Virus Disease.

Leendertz *et al.* (2015: 22) suggest that bats are intermediate hosts, which are occasionally exposed via another intermediate host or unknown reservoir and that viral emergence might be more related to environmental factors and other hosts than bats themselves. See also Caron *et al.* (2018: 5) who discuss a number of hypothetical transmission pathways between a maintenance host of EBOV and bats: Air-borne, vector-borne, food-borne (insects or fruits), water-borne, direct and environmental.

Hemamalani *et al.* (2025: 6), Matson *et al.* (2025: 4) and Sundaram *et al.* (2025: 1) confirmed that the permanent or primary reservoir of the Ebola virus is not yet known. Yet multiple publications, e.g. Umar and Diggle (2025: 5) still claim: "The natural reservoir host(s) of EBV are forest-dwelling fruit bats of the Pteropodidae family in Africa".

Dick and Dittmar (2014: 150) indicate that nycteribiid and streblid bat flies are known to infest the above mentioned fruit bats. These flies readily move from bat to bat, feeding on multiple individuals during the course of days and weeks. Possibly, the flies can uptake viral pathogens, which might remain viable within bat flies. If this is the case, host-specific flies can transfer such viruses among host bats within a population.

Babayan *et al.* (2018: 578) worked out a model that analyses virus genomes and links these to probable reservoir hosts. For the four Ebolaviruses, the model showed greater support for Pteropodiformi as reservoir than Vespertilioniformi, but Bundibugyo and Tai Forest ebolaviruses had equal or stronger support for primate reservoirs.

Analysing the literature data, Ponce *et al.* (2019: 3133) pointed out that for only three of the 23 outbreaks (13.0 %) the source animal was confirmed in a laboratory. Of the suspected source animals, 10 were primates and six bats (with three fruit bats and three insectivorous bats).

On 24 January 2019, a series of newspaper articles was published, where several scientists from EcoHealth Alliance were quoted (Simon J. Anthony, Jonathan Epstein) stating that in a mouth swab one Liberian *Miniopterus inflatus* (out of 150 tested) RNA material of the Zaire Ebolavirus was found. Epstein, however, pointed out that if the bat was a natural host for the virus, it would have been found in more than one bat. He also pointed out that the bat could have become infected by another bat species living in the same habitat. Fabian Leendertz (veterinary epidemiologist at the Robert Koch Institute - not involved in the study) indicated that the virus itself wasn't isolated but only about one-fifth of its genome (Grady, 2019; Kupferschmidt, 2019; Su, 2019). Schuh *et al.* (2019a: 2) also confirmed that no infectious virus was yet isolated from any bat species. This would indicate that the bats had either cleared virus infection prior to sampling or are 'dead-end' virus hosts. However, it might also be possible that current filovirus isolation techniques lack the sensitivity to recover infectious virus from specimens with low viral loads.

Gryseels *et al.* (2020: 2208) point out that many small mammals (not only bats) are difficult to identify at a species or genus level on the basis of morphology alone and emphasize the need of molecular identification of the host species when doing EBOV and other virus surveillance in small mammals.

Lee-Cruz *et al.* (2021: Suppl. Table A, D) considered the following species as potential reservoir or intermediate host species: *Chaerephon pumilus, Eidolon helvum, Epomophorus gambianus, Epomophorus labiatus, Epomophorus wahlbergi, Epomops franqueti, Hypsignathus monstrosus, Lissonycteris angolensis, Micropteropus pusillus, Miniopterus inflatus, Mops condylurus, Myonycteris torquata, Otomops martiensseni* and *Rousettus aegyptiacus*.

See also Tuttle (2017) for a further discussion on possible alternative virus hosts, who also pointed out (p. 48) that 'the knowledge base about emerging infectious diseases is extraordinarily biased by scientists' obsession with bats. This bias is encouraged by an additional, highly practical factor: there is no group of mammals easier to sample quickly or in large numbers than bats. Bats may love the dark, but they are all too easy to put under the spotlight of scientific scrutiny."

Sundaram *et al.* (2024: 1) showed that factors that most influenced whether a given host species range contained a site of a previous outbreak event were habitat suitability for *Ficus* and the diversity of cercopithecid primates. The richness of pteropodid bats had a strong effect on which species tested positive for antibodies, but had no effect on the outbreak risk.

In an extensive study covering various African countries, Peeters *et al.* (2023: 7) found antibodies to orthoebolavirus antigens in 14.1 to 48.1 % of the *Eidolon helvum* specimens and in 14.1 to 35.5 % of the *Rousettus aegyptiacus* specimens. In *Hypsignathus monstrosus* the numbers varies between 12.4 and 30.6 %. In the other species the prevalence was much lower: 3.1 - 13.1 % for *Myonycteris torquata* and 2.2 - 5.8 % for *Epomops* species. Among the insectivorous species the numbers were even much lower: *Chaerephon/Mops* (1.8 - 7.5 %) and *Miniopterus* (4.5 - 12.1 %).

Weber *et al.* (2023: Suppl. 51) scrutinised the literature and found that several African bat species tested positive for antibodies against *Orthomarburgvirus* and *Orthoebolavirus*. They also found quite a lot of positive PCR test results, but actual viruses were only reported in 24 out of 4908 tests for *Orthomarburgvirus* (0.5 %) [all for *Rousettus aegyptiacus*] and 0 out of 1687 tests for *Orthoebolavirus*.

Note: The Filoviridae study group of the International Committee on Taxonomy of Viruses (ICTV) has renamed the genus *Ebolavirus* to *Orthoebolavirus* to make the distinction with the Ebola virus species (EBOV). Similarly, the name of the genus *Marburgvirus* has been changed to *Orthomarburgvirus* (Peeters *et al.*, 2023).

Poxviridae

Ortopoxvirus

N'dilimabaka *et al.* (2024 1, 3) were unable to find any MPXV (mpox) DNA in 859 Gabonese bats,

belonging to 11 species (including *Rousettus aegyptiacus* and *Epomops franqueti*).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Munang'andu *et al.* (2011: 23) summarize rabies status in Zambia for the period 1985-2004, where only one single case is reported from an unidentified bat. See Adedeji *et al.* (2010) for an overview of the history, and epidemiology of rabies and rabies-like viruses.

Dah *et al.* (2023: 4, 6) examined the brains of 212 Cameroonian bats (76 *Eidolon helvum*, 10 *Chaerephon chapini*, 10 *Chaerephon leucogaster*, 96 *Chaerephon pumilus* and 20 *Scotophilus leucogaster*). 57 of these tested positive for rabies antigen.
Note: The above paper was later retracted by the editors of journal.

Turkson (2023: 1) investigated 328 rabies cases in Ghana between 2010 and 2017. Of these, 2 (0.6 %) were found in bats

Singano *et al.* (2025: 14) indicated that rabies detection studies should best be executed during the dry season as viral activity and transmission risks are likely higher in that season due to immigrating rabit bats into colonies.

DUV
In 2007 a bat flew against the face of a Dutch woman in Tsavo West National Park in Kenya. She noticed two superficial bleeding wounds. Twenty-three days after the incidence she presented herself with symptoms in a hospital in the Netherlands and died of rabies. The virus was identified as Duvenhage virus (Van Thiel *et al.*, 2009).

UTILISATION:
Kamins *et al.* (2011b: S102) report that in southeastern Ghana nearly one half of the population may eat bats, although bats do not appear in other studies on wildlife meat markets.

Friant *et al.* (2022) investigated the use of animals in medical and cultural practices in Nigeria. In some cases, bat fur was used to treat burns (although apparently only as a substitute for missing flying squirrel fur) (p. 10). Another use (p. 11) was cooked bat brain consumption to enhance children's intelligence.

In Tanzania, inhaling smoke of burning bats is sometimes used to treat pneumonia.

Aggrey *et al.* (2024: 13) found that the usage of bats as medicine was less than expected (compared to Asia) as 60% traditional medicine is used on the continent, but they attributed this to the low publication output on this subject.

Aggrey *et al.* (2024: 4, 5) also indicated that bats are considered valuable (especially in West and East Africa) because of their material and immaterial benefits, which include providing sufficient and nutritious food, income and trade generated values (e.g. guano), and tourism.

ANTHROPOPHILOUS:
Willett (1988) discusses the use of bat symbols in West African art, whereas Snyders (2022) reported on the importance of bat guano trade in the late XIX - early XXth century in the Cape province.

Euren *et al.* (2020) investigated the knowledge, beliefs, perceptions, and behaviours of Sierra Leonan people that may potentially protect them from or expose them to zoonotic spillover either by direct or indirect contact with bats.

Over a third (38.4 %) of the interviews conducted by Laverty *et al.* (2021: 77) with Namibian pastoralists contained detailed descriptions of myths and common meanings assigned to bats. Of these, 12.1 % were about bats bringing good luck or good rains, but 84.8 % referred to bats bringing bad luck or omens of injury, death, disease, or drought.

Balla [in Laugrand *et al.* (2023: 333)] mentioned local differences in attitudes towards bats in Cameroon: in the southern part of the country, the Beti, Bassa, Douala, Tikar, and some Bamileke groups hunt and eat different species of bats, and bats entering houses are considered a bad omen. In the northern part, the Kapsiki believe that bats cannot live in a village with conflict and witchcraft, and their presence close to humans would be a source of peace and prosperity. The bats also believed to bring fertility to crops on farms located near the trees where the bats live.

Balla [in Laugrand *et al.* (2023: 334)] (referring to Cros and Frérot, 2021) also mentioned that in French speaking West Africa (e.g., Burkina Faso) - in the aftermath of the Ebola epidemic - people preferred to speak of "sauve-souris" ("saving bat") rather than "chauve-souris" as a widely used anagram at that time was "souche à virus" (meaning "virus strain").

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Gabon, Guinea-Bissau,

Kenya, Liberia, Madagascar, Malawi, Mauritius, Senegal, Somalia, South Africa, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

†Family AEGYPTONYCTERIDAE Simmons, Seiffert and Gunnell, 2016

*2016. *Aegyptonycteridae* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 4, 8. Publication date: 9 May 2016. - Comments: Type genus *Aegyptonycteris* Simmons, Seiffert and Gunnell 2016.

TAXONOMY:
The supra-familial relationships for this family are yet unknown.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
These fossil bats have a late Eocene (Priabonian, ca. 37 Mya) age.

†Genus *Aegyptonycteris* Simmons, Seiffert and Gunnell, 2016

*2016. *Aegyptonycteris* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 6, 8. Publication date: 9 May 2016. - Etymology: From *Aegyptus*, Latinized Greek for "Egypt," and nycteris, Greek for "bat." The genus name refers to the country in which this new taxon was discovered (Simmons *et al.*, 2016: 8).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Simmons and Jones (2024: 17) estimated that some members of this genus might have attained a weight 125 g.

DIET:
Simmons and Jones (2024: 17) indicate that *Aegyptonycteris* was probably an omnivorous bat.

†*Aegyptonycteris knightae* Simmons, Seiffert and Gunnell, 2016

*2016. *Aegyptonycteris knightae* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 6 8, figs 3 - 5. Publication date: 9 May 2016. Type locality: Egypt: Western Desert: Fayum Depression, Birket Qarun Formation: Fayum Quarry BQ-2: 23 m level. Holotype: CGM 83740. Fragment of right maxilla with M2 and M3 (see: Simmons *et al.*, 2016: 8). - Etymology: Named in honour of Mary Knight, Managing Editor of the American Museum of Natural History Scientific Publications, in recognition of the enormous contributions she has made to dissemination of the results of scientific research over the years, as well as her lifelong devotion to the people and culture of Egypt (Simmons *et al.*, 2016: 8).

COMMON NAMES:
Dutch: Knight's Egyptische vleermuis. English: Knight's Egyptian bat

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Priabonian (37.97 - 33.23 mya) (see Brown *et al.*, 2019: Suppl.).

†Family NECROMANTIDAE Sigé, 2011

*2011. *Necromantidae* Sigé, Bull. Soc. Hist. Nat. Toulouse, 147: xxx. - Comments: Type genus †*Necromantis* Weithofer, 1887.

TAXONOMY:
Jones *et al.* (2024: 14) mention that most traditional classifications link this family to the Megadermatidae, but more recently a close relationship with the Emballonuroidae has been proposed.

†Genus *Necromantis* Weithofer, 1887

1888. *Necromanter* Lydekker, Zool. Rec., London, 71 - 56 [for 1887].
*1888. *Necromantis* Weithofer, Sber. Akad. Wiss. Wien, math. naturw. Kl., 96 (1) 5: 353 (for 1887).
1903. *Necronycteris* Palmer, Science, NS 17: 873. Publication date: 29 May 1903.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Simmons and Jones (2024: 16) estimated that some members of this genus might have attained a weight of 50 to over 100 g.

DIET:
Simmons and Jones (2024: 16) indicate that *Necromantis* was originally described as a scavenger

of carrion. Referring to Hand *et al.* (2012), they also indicate that these bats were probably specialized in hard prey items.

†*Necromantis fragmentum* (Ravel, 2016)

*2016. *?Necromantis fragmentum* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 363, figs 4, 5. Publication date: 30 September 2016. Type locality: Tunisia: Kassérine province: Djebel Chambi National Park: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: From the Latin "fragmentum" meaning fragment or debris, referring to the fragmented character of the material attributed to this species (see Ravel *et al.*, 2016: 364).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe: Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

SUBORDER PTEROPODIFORMI Van Cakenberghe, Kearney and Seamark, 2007

1821. *FRUCTIVORAE* J. E. Gray, London Med. Repos., 15 (1): 299. - Comments: Proposed as order and originally included the families Pteropidae J. Gray, 1821 and Cephalotidae J. Gray, 1821, both currently representing Pteropodidae J. Gray, 1821. Jackson and Groves (2015: 230) included it as synonym of the Pteropodidae.

1855. *FRUGIVORA* Giebel, Die Säugethiere …, xii, 991. - Comments: Originally included the genera *Hypoderma* É. Geoffroy, 1828 [= *Dobsonia* Palmer, 1898]; *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797]; *Macroglossus* F. Cuvier, 1824 [1821-1825]; and *Pteropus* Brisson, 1762 (see Jackson and Groves, 2015: 229). McKenna and Bell (1997: 295) synonymized it with Megachiroptera.

1866. *Pterocynes* Haeckel, Generelle Morphologie der Organismen, 2: clx. - Comments: *Nomen oblitum*. Proposed as suborder and originally included the "families" Pteropodida (including the genera *Pteropus* and *Macroylossus*) and Hypodermida (including the genus *Hypoderma*) Jackson and Groves, 2015: 229). McKenna and Bell (1997: 295) synonymized it with Megachiroptera.

1875. *MEGACHIROPTERA* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (95): 346. - Comments: Originally included the groups Pteropi (containing the genera *Pteropus* Brisson, 1762; *Cynopterus* F. Cuvier, 1824 [1821-1825]; *Cynonycteris* Peters, 1852 [= *Rousettus* J. Gray, 1821]; *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797]; *Epomophorus* E. Bennett, 1836; and *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797]) and Macroglossi (containing the genera *Macroglossus* F. Cuvier, 1824 [1821-1825]; *Eonycteris* Dobson, 1873; and *Notopteris* J. Gray, 1859) (see Jackson and Groves, 2015: 228). - Etymology: From the neuter plural scientific Latin substantive made up of the Greek adjective "*μέγα*" (mega) "big" and chiroptera, i.e. "big Chiroptera", in opposition to Microchiroptera ("small chiroptera") (see Lanza *et al.*, 2015: 18).

2001. *YINPTEROCHIROPTERA* Springer, Teeling, Madsen, Stanhope and De Jong, Proc. Natl. Acad. Sci. USA, 98 (11): 6423. - Comments: In part.

2004. *PTEROPODIFORMES* Hutcheon and Kirsch, J. mamm. Evolut., 11 (1): 44. - Comments: Originally included the families Pteropodidae J. Gray, 1821, Hipposideridae Flower & Lydekker, 1891, Rhinolophidae J. Gray, 1825, Megadermatidae H. Allen, 1864, and Craseonycteridae Hill, 1974 (see Jackson and Groves, 2015: 229).

*2007. *PTEROPODIFORMI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the suborder is based on *Pteropus* Brisson, 1762 (type of Pteropodidae Gray, 1821). (Current Combination).

2014. *Pteropodimorpha* Zagorodniuk, Proc. Theriol. School, 12: 8.

2018. *Yinpterachiroptera:* Skirmuntt and Katzourakis, Virus Research, 270 (197645): 2. Publication date: 1 July 2018. (Lapsus).

TAXONOMY:

The suborder name follows the typified name used by Hutcheon and Kirsch (2004b, 2006), but with the ending changed to follow the format proposed for standardization of nomenclature of higher taxa by Alonso-Zarazaga (2005). '-formes' indicates ordinal level, while ending '-formi' indicates subordinal level.

Ao *et al.* (2007: 257) provide the first cytogenetic signature rearrangement that supports the grouping of Pteropodidae and Rhinolophoidea in a common clade (i.e. Pteropodiformes or Yinpterochiroptera).

In their phylogenetic study on *Bartonella*, McKee *et al.* (2016: 390) estimated the posterior state transition rate for *gltA* sequences in this bacterium and found a very high median rate between the superfamilies Pteropoidea and Rhinolophoidea (2.77) and between the families Pteropodidae and Rhinolophidae (2.32).

Based on transcriptome RNA-seq data, Lei and Dong (2016: 2) estimated the split between Rhinophoidea and Pteropoidae at about 60 MYA.

Currently two Infraorders are recognized within the suborder PTEROPODIFORMI from Africa: **PTEROPODIFORMACEI** Van Cakenberghe, Kearney and Seamark, 2007 and **RHINOLOPHIFORMACEI** Van Cakenberghe, Kearney and Seamark, 2007.

COMMON NAMES:

Czech: kaloňotvaří.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Guan *et al.* (2025: 7) estimate that the divergence of the families within this suborder began about 55.38 mya.

DETAILED MORPHOLOGY:

The echolocating bats belonging to the Pteropodiformi can be distinguished from the Vespertilioniformi by the presence of a pectoral ring. This bony structure is formed by the fusion of the top bone of the breast bone (manubrium), the first two ribs and the last cervical and first two thoracic vertebrae (Jacobs (2016: 66-67).

MOLECULAR BIOLOGY:

Genetics

Volleth (2010: 308) reports the detection of two cytogenetic characters serving as synapomorphies for Pteropodiformi (i.e. Rhinolophoidea plus Pteropodidae), and indicates that the cytogenetic basis is a small paracentric inversion hardly detectable with banding

techniques, but clearly detectable with FISH (fluorescence in-situ hybridization) techniques.

VIRUSES:
Osborne *et al.* (2011: 8) indicate that "Yinpterochiroptera" [= Pteropodiformi] is the only suborder in which Betacoronaviruses are found, but they indicate that their conclusion might be biased as they only examined a subset of species of the New World, where no representatives of this suborder are occurring.

INFRAORDER PTEROPODIFORMACEI Van Cakenberghe, Kearney and Seamark, 2007

*2007. *PTEROPODIFORMACEI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Infraorder is based on *Pteropus* Brisson, 1762 (type of Pteropodidae Gray, 1821). (Current Combination).

TAXONOMY:
Currently only a single superfamily is recognised within the infraorder PTEROPODIFORMACEI: **PTEROPODOIDEA** Gray, 1821.

Superfamily PTEROPODOIDEA J. E. Gray, 1821

*1821. *PTEROPODOIDEA* J. E. Gray, London Med. Repos., 15 (1): 229. - Comments: The name of the superfamily is based on *Pteropus* Brisson, 1762 (type of Pteropodidae Gray, 1821), and originally included the genera *Pteropus* Brisson, 1762; and *Rousettus* J. Gray, 1821. (Current Combination).
2008. *Pteropoidea* Serra-Cobo, López-Roig, Bayer, Amengual and Guasch, Ratpenats. Ciència i mite, 31.

TAXONOMY:
Known families of the superfamily PTEROPODOIDEA: **PTEROPODIDAE** Gray, 1821.

COMMON NAMES:
Czech: kaloňovci, kaloni.

Family PTEROPODIDAE J. E. Gray, 1821

1821. *Cephalotidæ* J. E. Gray, London Med. Repos., 15 (1): 299. - Comments: Type genus: *Cephalotes* É. Geoffroy, 1810b [= *Nyctimene* Borkhausen, 1797].
*1821. *Pteropidæ* J. E. Gray, London Med. Repos., 15 (1): 299. Publication date: 1 April 1821. - Comments: Jackson and Groves (2015: 230) explains that the stem of the Greek *pous* (=foot) is *pod-*, so the stem of the latinised *Pteropus* is 'pteropod-', leading to the corrected name Pteropodidae introduced by Bonaparte (1837: 112).
1825. *Pteropina* J. E. Gray, Ann. Philos., 10 (5): 338. Publication date: November 1825. - Comments: Proposed as tribe and originally included the genera *Pteropus* Brisson, 1762; *Cynopterus* F. Cuvier, 1824 [1821-1825]; *Macroglossum* [sic = *Macroglossus*] F. Cuvier, 1824 [1821-1825]; *Cephalotis* [sic = *Cephalotes*] É. Geoffroy, 1810b [= *Nyctimene* Borkhausen, 1797]; and *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797] (see Jackson and Groves, 2015: 230). McKenna and Bell (1997: 295) synonymized it with Pteropodidae. Jackson and Groves (2015: 236) also mention it in the synonymy of the subfamily Pteropodinae.
1838. *PTEROPODIDAE* Bonaparte, Syn. Vert. Syst., in Nuovi Ann. Sci. Nat., Bologna, 2: 111. - Comments: Type genus: *Pteropus* Brisson, 1762. (Alternate Spelling).
1842. *Harpyidae* C. H. Smith, An introduction to the Mammalia, 15: 115. - Comments: Type genus: *Harpyia* Illiger, 1811 [=*Nyctimene* Borkhausen, 1797). Originally included the genera *Pteropus* Brisson, 1762; *Pachysoma* I. Geoffroy, 1828 [= *Cynopterus* F. Cuvier, 1824 [1821-1825]; *Macroglossus* F. Cuvier, 1824 [1821-1825]; *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797]; and *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797] (see Jackson and Groves, 2015: 230). Simmons (2005: 313) synonymized this name with Pteropodidae.
1866. *Hypodermida* Haeckel, Generelle Morphologie der Organismen, clx. - Comments: Originally included the genus *Hypoderma* É. Geoffroy, 1828 [= *Dobsonia* Palmer, 1898] (see Jackson and Groves, 2015: 230). McKenna and Bell (1997: 295) synonymized it with Pteropodidae.
1866. *Pteropi* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 256. - Comments: Proposed as family name and originally included the genera *Pteropus* Brisson, 1762; *Cynonycteris* Peters, 1852 [= *Rousettus* J. Gray, 1821]; *Pterocyon* Peters, 1861 [= *Eidolon* Rafinesque, 1815]; *Cynopterus* F. Cuvier, 1824 [1821-1825]: 248; *Megaerops* Peters, 1865; *Epomophorus* E. Bennett, 1836; *Macroglossus* F. Cuvier, 1824 [1821-1825]; *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797]; *Cephalotes* É. Geoffroy, 1810b [= *Nyctimene* Borkhausen, 1797]; and *Notopteris* J. Gray, 1859.
1866. *Pteropodida* Haeckel, Generelle Morphologie der Organismen, clx. - Comments: Originally included the genera *Pteropus* Brisson, 1762; and *Macroglossus* F. Cuvier, 1824 [1821-1825] (see Jackson and Groves, 2015: 230). McKenna and Bell (1997: 295) synonymized it with Pteropodidae.

1893. *Pteropi* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 53. - Comments: Proposed as tribe(?) and originally included the genera *Cynonycteris* Peters, 1852b: 25 [= *Rousettus* J. Gray, 1821]; *Pteropus* Brisson, 1762; *Pteralopex* Thomas, 1888; *Epomophorus* Bennett, 1836; *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797]; *Cynopterus* F. Cuvier, 1824 [1821-1825]; and *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797] (see Jackson and Groves, 2015: 231).

2024. *Petropodidae:* Taha and Soliman, Zool. Middle East, 70 (4): 281. Publication date: 7 November 2024. (Lapsus).

2025. *Pteripodidae:* Grunwald, Demos, Atagana, Volk, Monadjem, Meyo Okono, Ngueagni, Merrill, Bevers, Armstrong, Kilber, Talla, Bakwo Fils, Patterson, Ballhorn and Ruedas, Acta Chiropt., 26 (2): 280. Publication date: 12 February 2025. (Lapsus).

TAXONOMY:

The taxonomy of the Pteropodidae follows that of Bergmans (1988, 1989, 1991, 1994, 1997) and Simmons (2005: 313 - 350).

Corbet and Hill (1992: 55) refer to Handley (1980) for a discussion on the correct formation of the family name.

Between two and six subfamilies of Pteropodidae have been recognized (Simmons, 2005: 313) including: Cynopterinae K. Andersen, 1912, Epomophorinae K. Andersen, 1912, Harpionycterinae Miller, 1907, Nyctimeninae Miller, 1907, Macroglossinae Gray, 1866, Rousettinae Andersen, 1912, and Pteropodinae Grey, 1821 (Bergmans, 1997; Corbet and Hill, 1980, 1991, 1992; Hill and Smith, 1984; Koopman, 1993a, 1994; McKenna and Bell, 1997).

Recent phylogenetic studies agree that Macroglossinae and Pteropodine *sensu* (Koopman, 1993a, 1994; McKenna and Bell, 1997) are not monophyletic (Álvarez *et al.*, 1999; Giannini and Simmons, 2003; Hollar and Springer, 1997; Hood, 1989; Juste B. *et al.*, 1997; Kirsch *et al.*, 1995; Romagnoli and Springer, 2000; Springer *et al.*, 1995). Monophyly of cynopterines and empomophorines has also been questioned (Álvarez *et al.*, 1999; Hollar and Springer, 1997; Kirsch *et al.*, 1995; Romagnoli and Springer, 2000). Phylogenetic studies based on DNA hybridization and DNA sequences have found support for a large clade of endemic African taxa including genera previously placed in several different subfamilies/tribes based on traditional taxonomic groupings (Álvarez *et al.*, 1999; Giannini and Simmons, 2003; Hollar and Springer, 1997; Kirsch *et al.*, 1995; Romagnoli and Springer, 2000). Relationships among pteropodid genera are not yet fully resolved, however, and questions remain concerning the position of *Nyctimene*; *Paranyctimene*, *Eidolon*, and several SE Asian endemic genera (Simmons, 2005) . Based on a phylogenetic study of newly generated sequences of four nuclear loci, Almeida *et al.* (2011b: 86) found a basal split of Pteropodidae into 7 (maybe 8) main clades, but the relationships between them are not well resolved. The analyses performed by Almeida *et al.* (2011a: 7) revealed six principal clades and one independent lineage (for *Eidolon*). Some of their principal clades agree with previously proposed subfamilies: Cynopterinae, Harpyionycterinae, and Nyctimeninae. The other clades agree with Macroglossini, Epomophorinae + Rousettini, and Pteropodini + *Melonycteris*. Almeida *et al.* (2016: 73) recognize four main African clades: *Eidolon*, Scotonycterini (including the genera *Casinycteris* and *Scotonycteris*), African *Rousettus* (with three species) and the previously identified 'endemic African clade' (with nine genera: (*Stenonycteris, Plerotes, Myonycteris, Megaloglossus, Hypsignathus, Nanonycteris, Epomops, Epomophorus*, and *Micropteropus*), and suggest that a new classification on subfamilial and tribal levels is probably needed.

Simmons (2005: 313) suggests the relationships among the pteropodid genera are not yet fully resolved, and no subfamilial or tribal groups were recognized pending a thorough reevaluation of pteropodid classification.

Almeida *et al.* (2016: 83) provide the following classification: Harpyionycterinae (including the genera *Dobsonia, Aproteles, Boneia, Harpyionycteris*, Rousettinae (including the tribes Rousettini (*Rousettus*), Eonycterini (*Eonycteris*), Scotonycterini (*Scotonycteris, Casinycteris*), Epomophorini (*Epomophorus, Epomops, Hypsignathus, Nanonycteris, Micropteropus*), Stenonycterini (*Stenonycteris*), Myonycterini (*Myonycteris* (incl. *Lissonycteris*), *Megaloglossus*), and Plerotini (*Plerotes*)), and Eidolinae (*Eidolon*).

Hassanin *et al.* (2016: 521) indicate that two subfamiles occur in Africa: Pteropodinae (with one genus: *Eidolon*) and Rousettinae. The latter subfamily is subdivided in three tribes: Scotonycterini (*Scotonycteris* and *Casinycteris*), Rousettini (*Rousettus*), and Epomophorini, which is further divided in four subtribes: Epomophorina (*Epomophorus, Epomops, Hypsignathus, Micropteropus*, and *Nanonycteris*), Myonycterina (*Myonycteris* and *Megaloglossus*), Plerotina (*Plerotes*), and Stenonycterina (*Stenonycteris*).

They also estimate that the three tribes diversified about 7 - 8 Mya. They also indicate (p. 524) that this family has its origin in Southeast Asia, which is supported by: **1)** More than half of the species (94) are found in this region, **2)** The highest species density is found on the islands of Sumatra, Borneo and Sulawesi, **3)** the oldest fossil of fruit bats has been described in the Late Eocene/Early Oligocene of Thailand, and **4)** The molecular analyses indicate that all African species have a derived position with respect to their congeners from Asia and Oceania.

Almeida *et al.* (2020: 11) recognized eight subfamilies: Cynopterinae Andersen, 1912, Macroglossusinae Almeida *et al.*, 2020, Harpyionycterinae Miller, 1907, Rousettinae Andersen, 1912, Eidolinae Almeida *et al.*, 2016, Notopterisinae Almeida *et al., 2020*, Nyctimeninae Miller, 1907, and Pteropodinae Gray, 1821.

Currently (Simmons and Cirranello, 2024a) recognized genera of Pteropodidae: *Acerodon* Jourdan, 1837; *Aethalops*, Thomas, 1923; *Alionycteris* Kock, 1969; *Aproteles* Menzies, 1977; *Balionycteris* Matschie, 1899; *Boneia* Jentink, 1879; ***Casinycteris*** Thomas, 1910; *Chironax* K. Andersen, 1912; *Cynopterus* F. Cuvier, 1824; *Desmalopex* Miller, 1907; *Dobsonia* Palmer, 1898; *Dyacopterus* K. Andersen, 1912; ***Eidolon*** Rafinesque, 1815; *Eonycteris* Dobson, 1873; ***Epomophorus*** Bennett, 1836; ***Epomops*** Gray, 1870; *Haplonycteris* Lawrence, 1939; *Harpyionycteris* Thomas, 1896; ***Hypsignathus*** H. Allen, 1861; *Latidens* Thonglongya, 1972; *Macroglossus* F. Cuvier, 1824; *Megaerops* Peters, 1865; ***Megaloglossus*** Pagenstecher, 1885; *Melonycteris* Dobson, 1877; *Mirimiri* Helgen, 2005; ***Myonycteris*** Matschie, 1899; ***Nanonycteris*** Matschie, 1899; *Neopteryx* Hayman, 1946; *Nesonycteris* Flannery, 1993; *Notopteris* Gray, 1859; *Nyctimene* Borkhausen, 1797; *Otopteropus* Kock, 1969; *Paranyctimene* Tate, 1942; *Penthetor* K. Andersen, 1912; *Pilonycteris* Nesi, Tsang, Simmons, McGowen and Rossiter, 2021; ***Plerotes*** K. Andersen, 1910; *Ptenochirus* Peters, 1861; *Pteralopex* Thomas, 1888; ***Pteropus*** Brisson, 1762; ***Rousettus*** Gray, 1821; ***Scotonycteris*** Matschie, 1894; *Sphaerias* Miller, 1906; *Stenonycteris* Gray, 1870; *Styloctenium* Matschie, 1899; *Syconycteris* Matschie, 1899; *Thoopterus* Matschie, 1899.
Additionally, there is one extict genus: † Propotto Simpson, 1967.

COMMON NAMES:
Czech: kaloňovití, upírové, létací psi, bejložraví netopýři, létací lišky. Dutch: Grote fruitvleermuizen, Vliegende honden. English: Old World Fruit bats. Finnish: Hedelmälepakot. French: Prétopodidés, Chauves-souris frugivore de l'ancien monde. German: Flughunde, Flederhunde. Italian: Pteropòdidi, Pteròpidi. Norwegian: Flyvende hunder, kalong. Russian: Крылановые. Ukrainian: Летючі лисиці. Vietnamese: Họ dơi quạ.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Gunnell and Simmons (2013: 63) indicate that fossil records for Pteropodid bats are extremely poor. There are hardly any records older than Late Pleistocene-Holocene, although molecular data suggest that Pteropodids diverged from other bats no later than in the Early Eocene (ca. 50 million years ago). They suggest that this is probably due to the fact that most of the Pteropodid fossils are considered to be from Primates rather than from bats.

The family's stem and crown ages were reported by Shi and Rabosky (2015: 1537) to be respectively 56.6 and 40.2 mya, whereas Almeida *et al.* (2021: 234) fixed these at 55.4 and 25.3 mya, respectively.

Foley *et al.* (2014: 320) indicate that the Rhinolophoidea and Pteropodidae diverged approximately 59 mya.

CONSERVATION STATUS:
Tanalgo *et al.* (2023: 13) point out that intensely hunted bats (such as *Rousettus* and *Eidolon* remain under-protected due to their IUCN status of "least threatened" and being non-endemic. As such these are not prioritized in national conservation actions.

MAJOR THREATS:
Fruit bats are often persecuted for the damage they potentially cause to fruits. However, Mphethe *et al.* (2025: 1) indicate that - at least for litchi fruits in the RSA - the most damage is caused by weather and monkeys.

DENTAL FORMULA:
See Adeniyi *et al.* (2010).

DETAILED MORPHOLOGY:
Tongue
Morphological studies on the tongue structure of Old World fruit bats suggest that these bats are highly adapted to fruit and nectar diets and are able to change between a fruit and nectar diet when their preferred food is not available (Morrison, 1980; Birt *et al.*, 1997). Old World fruit bat species possess filiform papillae at the tip of the tongue, which is thought to increase the surface area for nectar collection (Birt *et al.*, 1997). Filiform papillae increase the gripping of

food on the tongue surface, thus efficiently moving food toward the pharynx (Birt *et al.*, 1997). Bats feeding on fruit also have a large tongue surface area, but generally lack tongue tip filiform papillae, and possess tridentate papillae (Birt *et al.*, 1997). Tridentate papillae are thought to be valuable when piercing through the skin of soft fruits (Birt *et al.*, 1997). Morrison (1980) suggested that fruit bats have a widened tongue and consequently larger tongue surface area that is used to squeeze fruit against the hard upper palate, thus releasing fruit juices.
See also Adeniyi *et al.* (2010).

SEXUAL DIMORPHISM:
Dobson (1873: 251) suggests that the hairs of the male's epaulettes of the Epomophori are long due to glandular excretions, similar to beard of male *Taphozous melanopogon*. The different colour, however, can (probably) not be explained by this.

ECHOLOCATION:
Although the use of clicking sounds as means of echolocation by *Rousettus aegyptiacus* has become well accepted over the past few years, Boonman *et al.* (2013a: 23) showed that this type of clicks were also produced by representatives of other genera they investigated: (*Eonycteris, Cynopterus* and *Macroglossus*, which convinced Boonman *et al.* (2013a) that the use of echolocation is more widely distributed than previously believed.

Boonman *et al.* (2014: 2962) provided evidence that suggests that all Old World fruit bats can produce clicks with their wings, resulting in a rudimentary echolocation system.

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) mentioned that the 2*n* value for the species belonging to this family varies between 24 and 58.

Genetics
Jiao *et al.* (2018: 4477) found that the bitter taste receptor genes (*Tas2rs*) in the Old World fruit bats underwent a massive loss (-11 genes out of the ancestral 27) in their common ancestor, but the remaining ones underwent subsequent diversification leading to an average number of genes in the present day species (e.g., 23 in *Eidolon helvum* and 31 in *Rousettus aegyptiacus*).

DIET:
In their study on figs as resources for tropical frugivorous vertebrates, Gautier-Hion and Michaloud (1989: 1826) concluded that these fruits are occurring in such distant patches, that only large frugivorous bats can use them as staple food.

Pettersson *et al.* (2004: 166) state that African pteropodid bats apparently feed more commonly from nectar sources visually observable from above the canopy (as compared with pollinating species from the New World). They also suggest that the absence of sulphur compounds in the floral scent of West African *C. pentandra* (as opposed to South-America) is the result of the different selective regimes of the pollinating bats.

Djossa *et al.* (2015: 286) found that the baobab tree (*Adansonia digitate* L.) needs pollinators (= fruit bats) to reach its optimal pollination success. They also concluded that the involvement of fruit bats is beneficial as they travel over long distances, which may help conserve the genetic diversity of this plant species, especially keeping in mind that the baobab tree is a multipurpose socioeconomically relevant plant for Sub-Saharan African rural communities. However, a study by Taylor *et al.* (2020b) revealed that - at least in southern Africa - fruit bats rarely pollinate baobab trees.

Oliveira *et al.* (2021: 436) reported Pteropodidae bats as known floral visitors/pollinators of *Parkia bicolor* A. Chev., 1908, *Parkia biglobosa* (Jacq.) R.Br. ex G.Don, *Parkia filicoidea* Welw., 1871 and *Parkia madagascariensis* R. Vig., 1949.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) report the following birds predating on "Pteropodidae": Chestnut-flanked sparrowhawk (*Accipiter castanilius* Bonaparte, 1853), Little sparrowhawk (*Accipiter minullus* (Daudin, 1800)), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850), African harrier-hawk (*Polyboroides typus* Smith, 1829), Crowned eagle (*Stephanoaetus coronatus* (Linnaeus, 1766)).

PARASITES:
Fain (1994: 1279) indicated that the Pteropodidae are hosts for two or three genera of Myobiidae: *Binuncus* (with subgenus *Probinuncus*) including 19 species of which 18 occur on Pteropodinae only, and one on Macroglossinae. The second genus is *Pteropimyobia* with five species of which 3 live on Macroglossinae and two on Nyctimeninae. The third genus - *Ugandobia* - contains nine species occurring on Emballonuridae and one species each occurring on Hipposideridae (*U. euthrix*) and on Pteropodinae (*U. balionycteris*). However, he believes that these two latter species were reported from the wrong host species due to "contamination of museum jars". Fain (1994:

1280) also mentions that the Myobiidae found on Megachiroptera are more evolved than those found on the Microchiroptera, indicating that the Myobiidae have probably originated on a primitive genus of the Microchiroptera and subsequently have passed to the Megachiroptera. He also reported this as peculiar since mites belonging to the Mesostigmata and Sarcoptidae are more primitive on Megachiroptera than on Microchiroptera.

HEMIPTERA
Cimicidae
Haeselbarth *et al.* (1966: 8) recorded *Afrocimex leleupi* Schouteden 1951 from fruit-bats in the "Grotte de Kakontwe" and "Grotte Dufrenne", Katanga, DRC.

DIPTERA
Streblidae
Ascodipteron semirasum Maa 1965 from a fruit bat in Kenya (Haeselbarth *et al.*, 1966: 106).

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 28 % of the species belonging to this family are confirmed viral carriers.

Nesi *et al.* (2012: 126) suggest that the high nucleotide distance between Ebola virus Côte d'Ivoire and Ebola virus Zaire can be correlated with the Plio/Pleistocene divergence between their putative reservoir host species, i.e., *Myonycteris leptodon* and *Myonycteris torquata*, respectively.

Akani *et al.* (2015: 614 - 615) state ". the first Ebola outbreak in Guinea in 2014 occurred in a site where there was recent deforestation due to the planting of massive oil palm plantations (Wallace *et al.*, 2014), exactly as it also occurred in the Democratic Republic of Congo in 2007 (see Leroy *et al.*, 2009). Therefore, it is likely that there is a direct noncausal link between oil palm plantations, fruit bats and Ebola outbreaks (Wallace *et al.*, 2014). Fruit bats may shift from using rainforest to utilizing oil palm plantations as foraging grounds once the forests became disturbed, especially where plantations are adjacent to rainforest patches. The intensified use of oil palm plantations by fruit bats may be due to the high food resource available due to the palm fruits". [**Note** (December 2024): As far as the editors are aware, no proof has yet been provided that fruit bats are indeed the culprits.]

ANTHROPOPHILOUS:
Muscarella and Fleming (2007) and Ramírez-Fráncel *et al.* (2021: 2) indicate that up to 34 % of (timber) plants that have economic importance in Africa are dispersed by pteropodid bats. Muscarella and Fleming (2007: 585) also point out that pteropodid bats help to promote regeneration of late successional plant species, because a large part of their diet consisted of hard, large-seeded fruits of forest canopy trees.

Torres *et al.* (2020: 282), however, point out that the effects on seed germination of ingestion by Pteropodidae is statistically not significant.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burkina Faso, Central African Republic, Gabon, Ghana, Kenya, Madagascar, Senegal, Tanzania.

Subfamily Eidolinae Almeida, Giannini and Simmons, 2016

*2016. *Eidolinae* Almeida, Giannini and Simmons, Acta Chiropt., 18 (1): 83, 84. Publication date: June 2016.

TAXONOMY:
This subfamily was created by Almeida *et al.* (2016: 84) to distinguish monophyletic groups within the Pteropodidae.

Currently recognized genera of Eidolinae: *Eidolon* Rafinesque, 1815.

Genus ***Eidolon*** Rafinesque, 1815

*1815. *Eidolon* Rafinesque, Analyse de la Nature, 45. - Comments: Type species: *Pteropus stamineus* E. Geoffroy Saint-Hilaire, 1803 (= *Vespertilio vampyrus helvus* Kerr, 1792). - Etymology: From the Greek "*ειδωλον*", meaning "image" or "phantom", evidently in allusion to its movements (see Palmer, 1904: 252; DeFrees and Wilson, 1988: 4).

1861. *Pterocyon* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1861: 423. - Comments: Type species: *Pterocyon paleaceus* Peters, 1861 (=*Vespertilio vampyrus helvus* Kerr, 1792). - Etymology: From the Greek "*πτερόν*", meaning wing and "*κύων*", meaning dog (see Palmer, 1904: 595).

1881. *Leiponyx* Jentink, Notes Leyden Mus., 3 (15): 60. Publication date: April 1881 [Goto Description]. - Comments: Type species: *Leiponyx büttikoferi* Jentink, 1881 (=*Vespertilio vampyrus helvus* Kerr, 1792). - Etymology: From

the Greek "*λείπω*", meaning to leave or to be wanting and "*ονυξ*", meaning claw, referring to the absence of a claw on the index finger (see Palmer, 1904: 367).

1882. *Liponyx* Forbes, Zoological Record, 18 Mamm: 13 (for 1881). - Comments: Emendation of *Leiponyx* Jentink, 1881. Preoccupied by *Liponyx* Vieillot, 1816; a bird (see Andersen, 1912b: 2; Meester *et al.*, 1986: 27). (Emendation).

2018. *Eidelon:* Van Damme, Benda, Van Damme, De Geest and Hajdas, J. nat. Hist., 52 (31-32): Suppl. Publication date: September 2018. (Lapsus).

2020. *Elidion:* Motayo, Oluwasemowo and Akinduti, PeerJ, 8 (e10434): 4. Publication date: 26 November 2020. (Lapsus).

TAXONOMY:
Revised by Bergmans (1991). See Simmons (2005: 320).

Almeida *et al.* (2011a: 11) suggest that *Eidolon* should be included in a subfamily of its own.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Eidolon*: ***dupreanum*** (Pollen, 1866); ***helvum*** (Kerr, 1792).

COMMON NAMES:
Afrikaans: Geel-vrugtevlermuis. Czech: plaví kaloni. English: Straw-coloured Fruit-bats, Eidolon fruit bats. French: Roussettes des palmiers. German: Palmenflughunde. Italian: Èidoli, Ptèropi fantasrna.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Shi *et al.* (2014: 285) refer to Howell and Coppens (1974), who reported the only fossil record for *Eidolon* from the Pliocene (ca. 3 mya) of Ethiopia. They also indicate (p. 279) that the two taxa (*helvum* and *dupreanum*) diverged in the mid-to-late Miocene. Almeida *et al.* (2016: 85) place the origin of the genus in the Miocene or Oligocene.

VIRUSES:
Flaviviridae
Luis *et al.* (2013: suppl.) mention the following Flaviviridae from "*Eidolon*": Entebbe bat virus, Uganda S virus, Usutu virus, West Nile virus, Yellow fever virus, and Zika virus.

Togaviridae
Alphavirus
Luis *et al.* (2013: suppl.) mention "from *Eidolon*".

Chikungunya virus
Luis *et al.* (2013: suppl.) mention "from *Eidolon*".

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Nigeria.

Eidolon dupreanum (Pollen in Schegel, 1867)

*1867. *Pteropus dupréanus* Pollen, in: Schlegel, Proc. zool. Soc. Lond., 1866, III: 419. Publication date: April 1867. Type locality: Madagascar: Nossi Bé island [ca. 13 20 S 48 15 E]. [Goto Description]. Lectotype: RMNH MAM.37230: ad ♀. Collected by: Douwe Casparus Van Dam and François Paul Louis Pollen; collection date: 18 August 1865. Lectotype assignment by Bergmans (1991: 169).
The RMNH catalog mentions two numbers: 37230.a (skull + loose bones) and 37230.b (mounted skin). Paralectotype: RMNH MAM.37229: ad ♂. Collected by: Douwe Casparus Van Dam and François Paul Louis Pollen; collection date: 17 August 1865. Paralectotype assignment by Bergmans (1991: 169). - Comments: Andersen (1912b: 8) mentions two cotypes in the Leyden Museum collected by Fr. Pollen and C.C. van Dam (see Schlegel, 1867: 419). Bergmans (1991: 169) named the female specimen (RMNH 37230) as Lectotype and the male (RMNH 27229) as Paralectotype.

1987. *Eidolon helvum dupraneum:* McHale, in: Wilson, Cave Sci., 14 (3): 114. Publication date: December 1987. (Lapsus).

2014. *Eidolon duprenum:* Gunnell, Simmons and Seiffert, PLoS ONE, 9 (2): e86712: 3. Publication date: 4 February 2014. (Lapsus).

? *Eidolon dupreanum:* (Current Combination).

? *Eidolon helvum dupreanum:* (Name Combination).

TAXONOMY:
Koopman (1993a: 140) mentioned Schlegel, 1867 as author, but Allen (1939a: 54), Peterson *et al.* (1995: 22) and Russ *et al.* (2001) mention Pollen, 1866, in Schlegel and Pollen, Proc. Zool. Soc. Lond., 1866: 419. Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1) mention Schlegel and Pollen, 1867 as authors, but in the references of the latter only Schlegel is mentioned as author. Reviewed by Bergmans (1991) and Peterson *et al.* (1995). See Simmons (2005: 321 and comments under *E. helvum* pg. 321).

COMMON NAMES:
Czech: kaloň malgašský. English: Madagascan Straw-coloured Fruit-bat, Madagascan Fruit Bat, Malagasy Straw-colored Fruit Bat. French: Roussette des palmiers malgache, Roussette malgache couleur paille, Roussette jaune de Madagascar, Rousette pailée de Madagascar. German: Madagaskar-Palmenflughund.

Malagasy: Malagasy: Andrehy, Angavo, Angoavy, Fanihy vato.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 43) found samples in deposits dated at 10,000 yrs old or younger from within the Anjohibe cave, Madagascar. Gunnell *et al.* (2014: 3) also refer to Goodman and Jungers (2013), who report material from the Andrahomana cave.

CONSERVATION STATUS:
Global Justification
This species is listed as Vulnerable (VU A2ad ver 3.1 (2001)) because it is estimated to have undergone a decline exceeding 30% over the past 20 years mainly from extreme pressure from hunting, causing it to abandon roosts, with known examples of local extirpation of roosts sites (Andriafidison *et al.*, 2008b; IUCN, 2009). These threats are expected to continue (Andriafidison *et al.*, 2020).

The mathematical predictor-rich model developed by Welch and Beaulieu (2018: 10) placed *Eidolon dupreanum* on the fourth position of the top ten bat species at risk of extinction worldwide.

Assessment History
Global
2018: VU A2ad ver 3.1 (2001) (Andriafidison *et al.*, 2020). 2008: VU A2ad ver 3.1 (2001) (Andriafidison *et al.*, 2008b; IUCN, 2009). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
In Madagascar its legal status is "animaux gibiers (game)".

MAJOR THREATS:
This species is subject to harvesting for bushmeat across its range and hunting occurs both at roosting and foraging sites (Jenkins and Racey, 2008). It is classed as a game species under Malagasy law and although it can only be legally hunted between the first of May and the first of September (Anonymus, 2007b: 6; Durbin, 2007; Randrianandrianina *et al.*, 2010: 412), this legislation is widely ignored and the bats are hunted throughout the year. Its roosts tend to be well protected from bushfires and it is able to survive in landscapes with severely depleted natural food supplies as long as alternative plants are available (Ratrimomanarivo, 2007). Hunting is therefore the main threat and was reported to account for a 30% desertion rate from 60 roosts (MacKinnon *et al.*, 2003). Although hunters report that deserted roosts are recolonized after a few years, there are several confirmed examples where this species has been extirpated at roost sites (MacKinnon *et al.*, 2003).

Randrianandrianina *et al.* (2010: 413) observed that at least 14 *E. dupreanum* specimens were captured each night at fruiting voandelaka tree (*Molinaea* sp.). However, Andrianaivoarivelo *et al.* (2022: 1914) state that current levels of hunting do not appear to threaten this species with extinction.

Cardiff and Jenkins (2016: 99) indicate that fires are used to expel *E. dupreanum* from their rocky roost sites.

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008b) [in IUCN (2009)] and Andriafidison *et al.* (2020) report this species is known from a number of protected areas (Goodman *et al.*, 2005a) including, Parc National d'Isalo, Parc National de Namoroka, Réserve Spéciale d'Ankarana and Réserve Spéciale de Cape Sainte Marie; however, hunting has been reported from within Réserve Spéciale d'Ankarana (Cardiff, 2006). Fernández-Llamazares *et al.* (2018: 273), similarly, reported hunting in and outside the Tsimanampetsotsa National Park, even in sacred caves. Roosts that are located in inaccessible rock outcrops pose significant challenges to hunters are relatively protected. Cave roosts are probably subject to highest hunting pressure and conservation measures should be focused at these sites (Andriafidison *et al.*, 2008b; IUCN, 2009).

Additional research is needed on natural history and in particular roosting ecology and movements (Andriafidison *et al.*, 2008b; IUCN, 2009).

GENERAL DISTRIBUTION:
Eidolon dupreanum is endemic to the island of Madagascar where it is widespread, albeit with a patchy distribution (MacKinnon *et al.*, 2003). It is found both along the coast and on the central high plateau and areas from where there are no records probably reflect inadequate survey coverage rather than a genuine absence. There are some areas within its range where the lack of crevices means there are no roosting opportunities (Goodman *et al.*, 2005a).

González-Gutiérrez *et al.* (2025: Suppl.) calculated that the entire distrtibution area of this species covers 467,539.89 km^2.

Native: Madagascar.

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 52) describe the baculum as a large flat structure, with the distal tip having a serrated or tooth-like structure that is wider than the proximal base; length: 6.59 ± 0.225 (6.41 - 6.84) mm, width: 4.21 ± 0.671 (3.48 - 4.80) mm.

SEXUAL DIMORPHISM:
Andrianaivoarivelo *et al.* (2022: 1914) indicate that males are about 10 % larger than females.

ECHOLOCATION:
Schoeman and Goodman (2012) identified three distinct call types: social calls 1, social calls 2 and echo clicks. Bats produce the echo clicks while flying towards the entrance of the cave, while the other two calls were emitted at roost sites and near the cave entrance. Based on the preliminary results, Schoeman and Goodman (2012) suggest that the social calls 1 and 2 were employed for social communication, whilst echo clicks may have been used in a sensory context, potentially as incipient echolocation to navigate in the dark cave.

MOLECULAR BIOLOGY:
Genetics
Wang *et al.* (2025b: 7) report that the total length of the genome is 2.29 Gb.

HABITAT:
Eidolon dupreanum has a patchy distribution which includes humid, dry deciduous and spiny forest is probably related to the availability of suitable roost sites and is rare or absent from a number of forests without rocky outcrops (Goodman *et al.*, 2005a; Jenkins *et al.*, 2007b; Schmid and Alonso, 2007). It continues to survive in highly modified landscapes with very little native vegetation remaining (Ratrimomanarivo, 2007), but appears to use native forest vegetation for food in preference to introduced plants (Picot *et al.*, 2007).

Dammhahn and Goodman (2013: 108) indicate that mid- to upper-canopy in forest and trees growing in open areas form the foraging habitat of this species.

HABITS:
Baum (1995: 337) reported that fruit bats (probably *E. dupreanum*) intensively visited *Adansonia suarezensis* trees in the forest at Beantely in the hour after dark, but also during the remainder of the night at a much lower frequency. Peak rates were about 14 visits per tree per hour (or ca. 0.5 visits / flower / hr), each lasting between 20 and 30 seconds. During each of the tree stopovers, up to nine flowers were visited.

While exiting roost, individuals flew within 50–100 cm of the ceiling, often settling and perching every 5–10 m along their flight patch and displacing in a leapfrog manner towards the cave entrance (Schoeman and Goodman, 2012).

ROOST:
It is known to roost in tree foliage, but is more usually found in rock fissures and caves (MacKinnon *et al.*, 2003, Andrianaivoarivelo *et al.*, 2022: 1914). Its roost sites are usually very high and located in cliffs and rock faces (Jenkins and Racey, 2008). In the Réserve Spéciale d'Ankarana, it used caves that were high and long with a good buffering capacity for temperature and humidity (Wilson, 1987b: 114; Cardiff, 2006).

Colonies contain between 10 and 500 bats (exceptionally 1,400), with an average of 200 (Andrianaivoarivelo *et al.*, 2022: 1914, Garbutt, 2022: 77).

The large roosts are generally over 60 km apart, suggesting that the bats forage within a radius of 30 km around the roost (Garbutt, 2022: 77).

See habits for roosting behaviour.

MIGRATION:
MacKinnon *et al.* (2003) suggested that *E. dupreanum* might be migratory because of regular variation in the occupancy and abundance of roosts.

DIET:
In a study, during three months (February, July and December), at four sites on the central Malagasy highlands, Ratrimomanarivo (2007) found the seeds of 13 plant species. Picot *et al.* (2007) reported that *E. dupreanum* ate mainly fruits (65%), although *Eucalyptus* spp. flowers were also consumed. Thirty plant species (14 identified and 16 unidentified), including six introduced species were utilized in the corridor of rainforest between Ranomafana and Andringitra National Parks, south-eastern Madagascar (Picot *et al.*, 2007). *Polyscias* spp. fruit (seeds) were the most frequently recorded plant in 70 % of the faecal samples (Picot *et al.*, 2007). Fruit is the main dietary component, but it also eats leaves and other plant parts (Picot, 2005; Picot *et al.*, 2007). Through the ingestion of pollen and small seeds, a significant ecological role is inferred (Picot, 2005; Ratrimomanarivo, 2007). *E. dupreanum* may be an important pollinator of threatened baobab trees (Baum, 1995).

Baum (1995: 339) mentions that *E. dupreanum* is believed to be one of the major pollinators of endemic baobabs *Adansonia grandidieri* and *Adansonia suarezensis* of Madagascar.

Picot *et al.* (2007) suggest that the alimentary tract is one intrinsic factor that influences seed dispersal, as they found a maximum seed size of 7 mm and mean size of 3.2 mm for *E. dupreanum* and the ecological services provided by this species appear to be limited by the dimensions of its intestinal tract.

Jenkins *et al.* (2007b: 213) [referring to Rakotonirainy (2001)] mention these bats visit fruiting trees of *Ficus soroceoides, F. pyrifolia*, and *F. guatteriifolia*. Hending *et al.* (2021b: 2) observed them feeding on *Ceiba pentandra* (kapok).

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Eidolon dupreanum*: *Allophylus cobbe* (L.) Forsyth fil., 1794, *Anthocleista* sp., *Cassinopsis madagascariensis*, *Ficus brachyclada* Baker, 1883, *Ficus lutea* Vahl, 1805, *Ficus pachyclada* Baker, 1887, *Ficus pyrifolia* Salisb., 1796, *Ficus reflexa* Thunb., 1786, , *Ilex mitis* (Linnaeus) Radlk., *Morus alba* Linnaeus, 1753, *Passiflora subpeltata* Ortega, 1798, *Polyscias* sp., *Polyscias ornifolia* (Baker) Harms, 1894, *Psidium cattleyanum* Afzel. ex Sabine, 1821, *Psidium guajava* Linnaeus, 1753.

Based on stable isotope analyses, Reuter *et al.* (2016c) found that *Pteropus rufus*, *Eidolon dupreanum* and *Rousettus madagascariensis* have broadly overlapping diets, although there are differences between *P. rufus* and *E. dupreanum*. Furthermore, they found that the diet shifted when these two species occurred sympatrically.

Population:

Structure and Density

The population size and local abundance of this species are not well known. Estimates of colony size are difficult to obtain because the bats are hidden during the day, but is usually in the range of between 10 and 500, with a median of 200 individuals (MacKinnon *et al.*, 2003). The maximum colony size of 1,400 is from Réserve Spéciale d'Ankarana (S. G. Cardiff unpubl. [in Andriafidison *et al.* (2008b; Andriafidison *et al.*, 2020)]).

Given the estimated adult survival, Brook *et al.* (2019a: 165) found that the population of *E. dupreanum* will only be able to persist if the field-based fecundity estimates were replaced by higher values reported in the literature for related species.

Trend

2018: Decreasing (Andriafidison *et al.*, 2020).
2008: Decreasing (Andriafidison *et al.*, 2008b; IUCN, 2009).

Reproduction and ontogeny:

Kaudern (1914: 11 - 12) reported that he was unable to shoot any pregnant female or females with young during his travels on Madagascar, which took place in the dry season (May to September), so he assumed they had their reproductive season in Spring or Summer.

Andrianaivoarivelo *et al.* (2022: 1914) reported births occur in December and January/

Parasites:

Brook *et al.* (2015a: 4) found *E. dupreanum* to be the host of *Cyclopodia dubia* (Westwood, 1835) (Nycteribiidae) and *Thaumapsylla* sp. fleas. In the bat flies (and the bats), DNA of a new *Bartonella* was found. The bat flies were also reported by Wilkinson *et al.* (2016), Ramasindrazana *et al.* (2017: Suppl.) and Atobatele *et al.* (2023: Suppl.). Szentiványi *et al.* (2019a: Suppl.) indicated that thes bat flies were also carrying Enterobacteriales and *Wolbachia* sp. bacteria.

Ranaivoson *et al.* (2015: 76) reported the presence of (*Hepatocystis* spp. (Haemospororida) in this species.

A flea of the genus *Thaumapsylla* Rothschild, 1907 (Ischnosyllidae) was reported by Duchemin *et al.* (2022: 1076).

Andrianiaina *et al.* (2025: 8) reported the following ectoparasites from 628 *Eidolon dupreanum* bats: Fleas (Siphonaptera) *Thaumapsylla* Rothschild, 1907, *Echidnophaga* Olliff, 1886, Bat flies (Streblidae): *Cyclopodia dubia* (Westwood, 1835), and mites: *Meristaspis* Kolenati, 1857, *Ornithodoros* Koch, 1837, "other mites". The bats were on average parasitized by 1.44 different ectoparasite taxa. *C. dubia* was primarily present late May/early June on female bats and late June on males.

Viruses:

Astroviridae - Astroviruses

Two novel astroviruses reported by Horigan *et al.* (2024: 9) did not group with viruses found in other Ynpterochiroptera, but rather with viruses found in Molossids.

Coronaviridae - Coronaviruses
BtCoVMAH051F/E. dupreanum/2011
In Madagascar, identified in faecal material (Razanajatovo *et al.*, 2015).

Herpesviridae
Alphaherpesvirinae
Simplexvirus
Alphaherpesvirus CS730G
In Madagascar 2006, isolated in Vero cells from throat swabs (Razafindratsimandresy *et al.*, 2009).

Paramyxoviridae
Henipavirus
Cedar (CedPV)
Brook *et al.* (2019b: 1004) reported the presence of reliable reactive antibodies to tested antigens in serum from *E. dupreanum* specimens.

Hendra (HeV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found Hendra virus with an infection rate of 19.2%.

Nipah (NiV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found Nipah virus with an infection rate of 19.2%. Kuzmin *et al.* (2011a: 5) suggest that their exposure to NiV might be the result of contact with infected *Pteropus rufus* specimens.

Tioman (TiV)
In Madagascar during 2003 - 2004, this virus was not detected (Iehlé *et al.*, 2007).

Picornaviridae
Kobuvirus
Gonzalez *et al.* (2025: 1) reported the detection of Kobuvirus RNA in Madagascan bats.

Rhabdoviridae – Rabies like viruses
Lyssavirus - Rabies related viruses
Andriamandimby *et al.* (2013: 3) reported that 17 bats tested positive for the detection of antibodies against Lagos Bat Virus (LBV) in two areas close to Antananarivo. Five of these also tested positive against European Bat Lyssavirus type 1 (EBLV-1).

UTILISATION:
E. dupreanum is hunted for meat in many parts of Madagascar (Ranivo, 2001; MacKinnon *et al.*, 2003). Hunting is undertaken by specialists (due to the roosting high in cliffs) who either access the roosts with wooden ladders (Jenkins and Racey, 2008) or light fires directly underneath the roosts and net or swat flying bats as they emerge (Ranivo, 2001). Alternatively, a hunter is lowered on a rope and hits the bats with a stick (Jenkins and Racey, 2008). Jenkins and Racey (2008) also indicate that guns and slingshots are used.

In the rainforests between PN de Ranomafana and PN d'Andringitra, several accounts of bat hunting were collected from villages (Picot, 2005). Although familiar with the location of the bat roosts, the local people rarely hunted or consumed the bats. Professional hunters visited a few times a year and occasionally offered bat meat to the village but most of the animals were taken to larger towns and sold for $ 0.4 US to restaurants and hotels. In this area oil residue from cooked bats is used as medicine for whooping cough (Jenkins and Racey, 2008). Further north in the highlands, Ranivo (2001) investigated the hunting of *E. dupreanum* at roost sites near Ambositra, Antsirabe and Ankazobe, where villages reported purchasing one and four times per year.

Pteropus rufus and *Eidolon dupreanum* appear to be the only species sold in restaurants, where they are either served individually, complete with head and wings, jointed, or are diced up into small pieces and accompanied by rice (Jenkins and Racey, 2008).

Ranivo (2001) found that hunting caused the bats to abandon traditional roost sites and local people noted declines in hunting returns.

Tackett *et al.* (2022: 7) [referring to Fernández-Llamazares *et al.* (2018) and Jenkins and Racey (2008)] report that fluids from *E. dupreanum* are used to "treat" whooping cough, baldness and coughs.

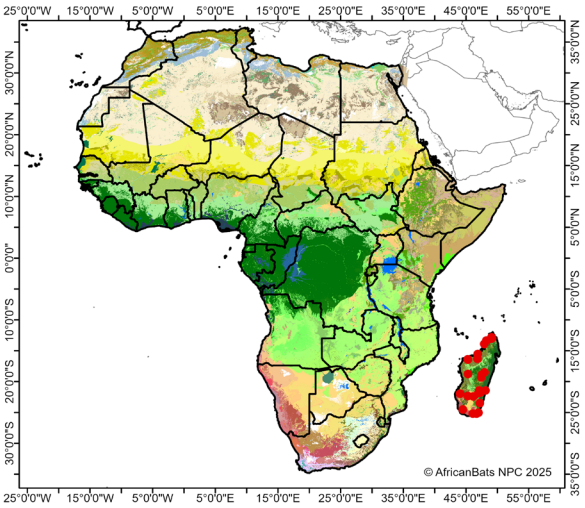

Figure 1. Distribution of *Eidolon dupreanum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Eidolon helvum (Kerr, 1792)

*1792. *Vespertilio vampyrus helvus* Kerr, in: Linnaeus, Animal Kingdom, 1 (1): xvii, 91. Publication date: February 1792. Type locality: Senegal: "Senegal". - Comments: Type locality fixed by Andersen (1907a: 504); see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1), Harrison and Bates (1991). Andersen (1912b: viii) indicates that the type was once in the Museum Leverianum, but is probably no longer in existence. - Etymology: From the Latin "helvus" (=dun-coloured), referring to the straw colour on their shoulders; the back, rump and hind limbs are normally various shades of brown (see DeFrees and Wilson, 1988: 4; Taylor, 2005). Lanza *et al.* (2015: 27) translate "helvus" to "dull-yellow".
1862. *Xantharpyia stramineus:* Gerrard, Catalogue of the bones of Mammalia in the collection of the British Museum, 58. (Name Combination).
1866. *Xantharpyia leucomelas* Heuglin, in: Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54: sect 1, pt 10, p 544. Type locality: Sudan: Kordofan: Bahr-el-Azrak: Bahr-el-Abiad: Sennaar. - Comments: Originally "Upper Nile lands", but subsequently fixed to Senaar by Koopman (1975): see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1).
1867. *Cynonycteris straminea:* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 866. - Comments: see Pousargues (1896: 257). (Name Combination).
1895. *Cynonicteris straminea:* Bocage, J. Sci. mat. phys. nat., ser 2, 4 (8): 4. Publication date: December 1895. (Lapsus).
1906. *R[oussettus (Xantharpyia)] stramineus:* Johnston, Liberia, Volume II: 690. (Lapsus).
1920. *Rousettus stramineus:* Haagner, South African mammals, 23. (Name Combination).
2015. *Pterocyon palaeaceus:* Lanza, Funaioli and Riccucci, The bats of Somalia and neighbouring areas, 27. (Lapsus).
2018. *Eidelon helvum:* Van Damme, Benda, Van Damme, De Geest and Hajdas, J. nat. Hist., 52 (31-32): Suppl. Publication date: September 2018. (Lapsus).
2019. *Eidolon hevlum:* Debata, Panda and Palita, Biodivers. Conserv., 28 (8-9 SI): 2386. Publication date: 13 February 2019. (Lapsus).
2020. *Elidion hevium:* Motayo, Oluwasemowo and Akinduti, PeerJ, 8 (e10434): 4. Publication date: 26 November 2020. (Lapsus).
2021. *Eidolon halvum:* Ohimain, Curr. Opin. Pharmacol., 60: 69. Publication date: 3 August 2021. (Lapsus).
2024. *Eidolon helsum:* Franco, dos Santos, de Sousa Verde, Calchi, de Mello, Lee, Días, Machado, Carvalho and André, Vet. Res. Commun., xxx (x): 8. Publication date: 24 September. (Lapsus).
? *Eidolon helvum:* (Current Combination).

TAXONOMY:
Includes *sabaeum* see Hayman and Hill (1971), Bergmans (1991), Harrison and Bates (1991), Simmons (2005: 321). Does not include *dupreanum*; see Bergmans (1991), Peterson *et al.* (1995) and Simmons (2005: 321), but also see Hayman and Hill (1971) who treated *dupreanum* Schlegel, 1866, from Madagascar and *sabaeum* Andersen, 1907, from Arabia as subspecies of *E. helvum* (Meester *et al.*, 1986). African forms reviewed in part by Juste *et al.* (2000); Palearctic forms reviewed by Horáček *et al.* (2000). The taxonomic status of populations in the Anr Mountains of Niger is unclear Simmons (2005: 321).

E. dupreanum is here retained as a separate species and *sabaeum* is considered an extralimital subspecies of *E. helvum* not occurring in Africa.

Juste *et al.* (2000) found that the population from Annobón is significantly smaller than the continental forms (and the specimens from the other islands in the Gulf of Guinea) and created a new subspecies for these: *Eidolon helvum annobonensis*.

Currently recognized subspecies of *Eidolon helvum*:
E. h. helvum (Kerr, 1792) - Afrotropics.
E. h. annobonensis Juste et al. 2000 - islands off Gulf of Guinea.
E. h. sabaeum K. Andersen, 1907 - Oriental.

COMMON NAMES:
Afrikaans: Geel vrugtevlermuis. Castilian (Spain): Zorra Voladora Amarilla. Chinese: 黄毛果蝠. Czech: kaloň plavý, upír bledý, kaloň palmový, kaloň úzkokřídlý. English: African Straw-coloured Fruit-bat, Straw-colored Fruit Bat, Straw-coloured Flying Fox, Pale Xantharpy, Yellow-haired fruit bat. Ewe (Ghana): Aguto. French: Roussette jaune, Roussette des palmiers africaine, Roussette paillée, chauve-souris paillée. German: Afrikanischer Palmenflughund, Palmenflughund, Afrikanischer strohfarbener Flughund. Italian: Èidolo paglierìno, Ptèropo fantàsma paglierìno. Kinande (DRC): Mulima. Malawian: Lichinji, Mleme. Portuguese: Morcego frugivoro gigante. Tanoboase (Ghana): ampane ankasa. Tshokwe (Angola): T shingunzu.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Hildebrand *et al.* (2010: 268) recorded this species from the Kumali site in southern Ethiopia.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened (NT ver 3.1 (2001)) because this species is in significant decline (but

at a rate of less than 30% over three generations (approximately fifteen years)) because it is being seriously over-harvested for food and medicine, making the species close to qualifying for Vulnerable, Under criterion A2d (Mickleburgh *et al.*, 2008dc; IUCN, 2009; Cooper-Bohannon *et al.*, 2020d).

The subspecies *E. h. sabaeum* (Andersen, 1907) is known only from Yemen and Saudi Arabia and is possibly threatened (see Bergmans, 1999).

Assessment History
Global
2019: NT ver 3.1 (2001) (Cooper-Bohannon *et al.*, 2020d). 2008: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2008dc; IUCN, 2009). 2004: LC (Mickleburgh *et al.*, 2004bh; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016e). 2004: considered a vagrant not assessed, doesn't breed in SA (Friedmann and Daly, 2004).

Sáo Tomé: Vulnerable (Rainho *et al.*, 2022: 603) due to its reduced range and habitat degradation.

MAJOR THREATS:
In general there are no major threats to this widespread and adaptable species. It is, however, locally threatened in parts of its range by severe deforestation, and more generally across West and Central Africa by hunting for food and medicinal use. It is the most heavily harvested bat for bushmeat in West and Central Africa, and one of the most frequently consumed mammals in this region (P. Racey *pers comm.* in Mickleburgh *et al.* (2008dc)). Large pre-migration colonies are considered particularly vulnerable to any threats. In some areas it is considered to be a pest species and roosting locations may be restricted by cutting down trees. Trees are also cut down in order to catch bats for the market (P. Racey *pers comm.* [in Mickleburgh *et al.* (2008dc)]). Kamins *et al.* (2010: 190) report that 41 hunters, they interviewed, killed about 35,000 bats in one year in southeastern Ghana. 95 meat vendors indicated that they sold over 100,000 bats as food in one year. These bats were captured in an area up to 200 km away from the markets where they were sold. Kamins *et al.* (2011a: 3000) update these figures, based on interviews with 551 Ghanaians, to a minimum 128,000 bats being sold yearly, up to 400 km away from the markets. MacDonald *et al.* (2011: Suppl. Table 1) indicate that, in rural markets in Cameroon and Nigeria, fresh bats were sold at 2.96 US$, or about 10.6 US$/kg, and smoked bats at 1.63 US$ or 5.82 US$/kg. In Côte d'Ivoire, Niamien *et al.* (2015a: 233) found that poachers only ate 5 % of their catch themselves, the rest was sold for 0.6 US$ per animal, leading to a daily revenue of 15 US$. They estimated that some 30,600 were killed each month, but luckily for the bats, they made some major calculation errors.

Hoffman and Cawthorn (2023: 50) mention this species as "the preferred food source" in western Africa.

On São Tomé, these bats are extensively harvested for household consumption (see Carvalho *et al.*, 2015: 1). Hayman and Peel (2016: 132) indicate that the smaller island populations [from São Tomé, Príncipe and Annobón] may more likely suffer from additive mortality in response to harvesting than populations from the nearby Bioko as these latter can still mix freely with the continental populations.

Musaba Akawa *et al.* (2017) followed the sale of *E. helvum* at a market in Kisangani (DRC) for one year and found that most of the bats were sold during one of the wet seasons (September-October), but low during the second wet season (March-April). They also found that while hunting was allowed from December through July, only 47 % of the total number of bats were sold during that period; 53 % was sold during the period that the hunt was closed.

Anonymus (2004f: 51) indicates that their colonies are unwelcome in towns and cities through fruit feeding, defoliation of roost trees, defecation on (commercial) buildings.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dc) [in IUCN (2009)] report that there are no known direct conservation measures in place, but in view of the species extensive range it seems probable it is present in some protected areas during migration. There is a need to identify and protect important roosting sites, and a better understanding of the migratory patterns of this species would be beneficial to any conservation activities. The highest priority is to limit the harvesting of this species to sustainable levels.

Cooper-Bohannon *et al.* (2020d) report that this species is present in a few protected areas across its range, usually for relatively short periods of time, with a large roosting colony in Kasanka National Park, Zambia. As this species appears to prefer anthropogenic landscapes, conservation of *Eidolon* should not be

approached in terms of traditional "creation of protected areas." *Eidolon* conservation requires a completely different approach and way of thinking to get local communities to accept and even protect their colonies. There is a need to identify and protect important roosting sites, and a better understanding of the migratory patterns of this species would be beneficial to any conservation activities. The highest priority is to limit the harvesting of this species to sustainable levels. This would include an extensive community engagement programme in areas of important roosts and engaging all stakeholders, including government in the importance of this species. Under the Convention of Migratory Species (CMS) *Eidolon helvum* is a listed species and as such should be afforded protection in signatory countries. A working group of these countries could form a species action plan and work together to improve protection of this species. Some countries with important roosts, such as Zambia are currently not signatories of CMS and work is being carried out to better understand why Zambia is currently not a signatory.

GENERAL DISTRIBUTION:
Eidolon helvum is broadly distributed across the lowland rainforest and savanna zones of Africa from Senegal in the west, through to South Africa in the south and Ethiopia in the east (possibly ranging into Djibouti and southern Eritrea). It is also present on the extreme southwest Arabian Peninsula, where it has been recorded from Yemen and Saudi Arabia (Harrison and Bates, 1991). Populations of this bat occur on several offshore islands including the Gulf of Guinea islands (Peel *et al.*, 2013a: 296) and Zanzibar, Pemba and Mafia (off Tanzania) (Bergmans, 1991; Simmons, 2005; O'Brien, 2011: 285). It has also been recorded at sea, 250 km from the nearest land (Anonymus, 2004f: 50). There is a possibly disjunct population in the Air Mountains of Niger. Distribution at northern and southern extremes of the range is patchy and erratic. It is also sparse or absent in large areas of the Horn of Africa, central East Africa, and elsewhere (Bergmans, 1991). *Eidolon helvum* is a migratory species in parts of its range; populations migrate from the West African forest north into the savanna zone during the major wet season. It ranges from sea level to around 2,000 m asl (Ruwenzori Mountains). In Cameroon, Dongmo *et al.* (2020: 51) reported it from mid-elevated areas (1,220 – 1,320 m). In South Africa, its distribution is mostly affected by precipitation seasonality (Babiker Salata, 2012: 49).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,091,925 km^2.

It has also been reported from the Cape Verde Islands (Jiménez and Hazevoet, 2010: 116), although Borloti *et al.* (2020: 2) suspected this report referred to a vagrant specimen.

Native: Angola (Crawford-Cabral, 1989; Lopes and Crawford-Cabral, 1992; Bergmans, 1991; Monadjem *et al.*, 2010d: 551); Benin (Capo-Chichi *et al.*, 2004: 161); Botswana; Burkina Faso (Kangoyé *et al.*, 2015a: 605); Burundi; Cape Verde Islands (Jiménez and Hazevoet, 2010: 116); Cameroon; Central African Republic; Chad; Congo (Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Schouteden, 1944; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 551); Côte d'Ivoire (Henry *et al.*, 2004: 24); Equatorial Guinea; Ethiopia; Gabon; Gambia (Kock *et al.*, 2002b: 78); Ghana; Guinea (Fahr and Ebigbo, 2003: 128; Decher *et al.*, 2016: 259); Guinea-Bissau (Bocage, 1892b; Veiga-Ferreira, 1948; Bergmans, 1991; Corbet, 1984: 30) ; Kenya; Lesotho; Liberia (Fahr, 2007a: 103); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 28; Bergmans, 1991; Monadjem *et al.*, 2010d: 551); Mali (Meinig, 2000: 104); Mauritania; Mozambique (Smithers and Lobão Tello, 1976; Cotterill, 2001e: 54; Monadjem *et al.*, 2010d: 551); Namibia (Bergmans, 1991; Monadjem *et al.*, 2010d: 551); Niger (Bergmans, 1991 in Cotterill, 2001e, 2001e: 55); Nigeria; Rwanda; São Tomé and Príncipe (Rainho *et al.*, 2010a: 24); Saudi Arabia; Senegal; Sierra Leone; South Africa (Monadjem *et al.*, 2010d: 551); Sudan; Swaziland; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 58); Yemen; Zambia (Ansell, 1974; Cotterill, 2001e: 54; Monadjem *et al.*, 2010d: 551); Zimbabwe (Monadjem *et al.*, 2010d: 551).

Presence uncertain: Djibouti; Eritrea.

GEOGRAPHIC VARIATION:
Peel *et al.* (2010b: 245) indicate that the non-migratory populations on the islands in the Gulf of Guinea (São Tomé and Príncipe, and Bioko and Annobón) show evidence of genetic differentiation from the continental (migratory) populations. They also indicate that two or three colonisation events to the islands have taken place.

Juste *et al.* (2000) found that the population from Annobón is significantly smaller than the continental forms (and the specimens from the other islands in the Gulf of Guinea) and created a new subspecies for these: *Eidolon helvum annobonensis*.

Dental Formula:

Popa *et al.* (2016: 847) described the replacement of the deciduous (milk) teeth by the permanent ones. The dentition consists of: Upper deciduous dentition: incisors I^1, I^2; canines C^1; premolars PM^1, PM^2, PM^3. Lower deciduous dentition: incisors I_1, I_2; canines C_1; premolars PM_1, PM_2, PM_3. Upper permanent dentition: incisors I^1, I^2; canines C^1; premolars PM^2, PM^3; molars M^1, M^2. Lower permanent dentition: incisors I_1, I_2; canines C_1; premolars PM_2, PM_3; molars M_1, M_2, M_3.

19 out of 94 skulls (20.2 %) examined by Esquivel *et al.* (2021: Suppl.) had an aberrant number of teeth (either Oligodontia or Polyodontia).

General description of cranial and dental morphology:

Thier and Stefen (2020) provide a detailed description of the skull of a subadult bats from São Tomé. Their conclusions include the presence of a large anterior upper premolar and the very unique peculiarity of the ectotympanic. They also reported differences in the palatine as compared with *Pteropus* skulls. Additionally, the processus postorbitalis is more pronounced and the coronoid is higher.

Detailed morphology:

Baculum

Rakotondramanana and Goodman (2017: 54) refer to Nwoha *et al.* (2000: 154), who found that the baculum in juvenile bats consists of two small paddlestone pieces located longitudinally close to each other at the distal third of the penis. In adult bats, the baculum consists of a large distal portion and a narrow proximal portion.

Brain

The average brain mass for this species is 4.30 g [n = 2, Chawana *et al.* (2013: 160)].

Tongue

The morphology of the tongue was studied by Igbokwe *et al.* (2020), who mention it to be relatively long with a rounded tip, and is covered by five types of mechanical papillae (including crown-like, trifid filiform, bulky, cone-shaped and long conical types).

Eye

The ocular morphology and the role of the choroidal papillae was studied by Paulat *et al.* (2022: 715). The latter are adapted for increased light sensitivity serving as a convex mirror.

Other

Huggel (1959) studied the blood pressure in the wings of *E. helvum* from Côte d'Ivoire. The normal pressure varied between 23 and 30 cm H_2O. This pressure was the same for the two types of blood vessels that are present in the wing (contracting or non-contracting). If there is some blocking, the pressure can double very quickly, and in one case it even tripled.

Nwoha (2000: 291) examined the pelvis of this bat and found sexual dimorphism both in the shape and size of these bones as well as in its development. In males, the ossification of the interpubic ligament already start in the juvenile stage, whereas in females this only begins with puberty.

Odukoya *et al.* (2009b: 175) investigated the biochemical differences in the two uterine limbs during pregnancy and found that the uterine limbs actively utilized different metabolic pathways according to the functions they subserve during pregnancy.

Adeniyi *et al.* (2012: 118) compared the lateral geniculate bodies (LGB) of *E. helvum* with those of *Rattus norvegicus* and *Manis tricuspis* and found some differences, which they attributed to the feeding habits, lifestyle as well as the nature of their habitat.

The morphometrics of the reproductive tract of male bats were examined by Danmaigoro *et al.* (2014a), whereas Danmaigoro *et al.* (2014b) examined the histology and the histometric anatomy. The morphology and seasonal changes of the bulbourethral gland were studied by Abiaezute *et al.* (2020a).

Abedi-Lartey *et al.* (2016: 18) found that the average gut passage time for small seeds was 116 ± 112 minutes (4 - 1,143 min). The dispersal distances for the small and large seeds were longer in rural areas than in urban areas, and for large seeds and small seeds in urban areas, they were also longer in the dry season than in the wet season. For small seeds in rural areas, they found that the distances were longer in the wet season than in the dry season.

Functional morphology:

Church and Warren (1968) indicate that wing membranes of *Eidolon helvum* are composed of long, prominent strands of elastin with collagen stretched in between, and that 2 x 2 cm holes in wings heal in 24 days.

Referring to Riskin *et al.* (2010), O'Mara *et al.* (2016: 10) mention that the wing camber of *E.*

helvum shows more variation than in non-migrating flying foxes. O'Mara *et al.* (2019a: 1) found that wingbeat frequency has the strongest positive relationship with ODBA (overall dynamic body acceleration) and that there is small, negative correlation between ODBA and airspeed. ODBA is also decreased with increasing tailwind.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 30.6 Pa, aspect ratio 6.9 and tip shape index of 1.2 for a wingspan of 78 cm and a wing area of 879 cm^2 and a body mass of 274 g.

Igado *et al.* (2015: 283) studied the tongue, hard palate and buccal cavity of this bat. They found that the overal distribution of lingual papillae was the same for both sexes, but the weight and the length of the tongue was higher in females (although the difference was not significant). Also the number of ridges on the hard palate showed a sexual dimorphism (see also the sexual dimorphism section).

The eyes of *E. helvum* contain approximately 280,000 retinal ganglion cells. The minimum angle of resolution was approximately 0.122° (ca. 4 mm at 1 m distance).

Based on a histological investigation, Mainoya and Howell (1979: 162) suggest that the neck skin patch in *E. helvum* - consisting of long and coarse hairs, and extending from the ventral surface of the neck to the shoulder area - plays a role in scent emission.

The microstructure of the skin was studied by Peter-Ajuzie *et al.* (2023).

SEXUAL DIMORPHISM:
In Nigeria, Igado *et al.* (2015: 285) examined the heads of 30 adult males and females and found the males to have larger values for overal weight, weight of the head, thickness of the tongue (at the torus), width of the tongue (at the root), width of the hard palate (at the commissures of the mouth), and width of the hard palate (at the anterior region and at the posterior half). Additionally, the number of palatine ridges was higher in males (♂♂: 8.33 ± 0.577; ♀♀: 7.667 ± 0.577). The width of the tongue at the apex was similar in both species, and the width of the tongue at the torus was significantly larger in females. In a previous study, Igado *et al.* (2012: 172) already found that males had higher values for most of the craniofacial and neurometric parameters they examined. The only parameter where females had higher values was the width of the left external nares (♀♀: 5.08 ± 0.55 mm; ♂♂: 5.0 ± 0.39 mm).

MOLECULAR BIOLOGY:
Genetics
Peel *et al.* (2010a) developed twenty microsatellite loci, from 142 individuals sampled from nine populations across Africa.

Teeling *et al.* (2017: 32) mention the estimated genome size for *E. helvum* to be 2.03 C, and the assembly size 1.44 Gb.

Wang *et al.* (2025b: 7) report that the total length of the genome is 1.84 Gb.

Karyotype
Mattey (1962) and Rushton (1970: 460) reported $2n = 34$.

Blood chemistry
The phosphate and oxygene binding capacity of the bat's haemoglobin was studied by Fodeke (2017).

Stasiak *et al.* (2018: 386) investigated he role of Hepcidin in the iron metabolism of *Eidolon helvum*, a species that rarely developed iron storage disease (hemochromatosis). They found that Hepcidin mRNA expression doesn't increase in response to iron administration in healthy animals.

Anosike *et al.* (2020: 181) studied the haematology and micronucleus assay of Nigerian *Eidolon helvum* specimens and they found increased levels of micronucleated polychromatic erythrocytes and normochromatic erythrocytes, which indicate genotoxicity and cytotoxicity. They higher monocyte counts they found suggest chronic inflammation.

Abalaka *et al.* (2023: 1) investigated the bioaccumulation of cadmium, lead and zinc in Nigerian *E. helvum* (primarily with regard to their indirect health risk to human consumers). The concentrations of these metals were respectively: 0.05 ± 0.01, 2.83 ± 0.35 and 0.42 ± 0.03 mg/kg.

HABITAT:
This adaptable species has been recorded from a very wide range of habitats. It is commonly found in moist and dry tropical rain forest, including evergreen forest habitats in the form of coastal (including mangrove) and riverine forest, through moist and dry savanna and mosaics of these and similar habitat types. Populations can persist in modified habitats and the species is often recorded in urban areas, such as wooded city parks (Mickleburgh *et al.*, 2008dc).

In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported that this species was only found in disturbed habitats in the Afromontane forest biome.

HABITS:
Calderón-Capote *et al.* (2020: 1) tracked the movements in four colonies (ranging in size from 4,000 to 10,000,000 animals) and found that average distance covered per night (9 - 99 km), number of foraging sites visited per night (2 - 3) as well as foraging and commuting times were largely independent of colony size. In general, all the bats returned to the same day roost each night.

Using tri-axial accelerometers, Costa *et al.* (2020: 1, 7) found that there was a higher chance that *E. helvum* made daytime flights when they were disturbed (e.g., by trapping or hunting) and also when there was a lot of sunlight (especially > 20 MJ/m^2). The latter was probably linked with the search for more shaded resting places. Rain nor wind had any influence on daytime flights.

ROOST:
Roosting trees often become defoliated due to the large number of bats inhabiting them and are therefore only used on a relatively limited temporal scale (Kunz, 1996: 42). The extent of the damage caused by the bats at the Awolowo University Campus, Ile-Ife, Nigeria, was studied by Ayoade *et al.* (2012: 405), who reported that premature defoliation, loss of branches and hence reduction in canopy foliage of the host trees led to the decline in the ability of the trees to provide many environmental and social services that contribute to the quality of life in cities and to serve as effective wind barrier.
At the same location, Ndebele *et al.* (2025: 8) found that *Eidolon helvum* preferred to roost in *Celtis zenkeri* (Engl., 1902) trees with a hight between 15 and 20 m (16.54 % of all observations). The second preferred tree species was *Delonix regia* (Boj. ex Hook.) Raf. (8.27 %), followed by trees of the Moraceae family (7.52 %).

Ayensu (1974: 716) mentions that Ghanaian *E. helvum* roosting in the palms do not feed on the fruits of the same palm tree but fly to another palm to feed. In Accra, the bats roost in large mahogany and neem trees at the 37 Military Hospital, the Department of Parks and Gardens and the 37 Military Barracks (Ohemeng *et al.* (2018: 3). Lawson *et al.* (2018: 110) also found them roosting in huge silk cotton trees (*Ceiba pentandra*).

In Côte d'Ivoire, Niamien *et al.* (2017a: 70) found that *E. helvum* prefers to roost in *Hevea brasiliensis* Müll. Arg. (Pará rubber tree - Euphorbiaceae) and *Mangifera indica* L. (Mango - Anacardiaceae) trees.

In Kigali (Rwanda), Leeuwerck (2019: 6) reported *E. helvum* roosting in *Araucaria* sp., *Elaeis guineensis, Jacaranda mimosifolia, Markhamia lutea, Casuarina equisetifolia, Terminalia mantaly, Cupressus lusitanica, Persea americana, Ficus benjamina, Syzygium guineense* and *Grevillea robusta*.

For western Kenya - the only colony site in Kenya - Webala *et al.* (2012: 3) suggested that tree density was an important factor in roosting-camp selection for *E. helvum*, and the removal of roost trees could have serious ramifications on their conservation in the region. This is especially important as colonies of *E. helvum* are rarely found in protected areas, but rather within human habitation. Webala *et al.* (2014: 85) found that, besides the density of the trees, also the number of branches on a tree was an important factor when selecting a roost site.

Peel *et al.* (2017: 77) provided information on distribution, migration patterns, roost size, age and sex composition of 29 *E. helvum* roosts from nine countries across tropical Africa. They indicate (p. 89) that roosts in urban areas are in zones where hunting is discouraged due to their human usage: hospital grounds, embassies, botanical gardens, hotels, palace gardens, zoos, and military, private or corporate compounds. These zones are usually locations where sufficient numbers of large, tall trees are present.

MIGRATION:
Cosson *et al.* (1996: 370) reported that *E. helvum* is not a year-round inhabitant of Mauritania, and is likely a migrant species. Lelant and Chenaval (2011d: 14) reported an impressive cloud consisting of thousands of animals in Nouakchott on 9 November 2010.

Hayman *et al.* (2010) who radio tracked an individual (EBOV-seropositive, see viruses below), showed typical migratory movements in this region of West Africa.

The drivers, routes and patterns of migration are unknown (Peel *et al.*, 2010a). It is unclear whether *E. helvum* has a panmictic population structure across a continuous distribution that shifts according to seasonal resource availability, or whether a finer substructure and specific migration routes exist (Peel *et al.*, 2010a; O'Toole *et al.*, 2021: 229). O'Toole *et al.* (2021: 231, fig 2)

suggest three hypotheses: one where the Mambila Mountains in the west and the Ethiopian highlands/Katanga Plateau are barriers (Elevation Hypothesis); one where the Congo, Niger, Nile and Zambezi rivers act as barriers (River Basin Hypothesis) and the Panmixia Hypothesis, where there is no limit to the gene flow for *Eidolon helvum*.

Hurme *et al.* (2022: 1) found that *E. helvum* timed its migration to move into highly seasonal landscapes to exploit short-lived explosions of food. For this, the bats may benefit from collective sensing of the environment to time migrations. Hurme *et al.* (2022) also warn that the decreasing bat numbers as well as various threats might cause this property of large colonies to be lost.

Daïnou *et al.* (2010) report that the distribution of *Milicia excelsa* (Moracea) is largely determined by the migration behaviour of the species main seed disperser *E. helvum*.

Based on stable hydrogen isotopes in the fur of 88 examined museum specimens from Sub-Saharan Africa, Ossa *et al.* (2012: 1) report that 22 % had migrated at least 250 km, with a mean distance of 860 km, and a maximum of over 2,000 km (for seven specimens).

For Zambia, Richter (2004: 70) suggests that trees of the genera *Uapaca* and *Syzygium* may be key in timing this species' migration, although she also indicates that the exact migratory cues for the species are unknown.

O'Toole *et al.* (2021: 229) indicate that there is no evidence for gender-specific migratory behaviour.

Isotopic data captured by Ossa Gómez (2012: 22) suggest that *E. helvum* has a core distribution around the Gulf of Guinea, with migration towards the north (Mauritania, Niger) during the months of May to September and towards the south (Tanzania, Zimbabwe, Zambia) during the months of October and December.

Pakuła *et al.* (2017: 2) report on a Straw-coloured fruit bat that was observed on a ship sailing along the coast of West Africa, indicating that these bats can be transported over long distances.

DIET:
Doutre and Sarrat (1973: 280) indicated that in West Africa, *E. helvum* has an outspoken preference for (over)ripe local fruits such as mangos, guavas, figs and bananas. They never saw them eat green fruits.

Ayensu (1974) reports on *E. helvum* visiting the following plants when foraging: *Parkia clappertonia* (Dawadawa), *Ceiba pentandra* (Silk-Cotton tree or Kapop tree), *Adansonia digitata* (Baobab), *Anacardium occidentale* (Cashew tree), *Ficus umbellata* (Fig tree), *Psidium guajava* (Guava tree), *Carica papaya* (Papaya or pawpaw), and *Azadirachta indica* (Neem tree).

Daïnou *et al.* (2010) mention that *E. helvum* feeds on the fruits of the Iroko trees (*Milicia excelsa*) in Cameroon, and suggest that the migratory behaviour of *E. helvum* is the primary mechanisim (seed dispersal) for the distribution of *Milicia excelsa* (Moraceae).

In Accra (Ghana), Dechmann *et al.* (2010: 121) found that seven tracked bats mainly fed on introduced and/or cultivated fruits (primarily neem - *Azadirachta indica*, but also on papaya, mango, oil palm and banana). Only two animals ate wild figs. They also found that the core foraging area was only 3.9 ha (2.2 - 4.9 ha) and included only a few food trees. This area was on average 18.6 ± 11.8 km (max: 37 km) from their roost.

Fahr *et al.* (2015: 1) found that *E. helvum* primarily fed on fruits of introduced trees during the wet season low population numbers, whereas nectar and pollen of native trees made up the major part of their diet during the dry season when population numbers peak.

O'Brien (2011: 264) mentions that *Syzygium* is a staple food for mainland African *E. helvum*, but also refers to DeFrees and Wilson (1988: 4), who indicate that they are also fond of *Ceiba pentandra*.

Investigations by Kankam and Oduro (2011: 22) in the Bia Biosphere Reserve in Ghana showed that *Antiaris toxicaria* [bark cloth tree, antiaris, false iroko, false mvule or upas tree] fruits processed by *E. helvum* still had some fruit pulp around them, and resulted in a far less degree of germination than seeds, which were processed by monkeys and were cleared of fuit pulp.

In Congo, Kipalu (2009: 16) observed *E. helvum* visiting and/or consuming fruits of the African custard-apple (*Annona senegalensis*), Borassus palm (*Borassus aethiopum*), Heart Fruit (*Hymenocardia acida*), African peach (*Nauclea diderichii*), African corkwood tree (*Musanga cecropioides*), and (*Caloncoba welwitschii*)

Lavin *et al.* (2009: 336) report on the prevention of ISD (Iron Storage Disease of hemochromatosis) in captive *E. helvum* specimens, which can result in organ damage

and possibly fatalities. The animals might succumb due to the extremely low iron concentrations in the wild diet as compared with the diet they have in captivity.

In Abidjan, Côte d'Ivoire, Niamien *et al.* (2009: 235) reported the following fruits to be present in the bat's droppings: Anacardiaceae: *Mangifera indica* L. (Mango); Arecaceae: *Elaeis guineensis* Jacq. (African oil palm); Caricaceae: *Carica papaya* L. (Papaya); Mimosaceae: *Parkia biglobosa* (Jacq.) R.Br. ex G.Don (African locust bean) [flowers]; Moraceae: *Ficus benjamina* L. (Weeping fig, Benjamin fig), *Ficus exasperata* Vahl (Sandpaper tree, forest sandpaper fig, white fig, or sandpaper leaf tree), *Ficus lutea* Vahl (giant-leaved fig, Lagos rubbertree), *Ficus polita* Vahl (Heart-leaved fig), *Ficus* spp., *Ficus sur* Forssk (Cape fig, broom cluster fig), *Ficus umbellata* Vahl; Myrtaceae: *Psidium guajava* L. (common guava, yellow guava, lemon guava) as well as leaves of *Araucaria excelsa* (Norfolk Island Pine, Star Pine - Araucariaceae). Niamien *et al.* (2017b: 187) added the fruits of *Eugenia jambos* L. (Rose apple, Malabar plum) and *Eugenia malaccensis* L (Malay apple) (Myrtaceaea) and leaves of *Platycerium* sp. (Polypodiaceae).

In western Kenya, Webala *et al.* (2012: 12) reported that *E. helvum* helped to disperse seeds of over 32 plant species belonging to 17 families: Anacardiaceae: *Mangifera indica* (Mango); Apocynaceae: *Saba comorensis* (Bungo fruit); Canellaceae: *Warburgia ugandensis* (Uganda greenheart); Caricaceae: *Carica papaya* (Papaya); Cucurbitaceae: *Momordica foetida*; Flacourtiaceae: *Flacourtia indica* (Madagascar plum, batoka plum, flacourtia, governor's plum, Indian plum); Guttiferae: *Garcinia buchananii* (Granite Mangosteen); Lauraceae: *Persea americana* (Avocado); Malvaceae *Ceiba pentandra* (Kapok); Meliaceae: *Melia azedarach* (white cedar); Moraceae: *Ficus amadiensis*, *Ficus asperifolia*, *Ficus lutea* (Giant-leaved Fig), *Ficus natalensis* (Natal Fig), *Ficus ovalifolia*, *Ficus ovata*, *Ficus sur* (Cape Fig), *Ficus sycomorus* (Sycamore Fig), *Ficus thonningii* (Strangler Fig, Common Wild Fig, Bark-cloth Fig), *Ficus vallis-choudae*, *Morus alba* (White Mulberry); Myrtaceae: *Psidium guajava* (Apple or common guava), *Syzygium cordatum* (Water berry), *Syzygium guineense* (Water berry); Fabaceae: *Crotolaria lanchnocarpoides*; Rosaceae: *Eriobotrya japonica* (Loquat), *Rubus apetalus*; Rubiaceae: *Vangueria apiculata* (Mutugundo Fruit); Rutaceae: *Teclea nobilis* (Small fruited Teclea), *Teclea trichocarpa* (Furry-fruited Teclea), *Toddalia asiatica* (Orange climber).

Webala *et al.* (2014: 90) removed *Ceiba pentandra* from the above list and added *Allophylus ferrugineus* (Sapindaceae).

Makau (2016: xii) found it to be the most effective disperser of guava seeds in western Kenya.

Seltzer *et al.* (2013: table S2) provides an overview of the plant species found beneath bat feeding roosts. For *E. helvum* these include *Elaeis guineensis* Jacq. (African Oil palm - Arecaceae), *Magnistipula butayei* De Wild (Chrysobalanaceae), *Parinari excelsa* Sabine (Guinea Plum - Chrysobalanaceae), *Antiaris toxicaria* Lesch. (upas tree - Moraceae), *Ficus natalensis* Hochst (Natal Fig - Moraceae), *Milicia excelsa* (Welw.) C. C. Berg (African Iroko - Moraceae), *Psidium guajava* L. (apple guava - Myrtaceae), *Syzygium guineense* (Willd.) D.C. ("water-berry", Snake bean tree - Myrtaceae) and *Maesopsis eminii* Engl. (Umbrella tree - Rhamnaceae).

Corlett (2017: 13) (referring to Abedi-Lartey *et al.*, 2016) reports that gut passage times for small seeds in caged bats had a median of 72 min and a maximum of 19 h. Combined with the long commutes these bats undertake, this results in a potential dispersal distance of 10 to 100 km. However, they also indicate that the estimated median dispersal distances (for larger seeds) is about 50 m. van Toor *et al.* (2019: R238) found that the bats dispersed seeds over distances of up to 95 km, with averages ranging from 12.6 to 21.4 km, depending on colony and season. For the colony in Accra (Ghana), they calculated that during the dry season the 152,000 bats accounted for 338,000 dispersal events during a single night and produced an average seed rain of 26.2 dispersal events per km^2. During the wet season, when only 4,000 bats are present, there are only 5,500 dispersal events per night.

In Senegal, Sow *et al.* (2020: 4) used molecular analyses to identify the presence of *Heliocheilus albipunctella* de Joannis) (Lepidoptera, Noctuidae) in the faeces of *E. helvum* foraging in millet fields (*Pennisetum glaucum* (L.) R. Br. (Cyperales, Poaceae)).

On São Tomé, Heleno *et al.* (2021: 6, Suppl.) found that *Eidolon helvum* dispersed seeds up to a maximum size of 57.83 mm (mean size 8.48 mm and mean weight 4.65 g). These seeds belonged to *Alchornea* cf. *cordifolia, Annona muricata, Anthocleista* cf. *scandens, Artocarpus altilis, Artocarpus heterophylla, Averrhoa carambola, Carica papaya, Cecropia peltata, Dacryodes edulis, Discoglypremna caloneura, Eriobotrya japonica, Erythrina* sp., *Ficus*

chlamydocarpa, Ficus exasperata, Ficus kamerunensis, Ficus sp., *Lycopersicon esculentum, Maesopsis eminii, Mangifera indica, Milicia excelsa, Musa* sp., *Musanga cecropioides, Persea americana, Psidium guajava, Santiria trimera, Spondias cytherea, Sterculia tragacantha*.

Leeuwerck (2019: 6) reported the following fruits being eaten by *E. helvum* in Kigali (Rwanda): *Mangifea indica, Carica papaya, Persea americana, Ficus sur, Ficus sycomorus, Ficus thonningii, Morus alba, Musa acuminata, Psidium guajava, Syzygium cordatum* and *Syzygium guineense*.

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Eidolon helvum*: *Carica papaya* Linnaeus, *Ficus asperifolia* Miq., 1848, *Ficus lutea* Vahl, 1805, *Ficus natalensis* Hochst., 1845, *Ficus ovata* Vahl, 1805, *Ficus sur* Forssk. 1775, *Ficus sycomorus* Linnaeus, 1753, *Ficus thonningii* Blume, 1839, *Ficus vallis-choudae* Delile, 1843, *Garcinia buchananii* Baker, *Mangifera indica* Linnaeus, *Melia azedarach* Blanco, 1837, *Morus alba* Linnaeus, 1753, *Psidium guajava* Linnaeus, 1753, *Syzygium cordatum* Hochst., 1844, *Syzygium guineense* (Willd.) DC., 1828, *Toddalia asiatica* (Linnaeus) Lam., 1797, *Vangueria apiculata* K.Schum., 1895, *Warburgia ugandensis* Sprague.

PREDATORS:
Mikula *et al.* (2016: 162) report that the Amur falcon (*Falco amurensis* Radde, 1863) and the Eurasian hobby (*Falco subbuteo* Linnaeus, 1758) were observed chasing *Eidolon helvum* bats in Kasanka forest, Zambia. Furthermore (supplemental data), they mention the following avian predators: Steppe eagle (*Aquila nipalensis* (Hodgson, 1833)), African hawk eagle (*Aquila spilogaster* (Bonaparte, 1850)), Common buzzard (*Buteo buteo* (Linnaeus, 1758)), Greater spotted eagle (*Clanga clanga* (Pallas, 1811)), Lesser spotted eagle (*Clanga pomarina* (Brehm, 1831)), Lanner falcon (*Falco biarmicus* Temminck, 1825) [with "*Eidolon* sp" from countries on the African continent as prey], Palm-nut vulture (*Gypohierax angolensis* (Gmelin, 1788)), White-backed vulture (*Gyps africanus* Salvadori, 1865), African fish eagle (*Haliaeetus vocifer* (Daudin, 1800)), Ayres's hawk-eagle (*Hieraaetus ayresii* Gurney, 1862), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850), Black kite (*Milvus migrans* (Boddaert, 1783)), Martial eagle (*Polemaetus bellicosus* (Daudin, 1800)), Crowned eagle (*Stephanoaetus coronatus* (Linnaeus, 1766)), Pied crow (*Corvus albus* Statius Muller, 1776).

POPULATION:
Structure and Density
In general this is a common species forming large colonies of thousands to even millions of individual. Hayman *et al.* (2011b: 1; 2012c: 1393) report on a colony of up to one million individuals being present in Accra, Ghana for approximately 6 months during the dry season, and Sørensen and Halberg (2001: 213) report 1.5 million fruit bats leaving the roost at sunset in the Kasanga National Park, Zambia. Racey (2004a: 2) indicates that the number bats at the same locality peak near the end of November to about 8 million (representing a total mass of 3,000 metric tons in one hectare of forest and consuming nearly 6,000 tons of fruit each night), after which they begin to fall rapidly. Within colonies they form tight clusters of up to 100 animals, although in particularly large colonies this clustering may not be so obvious. Colonies may show extreme roost-site fidelity. During migration this species disperses into small groups. There is evidence of a widespread decline (P. Racey *pers. comm.* in Mickleburgh *et al.*, 2008dc). A well-known colony in Kampala (Uganda) declined in numbers over a forty-year period from ca. 250,000 animals to 40,000 in 2007 (Monadjem *et al.*, 2010d). A trend which continued over the following years (Akite, 2009: 28-29).

For the colony at Accra, Hurme *et al.* (2022: 9) mentioned that the peak size reached 1,000,000 bats in 2007, but was reduced to 85,000 in 2015. More recent numbers point to a further decline to about 20,000 (see also https://www.eidolonmonitoring.com/monitoring/ghana for further details).

Based on emergence data for one roost on Príncipe (10,500 - 14,200 bats), Dallimer *et al.* (2006: 50) estimated a population density between 82 and 111 bats/km^2 for the entire island.

On Annobón, Peel *et al.* (2012: 3) reported colony sized of up to 1,500 animals. Rainho *et al.* (2022: 603) [referring to Peel *et al.* (2017] mentions a density of 156 - 159 ind/km^2 for Príncipe and of 94 - 176 ind/km^2 for Annobón.

Wood *et al.* (2012: 2885) indicate that while colonies in West Africa can be very large, these in East Africa appear to be smaller and more fragmented, and also seem to be less migratory.

Magloire *et al.* (2017: 890) reported on a colony from Abidjan (Côte d'Ivoire) counting on average 180,000 bats. They found that the colony size increased from August to November (from

200,000 to 300,000), stabilized from November to February and decreased from March to July (to 12,000). These fluctuations were linked to food diversity and abundance.

For their study on the distribution of Ebola viruses, Fiorillo *et al.* (2018: 8) estimated the density of a *E. helvum* colony to be about 180 bats/km^2.

On a much larger timescale, Chattopadhyay *et al.* (2019: 7) suggested that *E. helvum* would have taken advantage of the decreased aridity from the Last Interglacial (approximately 110 000 to 130 000 years ago) to the Last Glacial Maximum (approximately 20 000 years ago), which led to an increased population size. They also estimated the bat's suitable habitat percentage to 100 at LGM, 27.34 at LIG, 36.67 at Mid-Holocene (ca. 6 000 years ago) and currently 44.31.

Trend
2019: Decreasing (Cooper-Bohannon *et al.*, 2020d). 2008: Decreasing (Mickleburgh *et al.*, 2008dc; IUCN, 2009). 2004: Decreasing (Mickleburgh *et al.*, 2004bh; IUCN, 2004).

LIFESPAN:
Hayman *et al.* (2012c: 1399) examined the tooth cementum annuli and found three old specimens with an estimated age range from 13 to 15 years. They found that adult bats had a survival probability of about 0.83, whereas this was 0.43 for juveniles.

Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 21.8 years.

Hayman and Peel (2016:134) calculated that the mean life expectancy estimates across the colonies they studied to be ranging from 2.3 to 6.8 years, and that individuals may live up to 30 years of age.

Peel *et al.* (2017: 85) report on regional differences in the lifespan of *E. helvum*: Tanzania (Dar es Salaam: mean 6.4 yrs, max 15 yrs, n = 53 adults; Morogoro: 4.5, 8, 24), Ghana (6.0, 14, 76), Bioko (2.4, 6, 16), Príncipé (4.2, 10, 23), and São Tomé (4.8, 13, 57).

ACTIVITY AND BEHAVIOUR:
In Nigeria, *E. helvum* was reported to fly at least 24 km each night and often stopped at a number of locations between leaving the roost and arriving at the foraging site (Okon, 1974). Richter and Cumming (2006) reported flights of over 15 km for *E. helvum* in Kasanka National Park, Zambia. Richter and Cumming (2008: 172) reported that bats foraged as far as 59 km away from their roost. During their migration, one animal travelled 370 km in one night, but on average they travelled 29 km/day. The largest distance travelled by one bat, reported in that study, is 2,518 km in 149 days.

Sapir *et al.* (2014: 1) found that, in Ghana, *E. helvum* modified its flight in response to the wind vector (e.g., they decreased their airspeed in response to tailwinds so that their groundspeed remained nearly constant).

In Ghana too, Fahr *et al.* (2015: 1) found that *E. helvum* foraged locally during the wet season population low (ca. 4,000 animals traveling between 3.5 and 36.7 km) in urban areas with low tree cover. During the dry season population peak, some 150,000 individuals travelled between 24.1 and 87.9 km.

Carpenter (1986: 90) and McGuire and Guglielmo (2009: 1291) reported that the respiratory quotient for this species indicates that fat provided 77 - 92 % of the fuel during flight, and a decline in respiratory quotient during long flights may prove that fat is indeed the only fuel source following initial carbohydrate use. Carpenter (1986: 93) also indicates that at airspeeds of 5.5 to 6.5 m/s the heart beats at a frequency of 576 - 601 beats per minute, and at airspeeds between 5.5 and 7.0 m/s, these bats take 295 to 316 breadths per minute. From flight corridor tests, Riskin *et al.* (2012: 2946) determined the average flight speed to be 4.24 ± 0.91 m/s.

In captive groups, Carter and Leffer (2015: 3) found that 6 males spent 0.52 % of their awake time with social grooming. A group consisting of six females and two castrated males did not perform any social grooming at all.

REPRODUCTION AND ONTOGENY:
Haensel (1987) mentions a female bat that was caught on a ship 40 off the coast of Monrovia (Libera) and was transferred to the Berlin Zoo, where it gave birth to a young six months after its arrival.

For Uganda, Mutere (1967, 1968) reported pregnancies between October and February and births occurring between February and March.

For Congo, Bergmans (1979a: 165) reported two pregnant females on 6 December 1972.

Pakenham (1984: 24) mentioned two highly advanced pregnant females in November on Zanzibar.

Krutzsch (2000: 109) reports that various authors found that *E. helvum* has a monoestrous reproduction cycle, which is confirmed by Abiaezute *et al.* (2020b: 1), who studied the seasonal changes in the morphology of the seminal vesicles of this species, and found the secretory epithelial cells to be very active during the rainy season, whereas regeneration of degenerated epithelium occurred during the dry season.

Simbauni and Bernard (2001: 63) indicate that the reproductive cycle of *E. helvum* is characterized by a three-month period of delayed implantation (see also Badwaik and Rasweiler, 2000: 228; Racey and Entwistle, 2000: 383, O'Toole *et al.*, 2021: 229; Happold and Happold, 2023: 58) and that the pregnancy may last for 10 months. At birth, the young has about 18.4 % of the mother's body mass (48.6 g versus 263.5 g; see Kurta and Kunz, 1987: 82)..

Peel *et al.* (2013b: 7) indicate that *E. helvum* is panmictic across its continental African range, meaning that all individuals from over the entire range are potential partners. They found no indication that gene flow was more likely to occur among neighbouring populations than among distant populations (> 4,500 km). They conclude that *E. helvum*, therefore, has the largest reported panmictic unit of any mammal.

Szekely *et al.* (2015: Suppl.) report a gestation period of 275 days and indicate that weaning occurs after 65 days. At birth the young weighs 50 g and after gestation its weight has increased to 135 g.

In their overview, Peel *et al.* (2017: 82) report the estimated start of births in different countries: Annobón (mid-September), Malawi (mid-November), Príncipe (November-December), Tanzania (mid-December), São Tomé and Ghana (February-March), Uganda (March-April), Bioko (mid-April). They also indicate (p. 83) that females are reproductively active between the ages of 2 and 14 years.

MATING:
Webber *et al.* (2017: Suppl.) indicate that this species has a polygynandrous mating system.

PARASITES:
BACTERIA
Gram-negative bacterium
Pinus and Müller (1980) and Sara (2002: 41) reported *Citrobacter freudii*, *Escherichia coli*, *Klebsiella oxytoca*, and *Klebsiella pneumoniae*.

Nowak *et al.* (2017: 6) tested three bats from the Republic of Congo of which two tested positive for *E. coli*.

Obodoechi *et al.* (2021: 3) investigated the antimicrobial resistance of *E. coli* bacteria recovered from Nigerian bats.

Two out of 107 Nigerian *Eidolon helvum* specimens examined by Kamani *et al.* (2021: 4) tested positive for *Leptospira*

Gram-positive bacterium
Akobi *et al.* (2012: 1) found that 500 faecal samples of bats at the university of Ife-Ife, Nigeria were colonized by 107 isolates of *Staphylococcus aureus* strains with genotypic characteristics that are rarely found in humans. Held *et al.* (2016: 118) refer to a report from Nigeria, indicating that *E. helvum* can be colonized by *S. schweitzeri*. Monecke *et al.* (2022: 1) re-assigned the Nigerian *Staphylococcus* to the newly described *S. roterodami* Schutte *et al.*, 2021.

Spirochaetales
Reviewed in McCoy (1974), who listed *Borrelia* sp. Ogawa *et al.* (2015a: 143) report on the presence of at least two other spirochaete bacteria: *Leptospira borgpetersenii* and *L. kirschneri* in *E. helvum* which migrated from the Democratic Republic of the Congo to Zambia.

Bartonellae - Bacteria
Bartonella
Kosoy *et al.* (2010: 1877) and Bai and Kosoy (2012: 58) reported a prevalence of *Bartonella* spp. In *E. helvum* from Kenya of 23/88 (26.1%) cultured from blood samples. The level of *gltA* sequence identified between 16 *Bartonella* genotypes, but varied greatly, eight genotypes (sequence variants) were clustered around 4 clades (Kosoy *et al.*, 2010: 1878). Three novel *Bartonella* species have been isolated from *E. helvum* (Kosoy, 2010: 719). See also Kosoy (2010: 719) for further information.

Morse *et al.* (2012: 1719) refer to Billeter *et al.* (2012) for *Bartonella* sp. found in the bat fly *Cyclopodia greefi*, parasiting on *E. helvum* in Ghana. Billeter *et al.* (2012: 325) collected batflies (*Cyclopodia greefi greefi*) from *E. helvum* specimens from Ghana (see also Morse *et al.*, 2012), Bioko, and Annobón. Of these bat flies, 56.5 % (Ghana) to over 71 % (Bioko, Annobón) were carriers of *Bartonella* bacteria. Genetically, 65.9 % of the *Bartonella* sequences were identical or similar to sequences obtained in other studies (e.g., Kosoy *et al.*, 2010). One sequence was very similar to one obtained from a *E.*

helvum specimen collected in Kenya (Billeter *et al.*, 2012: 326 - 327).

Kamani *et al.* (2014: 628) tested 79 *E. helvum* specimens from Nigeria and found at least 44 testing positive for *Bartonella* DNA.

79 isolates studied by Bai *et al.* (2015: 7) revealed five genogroups (*E1* to *E5*) for *ribC*. An additional lineage (*Ew*) did not contain a fragment for *ribC*.

Mannerings *et al.* (2016: 923) report that the following *Bartonella* species were already isolated from *E. helvum* bats: *B. henselae, B. quintana, B. clarridgeiae, B. vinsonii vinsonii, B. elizabethae*, and *Bartonella* strain E1–105.

Olatimehin *et al.* (2018: 3) found *Staphylococcus aureus*, *Staphylococcus schweitzeri* and *Staphylococcus argenteus* in feacal samples from bats at the Obafemi Awolowo University, Ile-Ife, Nigeria.

Di Cataldo *et al.* (2020: 2) examined 51 Nigerian *Eidolon* bats and found 13 (45 %) to be infected by hemoplasma bacteria.

HAEMOSPORIDIA

Boundenga *et al.* (2018: 10581) reported 1 out of six examined *E. helvum* to be infected by *Hepatocystis* (16.67%) (see also Kamani *et al.*, 2022a: Suppl.).

In a study performed in Ibadan (Nigeria), Li *et al.* (2019a: 21) found six out of 109 *E. helvum* specimens (5.5%) infected with *Cryptosporidum* sp. and 16 (14.7%) infected by *Enterocytozoon bieneusi*; none were infected by *Giardia duodenalis*.

PROTOZOA

Kamani *et al.* (2022a: Suppl.) found 2 out of 67 bats examined in northern Nigeria to be infected by *Trypanosoma* cf. *livingstonei*.

ACARI

Laelapidae

Taufflieb (1962: 112) indicated that *Chelanyssus aethiopious* Hirst, 1921 was found once on a female *Eidolon helvum*, but this was never confirmed by subsequent findings. He considered this one-time occurrence as accidental.

Sarcoptidae

Nycteridocoptes pteropodi Rodhain and Gedoelst, 1923 was reported by Fain (1958: 236) from *E. helvum* specimens from Astrida (=Butare), Rwanda.

Spinturnicidae

Taufflieb (1962: 112) reported *Meristaspis kenyaensis* Radford, 1947.

Demodicidae

Bianco *et al.* (2019: 547) reported the first case of demodicosis, caused by *Demodex* sp. mites from bats in a captive colony at the Accra Zoological Gardens (Ghana).

HEMIPTERA

Cimicidae

Haeselbarth *et al.* (1966: 8) recorded *Afrocimex constrictus* Ferris & Usinger, 1957 associated with *E. helvum* near Ruiru, Kenya.

DIPTERA

Nycteribiidae

Penicillidia fulvida (Bigot, 1885) (see Haeselbarth *et al.*, 1966: 114). *Eucampsipoda africanum* Theodor, 1955, widely distributed over the Ethiopian region and recorded from localities in Senegal to the Sudan and southwards to the Cape (Haeselbarth *et al.*, 1966: 115). *Dipseliopoda setosa* Theodor, 1955 from Kenya and Tanzania (Haeselbarth *et al.*, 1966: 116). *Cyclopodia greeffi* was originally described by Karsch (1884) from an *E. helvum* specimen from São Tomé, and the adjacent islet of Rojas (see Urich *et al.*, 1922: 471). Urich *et al.* (1922) furthermore mentioned additional specimens from this bat fly, reported by Rodhain and Bequaert from *E. helvum* specimens from Leopoldville [= Kinshasa], DRC. *Cyclopodia greeffi* are found in a belt across central Africa, between lat. 10º south and north, while in West Africa it occurs further north up to lat. 20º (Haeselbarth *et al.*, 1966: 117). Billeter *et al.* (2012: 325) collected bat flies (*Cyclopodia greefi greefi*) from *E. helvum* specimens from Ghana (see also Morse *et al.*, 2012; Stuckey *et al.*, 2017: 22), Bioko, and Annobón (see above for bacteria results from this study). Reeves *et al.* (2020a: 328) reported this bat fly from a Namibian bat. Atobatele *et al.* (2023: 212) reported an average infestation of 3.7 ± 0.4 *C. greeffi* flies on bats from Nigeria during the wet season, which is significantly higher than during the dry season (1.6 ± 0.1).

Szentiványi *et al.* (2019a: Suppl.) indicated that these bat flies were also carrying the arthropod *Eupelmus urichi* (on São Tomé) and *Bartonella* bacteria (in Ghana).

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Eidolon helvum*: *Cyclopodia greeffi greeffi* Karsch, 1884, *Dipseliopoda setosa* Theodor, 1955,

Eucampsipoda africana Theodor, 1955, *Penicillidia (Penicillidia) fulvida* (Bigot, 1885).

SIPHONAPTERA
Ischnopsyllidae
Thaumapsylla breviceps Rothschild, 1907, described from Kenya and the DRC (Haeselbarth *et al.*, 1966: 186). *Thaumapsylla dina* Jordan, 1937 from the mountains of the Ruwenzori, Congo and Kenya (Haeselbarth *et al.*, 1966: 186). *Lagaropsylla consularis* Smit, 1957, traditional host being molossid bats, but it has also been recorded from this taxon (Haeselbarth *et al.*, 1966: 190).

Teinocoptidae
Teinocoptes eidoloni Fain, 1959 was reported by Fain (1967: 367) from *E. helvum* from Astrida (=Butare), Rwanda.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Eidolon helvum*: Adenoviruses, Astroviruses, Coronaviruses, Flaviviruses, Paramyxoviruses and Polyomavirus.

Willoughby *et al.* (2017: Suppl.) report the following viruses: Bundibugyo ebolavirus, Bunyamwera orthobunyavirus, Entebbe bat virus, Hendra henipavirus, Ife virus, Influenza A virus, Lagos bat lyssavirus, Mokola lyssavirus, Nipah henipavirus, Ntaya virus, Sudan ebolavirus, Tai forest ebolavirus, Usutu virus, West Caucasian bat lyssavirus, West Nile virus, Yellow fever virus, Zaire ebolavirus, Zika virus.

Nieto-Rabiela *et al.* (2019: Suppl.) reported the following viruses: Achimota virus, Bat coronavirus, Bat kobuvirus, Bat mastadenovirus, Bat paramyxovirus, Bat pegivirus, Bat simplexvirus, Chiroptera tetraparvovirus, *Eidolon helvum* papillomavirus, *Eidolon helvum* retrovirus, *Eidolon* paramyxovirus, Ife virus, Kumasi rhabdovirus [=Kumasi ledantevirus], Lagos bat virus, Polyomavirus [=*Eidolon helvum* polyomavirus 1], Poxvirus, Rotavirus A.

Yinda *et al.* (2016: 6) identified 5 divergent novel bat RVA strains from faeces collected in Cameroon. Four of these were genetically similar to each other and the last one was related to the Kenyan bat strain. They did not notice any diarrhea or other obvious signs of sickness in the bats.

Peel (2018: 1) estimated that maternally-derived immunity to Lagos bat virus and African henipavirus has a mean duration of about six months, which is much less than the acquired immunity for these viruses: 12 and 4 years respectively.

Yinda *et al.* (2018: 2) pooled 87 fecal samples of *Eidolon helvum* and *Epomophorus gambianus* from Cameroon into 25 groups. One group containing fecal samples of *E. gambianus* only yielded mainly phage viral reads, leading them to conclude that all the eukaryotic viral reads they encountered were from *E. helvum*. The viruses they found belonged to the following families: Alphaflexiviridae, Astroviridae, Baculoviridae, Caliciviridae, Caulimoviridae, Circoviridae, Coronaviridae, Dicistroviridae, Geminiviridae, Hepeviridae, Herpesviridae, Iflaviridae, Marnaviridae, Nodaviridae, Other Picornavirales, Papillomaviridae, Partitiviridae, Parvoviridae, Picobirnaviridae, Picornaviridae, Polydnaviridae, Reoviridae, Retroviridae, Secoviridae, Tombusviridae, Totiviridae, Tymoviridae, Unclassified eukaryotic virus, and Virgaviridae. Most of the identified partitiviruses and densoviruses constitute putative novel genera in their respective families.

In urine samples of a captive colony at Accra Zoo, Ghana, Gibson *et al.* (2021: 6) found paramyxoviruses belonging to the genus *Henipavirus* and *Pararubulavirus*. The same colony was followed by Jolma *et al.* (2021: 4), who found two viruses belonging to the genus *Pararubulavirus*, one to the genus *Orthorubulavirus* and five which were distantly related to *Henipavirus* (but to distinct to be assigned to that genus). The shedding pattern was cyclic, with peaks in late July and late January. During the 10 years that this colony was followed, none of the bats displayed any signs of illness.

In bats from Saudi Arabia, Mishra *et al.* (2019: 5) found evidence for the following viruses: Bat astrovirus, Bat papilloma virus, Bat Coronavirus, Bat polyomavirus, Me Hepe-Astro virus, Parechovirus, Rotavirus, Sapovirus, Teschovirus,

Raulino *et al.* (2022: 256) tested bats from Guinea, Cameroon and the DRC and found antibodies against Chikungunya virus , Dengue virus, O'nyong nyong virus, Usutu virus, West Nile virus and Zika virus. Meta Djomsi *et al.* (2023: 1) also tested *E. helvum* specimens from these three countries and found that 239 out of 733 (39.9 %) were positive for coronaviruses, which was the highest prevalence they found for the species they examined.

Cantoni *et al.* (2023; 1, 5) examined 304 serum samples from Nigerian bats captured for human consumption and found neutralizing antibodies

against henipavirus lineage GH-M74a, Nipah virus and bat influenza virus H17N10. One sample was positive for Ebola virus, but none were positive for Marburg virus or any coronavirus.

Adenoviridae
Sequences of *Eidolon helvum* adenovirus 1 attributed to the genus *Mastadenovirus* were found by Baker *et al.* (2013a: 98) in samples from bats from Ghana.

Conrardy *et al.* (2014) tested 9 bats from Kenya, none of which tested positive.

Ogawa *et al.* (2017: 2) isolated a new adenovirus from Zambian bats: *E. helvum* adenovirus 06-106 - EhAdV 06-106, which they also tentatively called: *Bat mastadenovirus H*.

Astroviridae
Babalola *et al.* (2020: 31) examined 180 bats from two localities in Nigeria, and found 17 (9.4 %) to be positive for Astroviruses.

Caliciviridae
Human Norovirus (HuNov)
Chigor *et al.* (2024: 3) [referring to Babalola *et al.* (2020)] reported this virus from Nigerian bats. The latter authors (p. 31) found 10 out of 180 bats to test positive for this virus.

Sapovirus (SaV)
From Cameroonian bats, Yinda *et al.* (2017a: 2) identified the complete genome of six highly divergent SaVs and one partial SaV, which probably represent two novel genogroups, that are only distantly related to any other known SaVs.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, six individuals for antibody to SARS-CoV in sera from Bandundu Province, DRC, none were found to be positive. In February 2008, Pfefferle *et al.* (2009) tested 212 fecal samples from bats from Ghana and all were negative for coronavirus (CoV) RNA. Tong *et al.* (2009) found 6/10 bats collected in 2006 positive for coronavirus RNA in Kenya (Kenya bat coronavirus BtKY20, Kenya bat coronavirus BtKY23, Kenya bat coronavirus BtKY24). 21 % (38 out of 181) of the Kenyan bats tested by Tao *et al.* (2017: 3) were positive for coronaviruses. In Nigeria during June 2008, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs, none tested positive.

Anthony *et al.* (2017b: Suppl.) mention beta-coronaviruses Eidolon_bat_CoV and Kenya_CoV_BtKY56.

Leopardi *et al.* (2016: 575) report on the first occurrence of CoV outside of Kenya: Nigeria.

Nziza *et al.* (2019: 156) found Eidolon bat coronavirus/Kenya/KY24/2006 in a rectal swap from Rwandan bats. Joffrin *et al.* (2020: 7) identified the Kenyan viruses as Beta-D coronavirus.

Lacroix *et al.* (2020: 7) found four out of nine Guinean *Eidolon* specimens to be positive for CoV.

For the two Congos, Kumakamba *et al.* (2021: 7) reported 23 out of 103 bats to test positive for coronaviruses.

Motayo *et al.* (2020: 4) assigned the Nigerian and Kenyan viruses to the subgenus Norbecovirus (sic). Shchelkanov *et al.* (2020b: 226) mention this as Eidolon bat coronavirus C704.

Eidolon bat coronavirus was detected in one of the nine Ghaianan *E. helvum* bats tested by Suu-Ire *et al.* (2022: 6).

Montecino-Latorre *et al.* (2022: 11) report that - in Ghana and Tanzania - virus shedding is not uniformly over the year, but is linked with the yearly reproductive cycle, particularly the weaning period.

Goharriz *et al.* (2025: 4) tested coronavirus RNA from bats from Nigeria and found this to be 99.75 % identical to a lineage D *Betacoronavirus* collected in 2017 from *E. helvum* bats from Ghana, and 99.48 % and 99.24 % identical to sequences from respectively Rwanda (2013) and Tanzania (2018).

Filoviridae - Filoviruses
Olival and Hayman (2014: 1770) found that *E. helvum* has a high seroprevalence of antibodies against several RNA viruses, but not filoviruses, especially when compared to other species in the same locations. They suggest that the migratory lifestyle of this species might prevent filovirus circulation. Peterson *et al.* (2007: 1547) indicate that the geographic distribution of *E. helvum* covers the entire distribution range of both Ebola and Marburg viruses. Hayman (2015: 6) points to the single, highly synchronous birth pulse per year, which prevents persistence of the virus in *E. helvum*.

Ebolavirus
Hayman *et al.* (2010) tested the blood of 262 individuals from Ghana for Ebola virus using indirect fluorescent tests for antibodies against EBOV subtype Zaire [= ZEBOV], one positive was found in a pregnant female. The positive reactivity for EBOV was confirmed using western blot against a recombinant nucleocapsid protein of EBOV-Zaire (Hayman *et al.*, 2010).

Funk and Piot (2014: 2) erroneously refer to Gire *et al.* (2014), who should have claimed that the 2014 Ebola outbreak in West Africa probably originated from a child infected by a straw-coloured fruit bat. However, as indicated by Jakob Fahr in the discussion following this paper, Gire *et al* (2014) never mention bats. The reference was then changed to Baize *et al.* (2014), but that paper (p. 1424) only refers to the "usual suspects": *Hypsignatus monstrosus, Epomops franqueti* and *Myonycteris torquata*. To date, there is no proof that the West African Ebola outbreak is directly related to bats.

In Zambia, Ogawa *et al.* (2015b: "1") found some serum samples that showed distinct specificity for Reston ebolavirus, which has thus far been found only in Asia.

Studying *E. helvum* genes, Ng *et al.* (2015a: 2) found that the *NCP1* gene, which encodes a protein that mammals need in order to move cholesterol within their cells, also turns out to be a receptor that the filoviruses must bind to before they can infect the cells. Ng *et al.* (2015b: 67) also mention that in *E. helvum* this gene has a single amino acid change, which turns them resistant to infection.

In the DRC, Lacroix *et al.* (2021: 7) searched for antibodies in 149 *Eidolon helvum* specimens and found between 7 and 50 of them to be positive.

Djomsi *et al.* (2022: 1) studied a colony of bats in Yaoundé (Cameroon) over a period of about a year, testing dried blood spots on a monthly basis. They found that the proportion of samples reacting with antigens increased with age from 0 - 9/220 (0 - 4.1%) in juveniles to 26 - 158/225 (11.6 - 70.2%) in immature adults and 10 - 225/372 (2.7 - 60.5%) in adult bats. Lactating females showed less antibody responses.

Becker *et al.* (2025: 7) mention that *Eidolon* bats have a mutation in their host receptor thet prevents EBOV entry.

Marburgvirus
Towner *et al.* (2007) tested 35 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 33 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found. Hayman *et al.* (2010) tested the blood of 262 individuals from Ghana for Marburg virus using indirect fluorescent tests for antibodies against MARV subtype Leiden, no positives were found.

Flaviviridae
Flavivirus
In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against West Nile virus (WNV) and non-specific Flaviviruses.

Malmlov *et al.* (2019: 3) refer to Simpson *et al.* (1968) who experimentally inoculated three *E. helvum* specimens with Zika virus, of which two became viraemic and seroconverted.

Fagre *et al.* (2021: 1) reported the presence of ZIKV sfRNA, but not NS5, in two Ugandan bats.

Gonzalez and Banerjee (2022: 10) mentioned the presence of Banzi virus.

Pegivirus (BPgv)
0 out of 8 bats from Cameroon, 1 out of 17 from the Democratic Republic of the Congo, 0 out of 11 from Kenya and 1 out of 50 animals from Nigeria examined by Quan *et al.* (2013: Table S5) were infected by clade H type *Pegivirus* (overall 2.3 %). For the same bats examined, they also found 1, 0, 1, and 5 specimens infected by clade K type *Pegivirus*.

Hantaviridae
In Zambia, Sarii *et al.* (2024: 14) found *Eidolon helvum* to be seropositive for Brno virus, Dakrong virus, Quezon virus, Robina virus and Xuan Son virus.

Herpesviridae
Alphaherpesvirinae
Simplexvirus
Dak An Y 7 – (3 isolates) Cameroon, 1971, isolated from pooled organs (Razafindratsimandresy *et al.*, 2009).

Betaherpesvirinae
Eidolon helvum herpesvirus 1 and 3 - Baker *et al.* (2013a: 96) identified 539 sequences related to herpesviruses, primarily from throat samples: 366 belonging to *betaherpesvirinae*.

Gammaherpesvirinae
Eidolon helvum herpesvirus 2
Baker *et al.* (2013a: 96) identified 539 sequences related to herpesviruses, primarily from throat samples: 171 to *gammaherpesvirinae*.

Nairoviridae
Orthonairovirus
Of the 167 specimens from Ghana tested by Müller *et al.* (2016: 3), 1 was positive for Crimean Congo haemorrhagic fever virus (CCHFV)

Orthomyxoviridae
Freidl *et al.* (2015) conducted serological studies on 100 *E. helvum* serum samples collected in Ghana in 2009/10. About 30% of the screened animals showed serological evidence to avian influenza subtype H9. According to Brunotte *et al.* (2016: 117), this suggests that bats can be naturally infected with classical IAV, although they did not find any evidence to support this hypothesis.

Papillomaviridae (PV)
Baker *et al.* (2013a: 97) found 408 sequences belonging to multiple papillomaviruses, of which two represented new forms.

García-Pérez *et al.* (2013: 51) cloned and sequenced the complete genome of a novel PV, EhelPV1, isolated from hair bulbs from a captive straw-colored fruit bat.

Mengual-Chuliá *et al.* (2012) reported on PV sequences from hair follicles of captive bats.

Paramyxoviridae - Paramyxoviruses
Nine individuals from Kenya were tested for paramyxoviruses by Conrardy *et al.* (2014). All nine were negative for paramyxovirus RNA.

Paramyxovirinae
Henipavirus
Hayman *et al.* (2008b) detected antibodies to both Nipah (NiV - 39 %) and Hendra (HeV - 22 %) [both members of the genus *Henipavirus* (see Hayman *et al.* (2011b: 1)] in bats collected in Ghana in 2007. Peel *et al.* (2012: 2) found antibodies against these viruses in bats on Annobón.

Drexler *et al.* (2009) detected henipavirus RNA and three novel viruses were identified. Drexler *et al.* (2012a: Suppl. Table 1) indicated that 42 out of 722 (5.8 %) bats collected in Ghana, the Central African Republic and Gabon tested positive for *Henipavirus*. 4.0 % (29) tested positive for *Rubulavirus* and 1.8 % (13) for *Pneumovirus*.

Pernet *et al.* (2014: 3) screened 44 Cameroonian bat serum samples for anti-NiV cross-neutralizing activity and found 21 (ca. 48 %) testing positive.

Pararubulavirus
Baker *et al.* (2012: 1348) describe two new Rubulaviruses: Achimota virus 1 (AchPV1) and Achimota virus 2 (AchPV2). They developed specific serological assays for these two viruses and found evidence of infection by both in *E. helvum* across sub-Saharan Africa and on islands in the Gulf of Guinea.

Baker *et al.* (2020: 2) reported a new virus (Achimota Pararubulavirus 3) from bats from Ghana.

Baker *et al.* (2011b: 855) indicate that a co-evolutionary relationship might exist between Chiroptera and *Paramyxoviridae*, based on an analysis of urine samples of *E. helvum* from Accra, Ghana.

Weiss *et al.* (2012a: suppl. 1) report on *Paramyxovirinae* sequences obtained from liver and urine samples from bats collected near Brazzaville (Republic of Congo), organs of one individual presented with two diverse paramyxovirus sequences.

From Zambia, Muleya *et al.* (2013: 611) report five new paramyxoviruses closely related to the genus *Henipavirus* and two related to the unclassified Bat paramyxoviruses from Ghana and Congo Brazzaville.

With the use of a seroneutralization assay, Pernet *et al.* (2014) found cross-neutralizing antibodies to Nipah virus in 48 % of sampled *E. helvum* bats collected in Cameroon.

Mbu'u *et al.* (2019: "1") mention the presence of Ghanaian bat henipavirus (designated Ghana virus - GhV) in Ghana.

Glennon *et al.* (2019: 1) followed a captive colony in Ghana for nine years and found that the observed dynamics of the henipavirus serology could only be explained by reinfection of the bats. They also found that the acute infectious period is extremely short (hours to days), and that immunity can last for about one to two years.

Orthorubulavirus
Achimota virus
Baker *et al.* (2012) describes two new paramyxoviruses isolated from *E. helvum*: Achimota virus 1 (AchPV1) and Achimota virus 2 (AchPV2).

Several rubulaviruses and rubula-related viruses were reported in several *E. helvum* individuals sampled from several African countries (Drexler *et al.*, 2012). Some of these sequences proved to

be closely related to human mumps virus and simian virus 5.

Kohl *et al.* (2018: 11) indicate that several yet unknown rubulaviruses might be present in these bats.

Markotter *et al.* (2020: 6) mentions Mumps virus-related viruses occurring in *Eidolon helvum*.

Pneumovirinae
Pneumovirus
Several individuals sampled in Ghana tested positive for a pneumovirus closely related to pneumonia virus of mice and grouped in a sister clade to human respiratory syncytial virus.

Parvoviridae
Canuti *et al.* (2011: 3) report a new virus (Eidolon-helvum-bat-Parvovirus-1 [Eh-BtPV-1]) from bats captured in Kumasi, Ghana. Baker *et al.* (2013a: 100) found 10 sequences, belonging to both the mammalian-infecting Parvovirinae (related to the genera *Erythrovirus* and *Betaparvovirus*) and the invertebrate-infecting Densovirinae.

Two out of 20 bats from Nigeria tested by Kamani *et al.* (2022b: 547) were positive for Eidolon helvum parvovirus 2 (BtPAR4), and 10 of these 20 bats were also positive for a novel virus (sabeidhel virus 1 - SBEHV-1) belonging to the genus *Amdoparvovirus*.

Peribunyaviridae
Orthobunyavirus
Fagre and Kading (2019: 4) report that Bunyamwera virus (BUNV) was isolated from this bat or that molecular and serologic evidence of it was found.

Picornaviridae
Eidolon-helvum-Picornavirus-1 contigs related to the genus *Kobuvirus* from 6 urine samples and one contig from a lung sample, and related to the genus *Enterovirus*, were reported by Baker *et al.* (2013a: 100).

In the faeces of Cameroonian bats, Yinda *et al.* (2017b: 3) identified 11 new picorna-like viruses of which some might represent new families [*] within the order Picornavirales: bat sapelovirus, bat kunsagivirus and bat crohivirus, bat iflavirus [Iflaviridae], bat posalivirus [Posa-like virus; *], bat fisalivirus [Fisa-like virus; *], bat cripavirus [Dicistroviridae], bat felisavirus [fesa-like virus; *], bat dicibavirus [bat dicistrovirus; *] and bat badiciviruses 1 and 2 [anagram from bat dicistrovirus; *].

Zeghbib *et al.* (2019: Suppl.) reported *Hepatovirus* from a bat from Ghana, and *Crohivirus, Kunsagivirus* and an unassigned (Sapelo-like) virus from Cameroon.

Polyomaviridae
Baker *et al.* (2013a: 100) assembled a sequence from a throat sample. Eckerle *et al.* (2014: 4) mention the presence of several, unassigned viruses of this family. Conrardy *et al.* (2014: 259) reported that one of the nine specimens tested in the Vihiga district (Kenya) tested positive for *Polyomavirus*. Tao *et al.* (2012) identified two novel species termed *Eidolon* PyV1 and 2, from Kenya in 2006.

Poxviridae
38 contigs related to *Molluscum contagiosum* [MC]), a human contagion, were reported by Baker *et al.* (2013a: 99). Baker and Murcia (2014: 1567) indicate that the bats do not show any clinical signs.

Reoviridae - Rotaviruses
Rotavirus
Esona *et al.* (2010: 1844) reported genetic characterization of a bat rotavirus (Bat/KE4852/07) detected in the faeces of *E. helvum*, which is a novel *Rotavirus A* species. This isolate contained a VP4 gene that probably originated from a human rotavirus, an NSP4 gene of likely human or animal rotavirus origin, and otherwise a unique genetic background requiring establishment of new genotypes for at least 7 genes (Esona *et al.*, 2010: 1845).

Sasaki *et al.* (2018: 104) compared genome segments of RVA from bats from Cameroon and Zambia and found these to be 97 to 99 % identical, suggesting that *E. helvum* is capable of dissimating RVA across long distances.

Simsek *et al.* (2021: 4) also found *Rotavirus A* in a bat from Gabon.

Orbivirus
Ife virus
In Nigeria 1971, the virus was isolated from the salivary glands, brain and blood (Kemp *et al.*, 1988). Also reported by de Jong *et al.* (2011: 11). Fagre *et al.* (2019: 2) indicated that this virus was also found in bats from Cameroon and the Central African Republic.

Retroviridae
Baker *et al.* (2013a: 100) reported on 292 sequences related to retroviridae, that were recovered from lung samples.

Rhabdoviridae

No rhabdoviruses were detected from 9 *E. helvum* bats sampled in Kenya Conrardy *et al.* (2014).

Lyssavirus - Rabies related viruses

2006 in Nigeria, Dzikwi *et al.* (2010: 269) tested 223 brains by direct fluorescent antibody (DFA) and mouse inoculation test (MIT) which tested negative for lyssavirus antigens. In Nigeria during June 2008, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluorescent antibody testing.

A literature review by Niu and McKee (2025: 235) revealed no seasonal pattern in shedding Lyssaviruses in *Eidolon helvum*.

Lagos bat virus (LBV)

Isolated in Nigeria (Boulger and Porterfield, 1958: 424 [1st detection]; Shope *et al.*, 1970; Kemp, 1975: 616; Hayman *et al.*, 2011a: 88; Fisher *et al.*, 2018: 242) and Senegal (Institute Pasteur, 1985; Hayman *et al.*, 2011a: 88). Antibodies detected in Ghana (Hayman *et al.*, 2008a); Kenya (Kuzmin *et al.*, 2008a; Kuzmin *et al.*, 2011b: 1467; Nadin-Davis *et al.*, 2011: 238), Annobón (Peel *et al.*, 2012: 3). In 2006, 105 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), where 24 tested positive (22.86 %) for neutralizing antibodies (Dzikwi *et al.*, 2010: 269). Hayman *et al.* (2010), who found an individual which tested positive for EBOV, also tested positive for LBV, but no antibodies against Mokola (MOKV).

Restif *et al.* (2012: 1091) report on how emerging infectious disease research can be undertaken when little prior knowledge exists, based on the occurrence of LBV in a population of *E. helvum* in Accra, Ghana.

Freuling *et al.* (2015: 44) point out that Lagos bat viruses belong to two phylogenetic lineages and that the presence of neutralizing antibodies might be missed if the test is performed with the most commonly used isolate.

Ameh *et al.* (2021: 1) examined 180 blood serum samples of Nigerian *E. helvum* specimens and found 133 (74 %) were able to neutralize as least one lineage of LBV: 36 % neutralized LBV-A, 49 % LBV-D, 45 % LBV-C and 24 % LBV-B. 75 % of the positive sera neutralized two or more lineages.

Kalemba *et al.* (2017: 409) reported that out of 18 bats examined from the DRC, six tested positive for lyssavirus neutralizing antibodies (LBV).

Hayman *et al.* (2018: 1) constructed a model to determine how host traits (e.g., maternally-derived antibodies, seasonal birthing) and viral traits (e.g., incubation periods) interact to allow LBV viruses to persist within bat populations.

Begeman *et al.* (2020: 1) experimentally infected *Eidolon helvum* specimens with different doses of the virus and found that the largest number of bats died in the group, which received the medium dose (10^{-1} $TCID_{50}$). Half of the bats inoculated with a higher dose ($10^{3.1}$ or $10^{4.1}$) survived, probably as a result of a stronger immune response to this higher dose.

Mokola virus (MOKV)

King *et al.* (1990: 168) found monoclonal antibodies for MOKV in bats from Nigeria and Senegal.

In 2006, 105 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), where 2 tested positive (1.9 %) for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Shimoni bat virus (SHIBV)

Kuzmin *et al.* (2011b: 1467) found 2 individuals testing seropositive on 9 animals tested between 2009 and 2010 in Kenya. Kalemba *et al.* (2017: 409) found four out of 19 bats examined from the DRC tested positive for SHIBV neutralizing antibodies.

Horton *et al.* (2014: Table S1) tested 8 Kenyan *E. helvum* specimens, but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Kumasi Rhabdovirus (KRV)

Kumasi ledantevirus

This new virus was detected by Binger *et al.* (2015: 4588) in the spleen and sera of *E. helvum* specimens from Kumasi in Ghana.

By means of Capture-Mark-Recapture (CMR) procedures, Hayman *et al.* (2012b: 2163) found that survival probabilities for lyssavirus seronegative and seropositive *Eidolon helvum* in Ghana were not significantly different.

King *et al.* (1990: 168) reported monoclonal antibodies for Duvenhage and Denmark bat virus from bats from Nigeria and Senegal.

Togaviridae

In their study covering Senegalese fruit bats, de Souza *et al.* (2024: 1490) reported the highest prevalence of Chikungunya virus (CHIKV) to occur in *Eidolon helvum* (15/82 = 18.3%).

???
Kemp (1975: 616 - 617) also mentions IbAn 67204 being isolated on 9 April 1971 from this species in Nigeria, and Herpes (YV6) virus in April 1971 and Dakar YV 177 in May 1971, both latter in specimens from Cameroon.

In their overview table, Maganga *et al.* (2014a: 8) report the following viruses were found on *E. helvum*: Lagos bat virus (LBV), Mokola virus, West Caucasian (WC) virus, Zaire Ebola virus (ZEBOV), Ife virus (Orbivirus), Hendra virus, Nipah virus (NPHV), Rubulavirus, Coronavirus, Rotavirus related, Simplexvirus, Parvovirus.

Peel *et al.* (2016) examined 2,827 bats from 9 countries over 8 years and focused on four viruses: Lagos bat virus (LBV), African henipaviruses, Achimota virus 1 (AchPV1) and Achimota virus 2 (AchPV2).

The genomic mining study by Cui and Wang (2015: 5793) revealed bornaviral elements built in the genome of *E. helvum.*

UTILISATION:
In Ghana *E. helvum* is a food source (Hayman *et al.*, 2008a). *Eidolon helvum* is the most heavily harvested bat for bushmeat in West and Central Africa, and this is believed to be a major factor in reported population declines (P. Racey *pers. comm.* in Mickleburgh *et al.*, 2008dc). Kamins *et al.* (2014) investigated the sociological characteristics of communities who interact with bats (specifically *E. helvum* in Ghana) to assess their attitudes and perceptions regarding bats and disease. Ohemeng *et al.* (2017: 184) indicated that local (Ghanaian) people preferred eating *E. helvum* over other bat species, because of their delicious taste.

In Benin, Dougnon *et al.* (2012: 85 - 86) found an average carcass weight of 89.27 ± 11.41 g (about 43 % of the body mass). The quality of the meat was evaluated (for 100g meat): Total mineral matter: 13.2 g, Lipids: 23.11 g, Protein: 56.8 g, Calcium: 55 mg, Sodium: 39 mg, Phosphore: 83 mg and Potassium: 75 mg, making it more fatty than *E. gambianus* meat (Lipids: 13.36 g). The authors suggest that the higher fat content is a result of the longer foraging distance covered by *E. helvum*.

See also threats section for additional information on utilization.

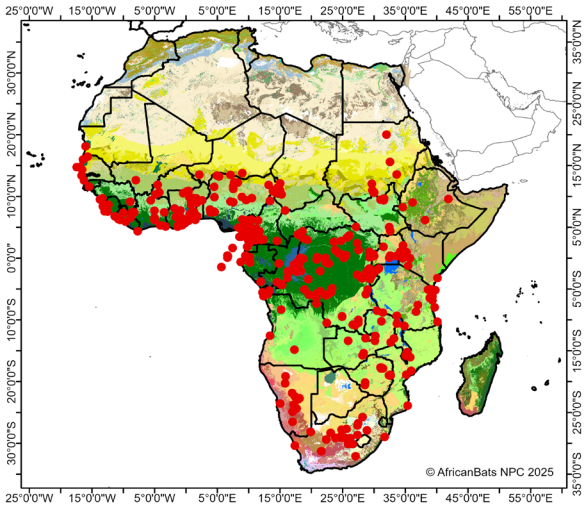

Figure 2. Distribution of *Eidolon helvum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Liberia.

Eidolon helvum annobonensis Juste, Ibáñez and Machordom, 2000

*2000. *Eidolon helvum annobonensis* Juste, Ibáñez and Machordom, Biol. J. Linn. Soc., 71: 373. Type locality: Equatorial Guinea: Annobón Island [01 24 N 05 38 E]. Holotype: EBD 17603M: ad ♀, skin and skull. Collected by: Javier Juste; collection date: 12 January 1987.
2022. *E[idolon].helvum annobonense:* Rainho, Meyer, Thorsteinsdóttir, Juste and Palmeirim, Current knowledge and conservation of the wild mammals of the Gulf of Guinea Oceanic Islands, 603. (Alternate Spelling).

TAXONOMY:
Rainho *et al.* (2022: 603) indicate that the animals from Annobón are significantly smaller than those from Príncipe and SãoTomé.

GENERAL DISTRIBUTION:
Native: Annobón.

POPULATION:
On Annobón, Peel *et al.* (2012: 3) reported colony sized of up to 1,500 animals.

Rainho *et al.* (2022: 603) [referring to Peel *et al.* (2017] mentions a density of 94 - 176 ind/km^2 for Annobón.

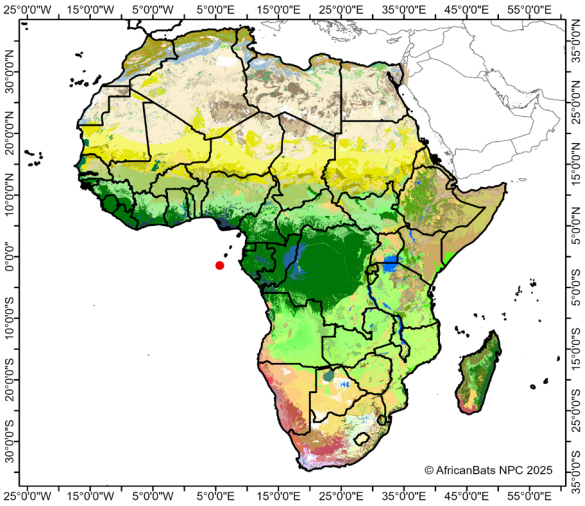

Figure 3. Distribution of *Eidolon helvum annobonensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Equatorial Guinea.

Eidolon helvum helvum (Kerr, 1792)

*1792. *Vespertilio vampyrus helvus* Kerr, in: Linnaeus, Animal Kingdom, 1 (1): xvii, 91. Publication date: February 1792. Type locality: Senegal: "Senegal". - Comments: Type locality fixed by Andersen (1907a: 504); see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1), Harrison and Bates (1991). Andersen (1912b: viii) indicates that the type was once in the Museum Leverianum, but is probably no longer in existence. - Etymology: From the Latin "helvus" (=dun-coloured), referring to the straw colour on their shoulders; the back, rump and hind limbs are normally various shades of brown (see DeFrees and Wilson, 1988: 4; Taylor, 2005). Lanza *et al.* (2015: 27) translate "helvus" to "dull-yellow".

1803. *Pteropus stramineus* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, 48. Type locality: Sudan: Sennaar [15 35 N 33 38 E, 425 m]. [Goto Description]. - Comments: Harrison (1964a: 44) refers to Sherborn to indicate that the 1803 paper has never been published. The next available date for this name is 1810: Ann. Mus. Nat. Hist., Paris, 15: 95.

Andersen (1912b: 12) mentions that the description in Geoffroy's 1813 paper was based on three specimens in the Paris Museum (nos 92 and 93 from an unknown locality, presented by Professor Fourcroy, and no 94 "de la collection du Stathouder") but these could not be traced by him. The description in the 1810 paper was based on two specimens, one believed to be from Timor (Péron and Lesueur), and the other without details (and possibly one of the cotypes of the 1803 description). Andersen (1912b: 12) also pointed out that "The 'Cat. Mamm. Mus. Nation. d'Hist. Nat.' (1803) was suppressed by Geoffroy himself, and the name *Pteropus stramineus* is therefore usually dated from his well-known paper in Ann. Mus. d'Hist. Nat. XV. (1810)."

Originally, the type locality was not specified, but it was subsequently fixed as Senaar by Koopman (1975: 357): see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1).

Harrison (1964a: 44) indicates that the type locality has been fixed by Temminck (1837b, Mon. Mamm. 2: 84), and Andersen (1912b: 12) mentions that the original type locality was "Timor" (based on the 1810 description), but that Temminck already corrected this to "Africa".

Jackson *et al.* (2021: 427) mention that no information is available on the whereabouts of the type specimens, but refer to illustrations by Charles-Alexandre Lesueur in the Muséum d'Histoire naturelle du Havre (Inv. no. 80035 - Fig. 159; two living animals and Inv. no. 80037 - Fig. 160; sketch of three animals).

1809. *Vespertilio caninus var. b* Goldfuss, Vergl. Naturbeschr., Säugethiere, 98. - Comments: Preoccupied by *V. caninus* Blumenbach, 1797: see Meester *et al.* (1986: 28).

1815. *Pteropus flavus* Illiger, Abh. Ak. Berlin, 90, 98. - Comments: *Nomen nudum* (see Andersen, 1912b: 809).

1861. *Pterocyon paleaceus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1861: 423. Type locality: Sudan: Sennaar [15 35 N 33 38 E, 425 m]. - Comments: Type locality originally as "Africa", but restricted to Senaar by Matschie (1899b: 62): see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1).

1861. *Pteropus mollipilosus* H. Allen, Proc. Acad. nat. Sci. Philad., 13 (11): 159. Publication date: prior to 28 December 1861. Type locality: Gabon: "Gabon". [Goto Description]. Holotype: ANSP MAM 1232/3324: ♂, skin and skull. Collected by: Paul Belloni Du Chaillu. - Comments: Originally mentioned as "Western Africa" by Allen (1861: 160), but restricted to Gabon (see Andersen, 1912b: 12). The type specimen was collected by Mr. Duchaillu, and is presumably in the Philadelphia Museum (see Andersen, 1912b: 12).

1865. *Pteropus palmarum* Heuglin, Leopoldina (Halle), 5 (3 & 4): 34. Publication date: June 1865. Type locality: Sudan: Sennaar [15 35 N 33 38 E, 425 m]. - Comments: Type locality originally as "Middle and Upper White Nile and between Senaar and Fazogli along the Blue Nile", but subsequently fixed as Senaar by Koopman (1975: 360): see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1). Andersen (1912b: 12) mentions that the type is probably no longer in existence.

1866. *Xantharpyia leucomelas* Fitzinger, in: Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 544. Type locality: Sudan: Kordofan province: Bahr-el-Azrak, Bahr-el-Abiad: Sennaar [15 35 N 33 38 E, 425 m]. - Comments: Type locality originally as "Upper Nile lands", but subsequently fixed to Senaar by Koopman (1975): see Meester *et al.* (1986: 28), DeFrees and Wilson (1988: 1). Andersen (1912b: 13) mentions that the specimen on which Fitzinger based himself is probably in the Munich Museum, and that a specimen belonging to the same series as the type is in the BM (1847.5.27.28; ad ♀; SK; purchased Parreys, from Sennaar).

1881. *Leiponyx büttikoferi* Jentink, Notes Leyden Mus., 3: 59, 60. Publication date: April 1881. Type locality: Liberia: St. Paul's river: Millsburg [06 33 N 10 38 W]. [Goto Description]. Holotype: RMNH MAM.27269: ad ♀, skull and alcoholic. Collected by: Johann Büttikofer and C.F. Sala; collection date: 18 October 1880. The RMNH catalog mentions two numbers: 27269.a (skull) and 27.269.b (wet specimen). - Comments: Type in RMNH.
1906. *R[oussettus (Xantharpyia)] buettikoferi:* Johnston, Liberia, Volume II: 690. - Comments: Bakwo Fils (2012: 690 - footnote) indicates that this name refers to the "very doubtfull *Leiponyx buettikoferi*" from Jentink. (Lapsus).
1906. *Roussettus buttikoferi:* Johnston, Liberia, Volume II: 690 - footnote. (Name Combination).
1953. *Pterocyon palaeceus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 44. - Comments: Lapsus: see Meester *et al.* (1986: 28). (Lapsus).
1975. *Pterocyon palaceus:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 357. - Comments: Lapsus: see Meester *et al.* (1986: 28). (Lapsus).
? *Eidolon helvum helvum:* (Current Combination).

GENERAL DISTRIBUTION:
See species, with the exception of SW Arabia.

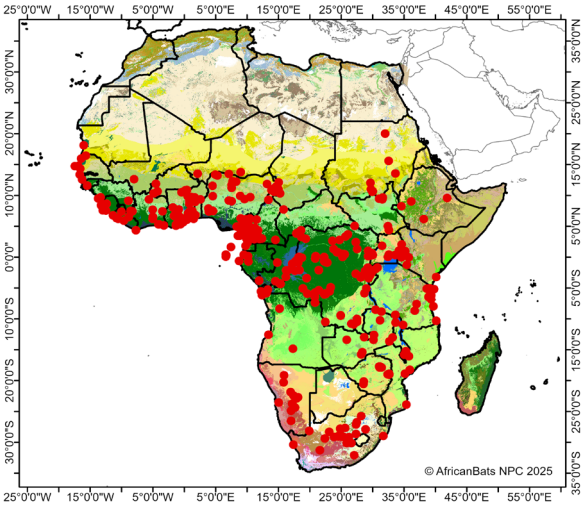

Figure 4. Distribution of *Eidolon helvum helvum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

†Subfamily Propottininae Butler, 1984

*1984. *Propottininae* Butler, Palaeovert., 14 (3): 118, 175. Publication date: 15 November 1984 [Goto Description]. - Comments: Recognized as a subfamily. (Current Combination).

TAXONOMY:
Currently recognized genera of Propottininae: *Propotto* Butler 1984.

†Genus ***Propotto*** Simpson, 1967

*1967. *Propotto* Simpson, Bull. Mus. comp. Zool., 136: 50 [Goto Description]. - Etymology: Meant to imply an antecedent but not necessarily ancestral relative of the potto. Although the valid generic name of the potto too is probably *Perodicticus*, *Potto* has also been used. The valid specific name of the potto is probably *Perodicticus potto* although several other names are also in use (Simpson, 1967). (Current Combination).

TAXONOMY:
Simpson (1967) originally described this as a new genus of primates, within the Lorisiforms. Walker (1969) re-examining the type, noted that it was not a Lorisiform, but rather a fruit bat.

Butler (1984: 178) believed it to be unlikely that *Propotto* is ancestral to any of the living Pteropodid genera.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
If *Archaeopteropus*, from the Oligocene of Italy, is removed from the Megachiroptera following Russell and Sigé (1970), *Propotto* becomes the oldest known member of the suborder (Butler, 1978).

†*Propotto leakeyi* Simpson, 1967

*1967. *Propotto leakeyi* Simpson, Bull. Mus. comp. Zool., 136: 50 [Goto Description]. - Etymology: Named for Dr. Louis Seymour Bazett Leakey, "in gratitude and admiration" (Simpson, 1967). (Current Combination).

TAXONOMY:
Simpson (1967) originally described this as a new species of primate, within the Lorisiforms. Upon re-examination of the type specimen, Walker (1969) noted that it was not a primate, but rather a fruit bat.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Miocene (Burdigalian - Brown *et al.*, 2019: Suppl.), Songhor (Simpson, 1967; Walker, 1969), probably Rusinga (Butler, 1978).

Subfamily Pteropodinae J. E. Gray, 1821

*1821. *Pteropodinae* J. E. Gray, London Med. Repos., 15: 299. (Current Combination).
1831. *Pteropodina* Bonaparte. - Comments: Introduced as tribe in the Vespertilionidae. Recognized as subtribe by Koopman and Jones (1970: 23) (see Jackson and Groves (2015: 236).
1835. *Pteropodae* Bonaparte, Iconogr. Fauna Ital. (Fascicolo 14 under *Dysopes cestonii*, second of four unnumbered pages). - Comments: Introduced as family (see Jackson and Groves, 2015: 236).
1866. *Epomophorina* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (v): 65. Publication date: May 1866. - Comments: Not included in Simmons (2005) since it was not proposed as family name, but as a subdivision within the Pteropodidiae (Simmons, pers. comm.).
1891. *Pteropodinae:* Flower and Lydekker, Mammals Living and Extinct, 650. - Comments: Proposed as subfamily. Originally included the genera *Epomophorus* E. Bennett, 1836; *Pteropus* Brisson, 1762; *Xantharpyia* J. Gray, 1843 [= *Rousettus* J. Gray, 1821]; *Boneia* Jentink, 1879 [= *Rousettus* J. Gray, 1821]; *Cynopterus* F. Cuvier, 1824 [1821-1825]; *Harpyia* Illiger, 1811 [= *Nyctimene* Borkhausen, 1797]; *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797]; *Pteralopex* Thomas, 1888 (see Jackson and Groves, 2015: 236).
1897. *Pteropinae* Trouessart, Cat. Mamm. Viv. Foss, 1: v, 77. - Comments: Bergmans (1997: 64) assigned it to Gray, 1821. Jackson and Groves (2015: 236) assigned it to Trouessart, 1897, but also mention a misspelling by Simpson (1945).
1912. *Cynopterinae* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, xix. Publication date: 23 March 1912. - Comments: Bergmans (1997: 69) considers this a valid subfamily in which he includes the genera *Cynopterus, Ptenochirus, Megaerops, Dyacopterus, Balionycteris, Chironax, Thoopterus, Sphaerias, Aethalops, Penthetor, Latidens, Alionycteris, Otopteropus, Haplonycteris*.
1970. *Cynopterini* Koopman and J.K. Jones Jr., Classification of Bats. - Comments: Not included in Simmons (2005) since it was not proposed as family name, but as a subdivision within the Pteropodidiae (Simmons, pers. comm.).

TAXONOMY:
Currently recognized genera of Pteropodinae: *Acerodon* Jourdan, 1837, *Desmalopex* Miller, 1907, *Macroglossus* F. Cuvier, 1824, *Melonycteris* Dobson, 1877, *Mirimiri* Helgen, 2005, *Neopteryx* Hayman, 1946, *Notopteris* Gray, 1859, *Pteralopex* Thomas, 1888, ***Pteropus*** Brisson, 1762, *Styloctenium* Matschie, 1899, *Syconycteris* Matschie, 1899.

TRIBE Pteropodini J. E. Gray, 1821

*1821. *Pteropodini* J. E. Gray, London Med. Repos., 15: 299.

TAXONOMY:
Includes the genera *Acerodon* Jourdan, 1837, *Neopteryx* Hayman, 1946, ***Pteropus*** Brisson, 1762 and *Styloctenium* Matschie, 1899.

Genus ***Pteropus*** Brisson, 1762

*1762. *Pteropus* Brisson, Regnum Animale, 2nd ed: 13, 53 [Goto Description]. - Comments: Type species: *Vespertilio vampirus niger* Kerr, 1792. Allen (1939a: 59), Corbet and Hill (1992: 57), and Simmons (2005) mention Brisson, 1762 [Règne Animal, ed. 2, pp. 13, 153] as author. This name was long time considered to be "not available" (see Hopwood, 1947). However, Opinion 1894 (ICZN, 1998: 64) ruled that the name (and authorship) is available. Not *Pteropus* Thunberg, 1815 (Insecta, Phasmatodea, Phylliidae - leaf insects); not *Pteropus* Jennings, 1828 (Aves, Gruiformes, Heliornithidae); not *Pteropus* Canestrini and Fanzago, 1878 (Arachnida, Mesostigmata, Spinturnicidae) (see Jackson and Groves, 2015: 238). - Etymology: From the Greek

"*πτερόπους*", meaning wing-footed, referring to the wing membrane which arises from the side of the back and the back of the second toe (see Palmer, 1904: 596; Jones and Kunz, 2000: 5). - Phonetics: te'-roh-poos. (Current Combination).

1799. *Spectrum* Lacépède, Tabl. Div. Subd. Orders Genres Mammifères, 15. - Comments: Type species: *Vespertilio vampirus* Linnaeus, 1758 (according to Miller and Wilson, 1997: 1; Jackson and Groves (2015: 238) or *Vespertilio vampirus niger* Kerr, 1792 (according to Andersen, 1912b: 61). Preoccupied by *Spectrum* Scopoli, 1777 [Lepidoptera, Sphingidae] (see Allen, 1939a: 59; Corbet and Hill, 1992: 57; Pavlinov *et al.*, 1995: 62; Miller and Wilson, 1997: 1; Jones and Kunz, 2000: 1). Not *Spectrum* Stoll, 1787 (Insecta, Orthoptera, Phasmatidae) (see Jackson and Groves (2015: 238). - Etymology: From the Latin "*spectrum*", meaning apparition or specter (see Palmer, 1904: 638).

1866. *Eunycteris* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (v): 64. Publication date: May 1866. - Comments: Type species: *Pteropus phaiops* Temminck, 1837 (=*Pteropus melanopogon* Peters, 1867).

1871. *Pselaphon* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 110. Publication date: 14 January 1871. - Comments: Type species: *Pteropus pselaphon* Layard, 1829, by monotypy. Not *Pselaphus* [= *Pselaphon*] Herbst, 1792 (Insecta, Coleoptera, Psephalidae) (Jackson and Groves, 2015: 238). - Etymology: From the Greek "*ψηλαφάω*", meaning to grope about (see Palmer, 1904: 588).

1899. *Sericonycteris* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 6, 30. - Comments: Type species: *Pteropus rubricollis* E. Geoffroy Saint-Hilaire, 1810 (= *Pteropus subniger* Kerr, 1792), by original designation (according to Miller and Wilson, 1997: 1) or subsequent designation (Palmer, 1904: 629; according to Jackson and Groves, 2015: 238). Originally described as a subgenus of *Pteropus*. Matschie dated his introduction on 14 May 1899. - Etymology: From the Greek "*σηρικόν*", meaning silk and "*νυκτερίς*", meaning bat (see Palmer, 1904: 627).

2011. *Pterocarpus* Mishra, Rout and Panda, Afr. J. Pharm. Pharmacol., 5 (1): 6. Publication date: January 2011. - Comments: Not of Jacquin, 1763, which is a pantropical genus of trees in the family Fabaceae (see http://en.wikipedia.org/wiki/Pterocarpus). (Lapsus).

TAXONOMY:

See Bergmans (1991) and Simmons (2005: 334). The International Commission on Zoological Nomenclature ruled in favour of rejecting Brisson (1762) but conserved several of the generic names including *Pteropus* (Opinion 1894; ICZN, 1998). Formerly included *arquatus* and *leucotis* which were transferred to *Acerodon* by Musser et al. (1982a).

O'Brien *et al.* (2009) examined the western Indian Ocean member of the genus *Pteropus*, based on three mitochondrial genes – cytochrome *b*, 12S rRNA, and a portion of the control region. The combined data set indicates the lack of reciprocal monophyly in western Indian Ocean *Pteropus*. With the exception of *P. livingstonii* and *P. voeltzkowi*, the other regional taxa demonstrate little genetic differentiation. The resulting poytomy indicates rapid and presumably recent divergence. Almeida *et al.* (2014: 83) studied the cytochrome *b* and the 12S rRNA mitochondrial genes sequences for all *Pteropus* species and some additional sequences of the nuclear RAG1, vWF, and BRCA1 genes for a subsample of taxa. Their conclusions were that the genus as a whole is monophyletic (originating in the Miocene), but also that the monophyly of the traditional species-groups could not be substantiated. They subdivided the genus in 13 species groups, where *livingstonii* and *voeltzkowi* are the only members of the "*livingstonii*" group. *aldabrensis, niger, rodricensis, rufus*, and *seychellensis* are part of the "*vampyrus*" group, whereas the extinct *subniger* could not be tested and is tentatively placed in an "*incertae sedis*" group.

Almeida *et al.* (2025: Suppl.) recognized two *Pteropus* species groups occurring in Africa: *livingstonii* (*P. livingstonii, P. voeltzkowi*), *vampyrus* (*P. rodricensis, P. rufus, P. aldabrensis, P; comorensis, P. niger, P. seychellensis*).

Currently (Simmons and Cirranello, 2024a) recognized species of *Pteropus*: *admiralitatum* Thomas, 1894 – Solomon Isls; Admiralty Isls, New Britain, and Tabar Isl (Bismarck Arch.) (Simmons, 2005: 334); ***aldabrensis*** True, 1893; *alecto* Temminck, 1837 – Sulawesi, Saleyer Isl, Lombok, Bawean Isl, Kangean Isls, Sumba Isl, and Savu Isl (Indonesia); north and east Australia; south New Guinea (Simmons, 2005: 335); *allenorum* Helgen, Helgen and Wilson, 2009; *anetianus* (Gray, 1870) – Vanuatu including Banks Isls (Simmons, 2005: 335); *aruensis* Peters, 1867 – Aru Isls (Indonesia) (Simmons, 2005: 335); *brunneus* Dobson, 1878 – Percy Isl., Queensland (Australia) (Simmons, 2005: 335); *caniceps* Gray, 1870 – Halmahera (Indonesia) (Simmons, 2005: 335); *capistratus* Peters, 1876 – Bismarch Arch. (Papua New Guinea) (Simmons, 2005: 336); *chrysoproctus* Temminck, 1837 – Ambon, Buru, Seram, and small islands east of Seram (Indonesia) (Simmons, 2005: 336); *cognatus* K. Andersen, 1908 – Makira and Uki Ni Masi Isls (Solomon Isls) (Simmons, 2005: 336); *conspicillatus* Gould, 1850 – north Moluccas (Indonesia), New Guinea and West Papuan Isls (Raja Ampat Isl, off northwest coast of New Guinea), northeast Queensland (Australia) (Simmons, 2005: 336); *coxi* Helgen, Helgen and Wilson, 2009; *dasymallus* Temminck, 1825 – Taiwan, Ryuku Isls, and extreme southern Kyushu (Japan), Batan, Dalupiri, and Fuga Isls

(Philippines) (Simmons, 2005: 337); *ennisae* Flannery and White, 1991 – New Ireland; *faunulus* Miller, 1902 – Nicobar Isls (India) (Simmons, 2005: 337); *fundatus* Felten and Kock, 1972 – Banks Isls (Vanuatu) (Simmons, 2005: 337); *gilliardorum* Van Deusen, 1969 – New Britain Isl. and New Ireland (Bismarck Arch.); *griseus* (E. Geoffroy Saint Hilaire, 1810) – Timor, Samao Isl, Dyampea Isl, Bonerato Isl, Saleyer Isl, Paternoster Isls, Pelang Isl, Sulawesi, and Banda Isls (Indonesia) (Simmons, 2005: 337); *howensis* Troughton, 1931 – Ontong Java Isl (Solomon Isls) (Simmons, 2005: 338); *hypomelanus* Temminck, 1853 – Andaman and Maldive Isls, New Guinea through Indonesia to Vietnam and Thailand, and adjacent islands, Philippines (Simmons, 2005: 338); *intermedius* K. Andersen, 1908 – southern Burma and western Thailand (Simmons, 2005: 338); *keyensis* Peters, 1867 – Kai Isls (Indonesia) (Simmons, 2005: 339); ***livingstonii*** Gray, 1866; *lombocensis* Dobson, 1878 – Lombok, Sumbawa, Komodo, Flores, Lembata, Pantar, Alor and Timor Isls (Indonesia) (Simmons, 2005: 339); *lylei* K. Andersen, 1908 – Thailand, Vietnam, Cambodia (Simmons, 2005: 339); *macrotis* Peters, 1867 – New Guinea, Aru Isls (Indonesia), Boigu Isl (Australia) (Simmons, 2005: 340); *mahaganus* Sanborn, 1931 – Bougainville Isl (Papua New Guinea), Ysabel Isl and Choiseul Isl (Solomon Isls) (Simmons, 2005: 340); *mariannus* Desmarest, 1822; *medius* Temminck, 1825 – Maldive Islands, India (incl. Anadaman Islands), Sri Lanka, Pakistan, Bangladesh, Burma (= Myanmar), Nepal, China (incl. Tsinghai [= ?Qinghai]): *melanopogon* Peters, 1867 – Amboina, Buru, Seram, Banda Isls, Yamdena (= Timor Laut), and adjacent islands (Indonesia) (Simmons, 2005: 340); *melanotus* Blyth, 1863 – Nicobar and Andaman Isls (India), Engano Isl and Nias Isl (Indonesia), Christmas Isl. (Simmons, 2005: 340); *molossinus* Temminck, 1853 – Pohnpei (= Ponape) and possibly Mortlock Isls (Caroline Isls, Micronesia) (Simmons, 2005: 341); *neohibernicus* Peters, 1876 – Bismarck Arch. and Admiralty Isls (Papua New Guinea), New Guinea, Misool and Gebi Isls, Gag Isl (Simmons, 2005: 341); ***niger*** (Kerr, 1792); *nitendiensis* Sanborn, 1930 – Nendö and Tömotu Neo (in the Santa Cruz Isls, Solomon Isls) (Simmons, 2005: 341); *ocularis* Peters, 1867 – Seram and Buru (Indonesia) (Simmons, 2005: 341); *ornatus* Gray, 1870 – New Caledonia and Loyalty Isls (Simmons, 2005: 342); *pelagicus* Kittlitz, 1836; *pelewensis* K. Andersen, 1908 – Pelew Isls (Micronesia) (Simmons, 2005: 342); *personatus* Temminck, 1825 – North Molucca Isls (Halmahera and Obi Isl groups), and Gag (Simmons, 2005: 342); *pilosus* K. Andersen, 1908 – Pelew Isls (Micronesia) (Simmons, 2005: 342); *pohlei* Stein, 1933 – Yapen, Biak-Spiori, Numfoor, and Rani Isls (off northwestern New Guinea) (Simmons, 2005: 342); *poliocephalus* Temminck, 1825 – Eastern Australia, from southern Queensland to Victoria (Simmons, 2005: 342); *pselaphon* Lay, 1829 – Bonin and Volcano Isls (Japan) (Simmons, 2005: 342); *pumilus* Miller, 1911 – Philippines (except Palawan region), Talaud Isls (Indonesia) (Simmons, 2005: 343); *rayneri* Gray, 1870 – Bougainville and Buka Isls (Papua New Guinea), Solomon Isls (Simmons, 2005: 343); *rennelli* Troughton, 1929 – Rennell Isl (Solomon Isls) (Simmons, 2005: 343); ***rodricensis*** Dobson, 1878; ***rufus*** E. Geoffroy Saint-Hilaire, 1803; *samoensis* Peale, 1848 – Fiji Isls, Samoan Isls (Simmons, 2005: 344); *scapulatus* Peters, 1862 – Australia, southern New Guinea, accidental on New Zealand (Simmons, 2005: 344); ***seychellensis*** A. Milne-Edwards, 1877; *speciosus* K. Andersen, 1908 – Philippines, Besar and Mata Siri (Java Sea), Talaud Isls (Simmons, 2005: 344); ***subniger*** (Kerr, 1792); *temminckii* Peters, 1867 – Buru, Ambon, Seram (Indonesia), nearby small islands, perhaps Timor Isl (Indonesia) (Simmons, 2005: 345); *tokudae* Tate, 1934 – Guam (Mariana Isls, USA) (Simmons, 2005: 345); *tonganus* Quoy and Gaimard, 1830 – Karkar Isl (off northeastern New Guinea) and Rennell Isl (Solomon Isls), south to New Caledonia, east to Cook Isls (Simmons, 2005: 345); *tuberculatus* Peters, 1869 – Vanikoro Isl (Santa Cruz Isls, Solomon Isls) (Simmons, 2005: 345); *ualanus* Peters, 1883 – Kosrae (Micronesia) (Simmons, 2005: 345); *vampyrus* (Linnaeus, 1758) – Vietnam, Burum, Malay Peninsula, Borneo, Philippines, Sumatra, Java, and Lesser Sunda Isls, adjacent small islands including Anak Krakatau (Simmons, 2005: 346); *vetula* Jouan, 1863 – New Caledonia (Simmons, 2005: 346); ***voeltzkowi*** Matschie, 1909; *woodfordi* Thomas, 1888 – New Georgia group, Russell and Florida Isls, Guadalcanal, Malaita (Solomon Isls) (Simmons, 2005: 346).

Common Names:

Czech: praví kaloni, upírové. Dutch: Kalongs. English: Flying-foxes, Flying Foxes. French: Renards volants, Roussettes géantes. German: Flugfüchse.

Palaeontological or archaeological records:

The origin of *Pteropus* can be found some 7 - 8 mya, and the current distribution of the genus was achieved over the past 2 million years (Almeida *et al.*, 2025: 2).

General distribution:

McNab (2009: 156) indicates that *Pteropus* "is primarily an island taxon, with 55 species (of the 57 species or 96.5 %) having some or all of their distribution on islands". Furthermore, McNab

(2009: 158) states that the distributional pattern of *Pteropus* on islands is extremely variable, with some species being limited to small islands (e.g., *P. voeltzkowi* on Pemba, *P. livingstonii* on Anjouan and perhaps on Mohéli in the Comoros, *P. rodricensis* on Rodrigues, and *P. niger* on Mauritius, and other (Asian) species on islands that are hundreds or even thousands of kilometers apart.

BIOGEOGRAPHY:
Kingdon (1989) suggested that *Pteropus* doesn't occur in central parts of the continent since it might depend on seawater as source of salts. This is rejected by McNab and Armstrong (2001: 710) as this would not explain why there are no representatives of this genus in the African coastal areas.

Almeida *et al.* (2025: Suppl.) [referring to Tsang *et al.* (2019)] indicate that the genus originated in Wallacea, and subsequently expanded to all other areas.

PARASITES:
Dick *et al.* (2023: 74) mentioned that nycteribiid fly *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817) has been found on *Pteropus* sp. from the Comoros.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Ethiopia, Madagascar, Mauritius, Réunion, Seychelles, South Sudan, Tanzania.

Pteropus aldabrensis True, 1893

*1893. *Pteropus aldabrensis* True, Proc. U.S. Natl. Mus., 16 (948): 533. Publication date: 14 July 1893. Type locality: Seychelles: Aldabra Island. Syntype: USNM 20984: ♂, skin and skull. Collected by: Dr. William Louis Abbott; collection date: 26 September 1892. Syntype: USNM 20985: ♂, skin and skull. Collected by: Dr. William Louis Abbott; collection date: 1892. - Comments: USNM 20984/36053 + 20985/36054: "cotypes" (syntypes); ad ♂♂, SS; coll. W.L. Abbott, 26 September 1892 and 5 October 1892: see Poole and Schantz (1942: 139), who also indicate "No type is specified in the original description, but these two specimens are mentioned by number and are therefore regarded as cotypes." Catalogued 30 June 1893: see Lyon and Osgood (1909: 256). Fisher and Ludwig (2015: 52) mention that *Proc. U.S. Natl. Mus.* **16**: 1, (published on 14 July 1893) was a "Preprint" of *Proc. U.S. Natl. Mus.* **16**: 533, which was published on 21 October 1893. (Current Combination).

1971. *Pteropus seychellensis aldabrensis:* Hill, Phil. Trans. Roy. Soc. Lond., B 260: 574. (Name Combination).

? *[Pteropus seychellensis] aldabrabensis:* Honacki, Kinman and Koeppl, Mammal species of the world: A taxonomic and geographic reference, 124. - Comments: Honacki *et al.* (1982: 124) mention "*aldabrabensis*" in the list of included taxa, and mention "*P. aldabrensis* (sic)." in the list with ISIS numbers. Bergmans (1991: 154) states it isn't clear to him why Honacki *et al.* (1982) changed the spelling. (Emendation).

TAXONOMY:
Bergmans (1991) showed that *P. aldabrensis* differs strongly from *P. seychellensis*, a view followed by Simmons (2005: 334).

O'Brien *et al.* (2009) suggested that *P. aldabrensis*, *P. rufus*, *P. niger* and *P. seychellensis* (including *comorensis*) should be considered geographical forms of a single species *P. giganteus* (Brünnich, 1782) from the Indian subcontinent, Maldives and Andaman archipelagos.

O'Brien (2011: 261) indicates that the last complete inundation of the Alabra atoll occurred some 125,000 years ago, and that the diversification of *Pteropus* in the area is therefore of recent age.

Almeida *et al.* (2014: 83) places this in the '*vampyrus*' group.

COMMON NAMES:
Castilian (Spain): Zorro volador de Aldabra. Czech: kaloň aldabránský. English: Aldabra Flying Fox, Aldabra Flying-fox. French: Renard volant d'Aldabra. German: Aldabra-Flugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN B1ab(i,ii,iii)+2ab(i,ii,iii); D ver 3.1 (2001)) because 100% of its global population is known from only a single location and population (Aldabra Atoll). It has an extent of occurrence (EOO) of 374 km^2 and an even smaller area of occupancy (the Aldabra Atoll has a land area of 155.4 km^2). The number of mature individuals is estimated to be 200-250 bats (assuming a stable population since 1968). The average height above sea level on the atoll is 8 meters. The increasing impacts and risk of climate change, from stochastic events due to increased frequency of major storms and the loss, shifting habitats and rainfall patterns, and degradation of important roost and foraging habitat due to sea-level rise is projected to increase over the next 16.2 years (two generations; generation length = 8.1 years, Pacifici *et al.*, 2013).

Critically Endangered - C2a(ii): see Jones *et al.* (2009b: 506). Conenna *et al.* (2017: Suppl.) mention its status as Vulnerable (VU).

Assessment History
Global
2019: EN B1ab(i,ii,iii)+2ab(i,ii,iii); D ver 3.1 (2001) (Waldien and Bunbury, 2020). 2008: VU D2 ver 3.1 (2001) (Mickleburgh *et al.*, 2008dh; IUCN, 2009). 2004: CR C2a(i) ver 3.1 (2001) (Mickleburgh *et al.*, 2004cv; IUCN, 2004).

Regional
None known.

Legal stutus
CITES - Appendix II.

MAJOR THREATS:
The limited historic population data, and with no current population data, the global population is assumed to be relatively stable since 1968 based on Hutson (2004a evaluation. However, as it is a range-restricted species, it is considered to be especially vulnerable to threats emerging from climate change including stronger tropical cyclones as well as sea-level rise. Climate change is projected to result in the degradation and loss of the limited foraging and roosting habitat available to the bats (Mickleburgh *et al.*, 1992; Hutson, 2004a; Justin Gerlach *pers. comm.*, 2008; Mickleburgh *et al.*, 2008dh; IUCN, 2009). As of 2019, research is underway to model land area and habitat changes under different scenarios of sea level rise (Waldien and Bunbury, 2020).

Waldien and Bunbury (2020) report Invasive species have been and continue to be a significant threat to island habitats and suggest research and control measures are needed to mitigate negative impacts.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dh) [in IUCN (2009)] report that although the species is not directly protected (Tony Hutson *pers. comm.,* 2008), the Aldabra Atoll is a highly protected UNESCO World Heritage site and a Special Reserve under the Seychelles National Parks and Nature Conservancy Act (Mickleburgh *et al.*, 1992; Hutson, 2004a: 128). There is a distinct need for additional research into the total population number of this restricted range species and to monitor any changes in abundance (Hutson, 2004a: 128).

Currently, *Pteropus aldabrensis* is not directly protected in the Republic of Seychelles. However, it is listed on CITES Appendix II. Further, Aldabra Atoll is a highly protected UNESCO World Heritage site and a Special Reserve under the Seychelles National Parks and Nature Conservancy Act (Mickleburgh *et al.*, 1992; Hutson, 2004a). It is effectively managed by the Seychelles Islands Foundation that has a number of conservation initiatives underway. Currently, there are no initiatives underway to specifically and directly address the needs of *P. aldabrensis*, although some initiatives likely provide both direct and indirect benefits. Consideration should be given to provide the species legal protection. Fundamental research is needed on the species ecology, how the bats use the different islands/habitats within Aldabra Atoll, its life history, population status, effective population size through research into the species genetics, trends through time. A robust yet viable monitoring program is needed to provide important management guidance and to ensure the population is sustainable. Research is also needed into the impacts of invasive species and implications from climate change and sea level rise (Waldien and Bunbury, 2020).

GENERAL DISTRIBUTION:
Pteropus aldabrensis is endemic to the Aldabra Atoll (approximately 150 km^2) in the Seychelles. Bats have been recorded from all main islands and have been observed flying between islands of the atoll (Hutson, 2004a; von Brandis, 2004).

Native: Seychelles [Aldabra].

BIOGEOGRAPHY:
See O'Brien *et al.* (2009) for further details.

MOLECULAR BIOLOGY:
Genetics
See O'Brien *et al.* (2009) and Almeida *et al.* (2014).

ROOST:
Racey and Nicoll (1984) [in O'Brien (2011: 262)] indicate that *P. aldabrensis* roosts in coconut palms, figs and *Sideroxylon inerme*.

DIET:
Hutson (2004a: 127) mentions that fruits of the following plants are eaten: *Ficus lutea, F. rubra* (as *F. avi-avi*) and *F. reflexa, Calophyllum inophyllum, Terminalia catappa, Mystroxylon aethiopicum*, and also flowers of *Cocos nucifera* and *Agave sisalana*. Roberts and Seabrook (1989) [in Courts (1998: 188)] report that *P. seychellensis aldabrensis* licked coccoids (*Icerya seychellarum*) from the leaves of infested *Ficus* trees, probably to supplement their diets.

POPULATION:
Structure and Density
The historic global population is reported to consist of only a few hundred animals (Cheke and Dahl, 1981; Carroll, 1985). No major colonies

were located in 1968 with the largest roosting group on the small lagoon islet of Ile Michel that was probably well under 100 animals Hutson, 2004a). There were fewer than 250 adult animals estimated in 1968 and the majority of the population was likely located on the relatively little explored Malabar Island (26 km^2) Hutson (2004a). In 1968 the largest group of fewer than 100 bats were dispersed among coconut palms on the small lagoon islet of Ile Michel (A.M. Hutson, pers. obs. in Waldien and Bunbury (2020)). von Brandis (2004) reports that groups of 40-50 bats have been recorded in Casuarina trees, with the largest group of more than 100 animals reported at the eastern end of Malabar Island in 1995. Conrad Savy (*pers. comm.,* 2008) indicates that the bats were commonly seen in good numbers during 2001 (Mickleburgh *et al.*, 2008dh; IUCN, 2009). A quality estimate of the global population is lacking as past efforts reflect anecdotes from larger roosts across several years and do not account for the tendency of the bats to move among roosts and disperse into smaller groups (Waldien and Bunbury, 2020). A robust, repeatable, and sustainable monitoring program is needed to inform conservation and management of this range-restricted species. Given the paucity of historic population data and no current estimates, this assessment assumes a stable global population of 200-250 adult animals since 1968 based on Hutson (2004a) evaluation with a projected future decline due to habitat loss associated with sea level rise and other climate change impacts.

Trend
2019: Stable (Waldien and Bunbury, 2020).

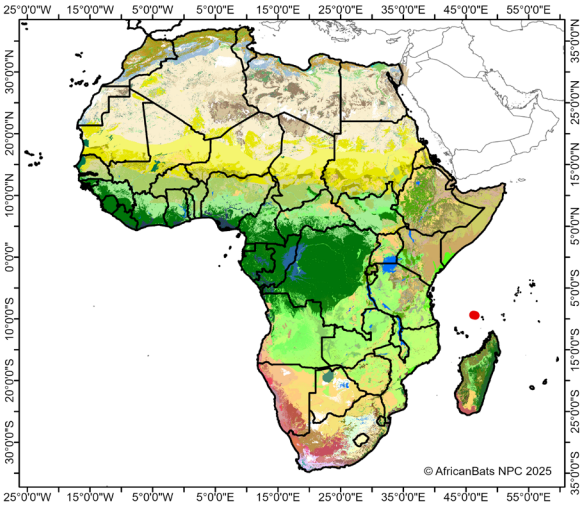

Figure 5. Distribution of *Pteropus aldabrensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Seychelles.

Pteropus livingstonii J. E. Gray, 1866

*1866. *Pteropus livingstonii* J. E. Gray, Proc. zool. Soc. Lond., 1866, I: 66. Publication date: May 1866. Type locality: Comoros: Anjouan Island. Holotype: NHMUK 1863.12.11.2: ad, skin and skull. Collected by: Dr. Livingstone. Presented/Donated by: Earl Russell. See Andersen (1912b: 250). (Current Combination).
1971. *Pteropus livingstonei:* Hayman and Hill, Mammals of Africa: Chiroptera, 10. (Lapsus).

TAXONOMY:
See Bergmans (1991), Simmons (2005: 339) and Smith and Leslie (2006: 1).

P. livingstonii together with *P. voeltzkowi* form the most distinct and ancient lineage of the western Indian Ocean *Pteropus* spp. (O'Brien *et al.*, 2009). The phylogenetic analyses performed by Chan *et al.* (2011: 7) suggest that both are sister species. This is supported by Almeida *et al.* (2014), who places this in the '*livingstoni*' group.

COMMON NAMES:
Castilian (Spain): Zorro Volador De Livingston. Czech: kaloň komorský. Dutch: Zwarte Komorenkalong, Schoudervlekkalong. English: Comoro Black Flying Fox, Comoro Flying Fox, Black Flying- fox, Livingstone's Flying Fox, Comores Flying Fox. French: Renard volant des Comores, Renard volant noir, la roussette de Livingstone. German: Livingstones Flugfuchs.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
No fossils are known (Smith and Leslie, 2006: 2).

CONSERVATION STATUS:
Global Justification
Sewall *et al.* (2016) provided the following justification for listing as Critically Endangered because of a serious population decline suspected from catastrophic habitat decline caused by cutting of trees for fuelwood and construction, and by conversion of all but the steepest upland areas to agricultural use; extensive declines in area of occupancy, extent of occurrence and quality of habitat.

True population change in *P. livingstonii* is unknown and data on habitat change over time is limited. However, the species qualifies for CR under the A2c criterion because best estimates indicate habitat loss has exceeded 80% over the past three generations (estimated generation length: 8.1 years/generation), because remaining

habitat is increasingly degraded and fragmented, and because declines in the extent and quality of habitat are continuing.

P. livingstonii also meets the Endangered threshold under a second criterion, B1. The geographic range is small, such that the current extent of occurrence is estimated to be 1,856 km^2, less than the EN threshold of 5,000 km^2 under criterion B1. In addition, the habitat is severely fragmented, and there have been clear, continuing, observed declines in extent of occurrence, area of occupancy, habitat quality, and number of locations. Declines in number of mature individuals are also inferred from these declines in habitat. Therefore, this species would also be listed as EN under criterion B1ab(i, ii, iii, iv, v).

Daniel *et al.* (2016: 742) supports the species listing as "Critically Endangered".

Assessment History
Global
2016: CE A2c ver 3.1 (2001) (Sewall *et al.*, 2016). 2008: EN A2c; B1ab(iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2008t; IUCN, 2009). 2004: CR A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004p; IUCN, 2004). 2002: CR A1c+2cd, B1+2c, C2a (Mickleburgh *et al.*, 2002a: 22). 1998: EN A1c+2cd, B1+2c, C2a (Trewhella *et al.*, 1998: 32). 1996: CR (Baillie and Groombridge, 1996). 1994: EN (Groombridge, 1994). 1993: EN (World Conservation Monitoring Centre, 1993). 1990: EN (IUCN, 1990). 1988: EN (IUCN Conservation Monitoring Centre, 1988).

Regional
None known.

Legal Status
CITES - Appendix II, see Smith and Leslie (2006: 4) for discussion.

MAJOR THREATS:
The species is threatened by the continuing degradation of its forest habitat by conversion of land to agricultural use, especially the use of lowland areas for export crops (such as cloves). In degraded forest the species is outcompeted by the bat *Pteropus seychellensis* (Mickleburgh *et al.*, 2002a). Tree felling has additionally destroyed a number of roosts (Trewhella *et al.*, 2005). There is also increased disturbance because of human population growth, however, the species is not hunted for food (Trewhella *et al.*, 2005). The small remaining population is additionally potentially threatened in its restricted range by the effects of tropical cyclones (Mickleburgh *et al.*, 2008t; IUCN, 2009). Since Anonymus (2000: 30) points out that this species generally roosts and feeds in native trees, the destruction of these forests can have a devastating effect, especially since *P. livingstonii* uses different tree species for food during different seasons.

Sagot and Chaverri (2015: 1670) mention roost loss or disturbance, and habitat degradation or loss as major threats for this species. Daniel *et al.* (2016: 743) indicate that the estimated forest loss between 2000 and 2010 was 9.3 % per annum.

Pteropus livingstonii is threatened principally by the continuing degradation, fragmentation, and loss of its forest habitat (Sewall *et al.*, 2007). Over the last few decades, the Comoros have undergone a sustained, rapid deforestation, resulting in the loss of nearly all its native forests. Data quality on rates of habitat loss is poor (FAO, 2010), but best estimates are that during the past 20 years alone, the country has lost 75% of its remaining forests, the fastest rate of any country in the world (UNDP, 2013). This habitat change is caused by cutting of trees for fuelwood and construction, and by conversion of all but the steepest upland areas to agricultural use (for subsistence agriculture and for export crops such as cloves) (Weightman, 1987; Sewall *et al.*, 2007; Sewall *et al.*, 2011b; Doulton *et al.*, 2015). With continuing habitat change, this species has retreated to higher elevations (above 450 m asl on Anjouan and above 250 m asl on Mohéli). Even above these elevations, forest habitat on both islands, and especially Anjouan, has undergone extensive and continuing habitat degradation, fragmentation, and loss (Sewall *et al.*, 2007, Sewall *et al.*, 2011a; R. Young *unpublished*), leaving large areas increasingly unsuitable for this species. Human pressures on native forests are expected to continue, as the growth rate of the human population remains high, with an annual increase of 2.5% (UNDP, 2013).

Roost sites represent critical habitat for *Pteropus livingstonii* (Granek, 2002; Sewall *et al.*, 2007; Sewall *et al.*, 2011b), yet tree felling has destroyed a number of roosts, leading to displacement of bats to less impacted areas, often at higher elevations (Trewhella *et al.*, 2005; Sewall *et al.*, 2011b). Of 23 roosts occupied in 2007 (Sewall *et al.*, 2007), three roosts have been abandoned due to clear felling of forest in the past five years, and only one new but very small roost (15 bats) has been uncovered despite extensive searching effort (Daniel *et al. in prep.*). This new roost was found in a patch of degraded forest at 1050 m, the first to be found at such a

high elevation and is believed to have been established very recently. On Anjouan, forest clearance, underplanting or significant soil erosion following deforestation upslope of the roost was found within 50 m of all but one of the 16 occupied roosts (Daniel *et al., in prep.*). Further, the replacement of native forests with agricultural lands on Anjouan and Mohéli may render formerly inaccessible roost sites on Anjouan and Mohéli more accessible, possibly exposing roosts to increased levels of human disturbance. Finally, the loss of native forests has resulted in impermanence or complete drying of nearly all rivers on Anjouan and many on Mohéli (Louette, 2004; Fernandez Astudillo, 2012). As *P. livingstonii* roosts are often associated with rivers and other humid environments, a factor which may be related to their thermal sensitivity (Granek, 2002), this loss of rivers may additionally affect the quality of roosting habitat.

Mandl *et al.* (2019: 257) indicate that only three of the 15 known roost sites on Anjouan are not under immediate threat from agricultural activities and timber logging.

There is no evidence that the species is hunted for food (Trewhella *et al.*, 2005), a key factor affecting other fruit bat species (Mickleburgh *et al.*, 1992). This may be due in part to cultural taboos among the majority of the population that surround consumption of fruit bats. However, the apparent lack of hunting may also be due in part to *P. livingstonii*'s habit of roosting in inaccessible areas remote from towns; some limited hunting of the other two fruit bat species in the Comoros has been occasionally recorded (Sewall *et al.*, 2003, B.J. Sewall, *pers. obs.*). It is unclear if the increased access to formerly inaccessible roost areas could expose the bats to any hunting pressure in the future, but any such hunting would likely first affect *P. livingstonii* congener, *P. seychellensis comorensis*, which sometimes roosts and forages in visible locations in or near towns.

On the other hand, Walsh (2007: 100) reported that *P. livingstonii* is reported to be catapulted by young boys for sport and food. He also suggests (p. 103) that the eating of bats on the Comoros is a recent introduction by Malagy speakers.

The mean surface temperature of the Comoros is thought to have increased about 1° C since 1900 and is expected to increase by 1-3° C more by 2100 due to global climate change (IPCC, 2013). It is unclear whether or how such changes will affect *P. livingstonii*, but since thermal characteristics are important components of roost suitability for this and other Pteropus species (Pierson and Rainey, 1992; Granek, 2002) predicted temperature increases could affect availability of suitable roosting habitat.

P. livingstonii has a small population, which is found within a restricted range (solely on two small, adjacent islands). The species is therefore susceptible to single threatening processes, like cyclones, that could simultaneously or rapidly affect its entire range (Sewall *et al.*, 2007). Further, the species may have naturally taken advantage of elevational differences in tree fruiting phenology to compensate for seasonal variation in fruit availability (Sewall, 2002). Thus, the loss of large areas of foraging habitat including all the lower parts of its elevational range, could result in seasonally restricted food availability.

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008t) [in IUCN (2009)] report that a species action plan developed by the NGO Action Comoros is being implemented for this species (Sewall *et al.*, 2003). A national environmental education programme has been implemented to raise awareness of this species (Trewhella *et al.*, 2005). National legislation to protect this species is being developed (Trewhella *et al.*, 2005) and work has begun to establish a forest reserve for this bat on Moheli and on evaluating a site for a reserve on Anjouan (Trewhella *et al.*, 2005). Sewall (2004: 10) suggests that the protection of specific "bat trees" can already provide a short-term solution.

Based on a study of mitochondrial and microsatellite markers, Ibouroi *et al.* (2018a: 1425) conclude that - for conservation purposes - the *S. livingstonii* populations from Anjouan and Mohéli should be considered as two separate management units, and that the focus should be targeted on the Anjouan population.

A detailed conservation plan for the species, the Conservation Action Plan for Livingstone's Flying Fox (Sewall *et al.*, 2007) was developed by the non-governmental organizations Action Comores Anjouan and Action Comores International, and a consortium of other conservation groups, through a participatory process involving a broad range of stakeholders. The plan identifies a conservation strategy with several key elements, including habitat protection, forest management, environmental education, population monitoring, ecological research, ex-situ breeding, and conservation partnerships. This conservation plan was adopted by the government of the Union of the Comoros as the national conservation strategy for this species and has served as a guide for conservation action.

A long-term comprehensive citizen science program involving Comorian villagers in population monitoring for this species was led by Action Comores Anjouan and Action Comores International between 1992 and 2006. Population surveys and habitat evaluation around roost sites was conducted by Engagement Communautaire pour le Développement Durable of the Bristol Zoological Society and Durrell Wildlife Conservation Trust between 2009 and 2012, and by Dahari more recently. A national environmental education programme was implemented by Action Comores Anjouan and Action Comores International, and it was successful in raising local and international awareness of this species and the threats it faces, in improving training of local personnel, and in increasing local participation in conservation and science programs (Trewhella *et al.*, 2005). A small community-based ecotourism program for this species has been implemented on Mohéli by Projet Conservation de la Biodiversité et Développement Durable and local communities and is maintained by the local community in Ouallah 2 (Sewall *et al.*, 2011b; Doulton *et al.*, 2015). Dahari is implementing integrated landscape management around the southern forest block of Anjouan; this involves sustainable land management at the roosting and foraging habitat of this species and a pilot program of payment for ecosystem services both within the Moya Forest area (Doulton *et al.*, 2015). Research by Dahari and partners into feeding ecology and the genetics of roost-site populations is also planned.

Since 1992, there is an active captive-breeding programme underway for this species, initiated by the Durrell Wildlife Conservation Trust. The program began with 17 founder individuals (7 females and 10 males) captured from the wild on Anjouan during 1992-1995 (Clark *et al.*, 1997). The captive population of *P. livingstonii* subsequently expanded at a slower rate than other fruit bat species in captive breeding programs (e.g., *P. rodricensis*), at least initially (O'Brien, 2011). However, by 2014, the *P. livingstonii* captive population had reached 59 individuals (22 females and 37 males) housed at four institutions (Durrell Wildlife Conservation Trust [Jersey, U.K.]; Bristol, Clifton, and West of England Zoological Society [Bristol, U.K.]; North of England Zoological Society [Chester, U.K.]; and Lisieux Cerza [Lisieux, France]) (Glendewar, 2014).

Richdon *et al.* (2024: 395) assessed the genetic diversity of the captive population and found this to be very similar to the wild populations of this bat, which would suggest that reintroduction from the captive population could be viable.

This species receives the highest level of legal protection available within the Union of the Comoros. It is listed as an 'integrally-protected species' (list 1 of RFIC 2001), which prohibits the capture or detention of *P. livingstonii* individuals without a permit. This law also expressly prohibits the killing of flying fox individuals; transport, purchase, sale, export or re-export of live or dead flying fox individuals or body parts; all disruption during the period of reproduction and raising of young; and the destruction of roosts (RFIC, 2001). The Union of the Comoros also ratified the Convention on Biological Diversity in 1994, and in response has developed a National Biodiversity Conservation Strategy (Roby and Dossar, 2000). This strategy highlights the importance of, threats to, and conservation recommendations for fruit bats of the Union of the Comoros (Sewall and Granek, 2000). *P. livingstonii* is also listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, or CITES (UN, 1973), which prevents international trade in specimens of this species without a permit. In practice, however, enforcement activities within the Comoros for these laws and treaties have been very limited in scope (Sewall *et al.*, 2007).

P. livingstonii also does not occur in any protected areas. However, critical roosting habitat at seven key roost sites that together harboured more than half the population was identified during the development of the conservation action plan (Sewall *et al.*, 2007). Habitat conservation of these roost sites was identified as a key goal in this plan. As part of its implementation, Action Comores Anjouan and the Comoros Forest Reserves Project conducted a conservation assessment to identify the two highest-priority sites (roost sites Yiméré on Anjouan and Hassera-Ndrengé on Mohéli), where the establishment of protected areas for roost habitat would be both highly beneficial to biodiversity conservation and highly feasible (Sewall *et al.*, 2011a). These two groups also completed conservation planning for protection of critical roosting habitat at all seven of these critical roost sites (Sewall *et al.*, 2011b). Implementation efforts by Action Comores Anjouan and partners to conserve habitat around critical roosting habitat on Anjouan and Mohéli are under development. A project to establish larger reserves to protect rainforest and cloud forest on both Anjouan and Mohéli, which would include roosting and foraging habitat for this species, has been proposed by the United Nations Development Programme, the Global

Environmental Facility, and the Comorian government. The success of habitat conservation and restoration efforts will be particularly critical to the long-term prospects for this species.

GENERAL DISTRIBUTION:
Pteropus livingstonii is endemic to two of the four Comoro Islands: Anjouan (formerly Johanna) and Moheli (Trewhella *et al.*, 2001; Smith and Leslie, 2006: 1). On Anjouan, the species avoids lower parts of the island below 300 to 1100 m asl, and on Moheli between 150 to 700 m asl.

Native: Comoros (Cheke and Dahl, 1981; Clark *et al.*, 1997; Trewhella *et al.*, 2001; Smith and Leslie, 2006: 1; Goodman *et al.*, 2010c: 124).

GEOGRAPHIC VARIATION:
See Smith and Leslie (2006: 1).

General description of exernal morphology:
See Smith and Leslie (2006: 1).

DETAILED MORPHOLOGY:
Brain
Segura-Cortijos *et al.* (2022: 152) mention the following average weights for male and female: wild captured animals: 587 ± 96; 673 ± 90 g; captive: 914 ± 164, 862 ± 162 g; maximum in captivity: 1163 ± 294, 1139 ± 291g; minimum in captivity: 712 ± 123, 668 ± 128 g.

Heart
Dickson *et al.* (2016: 963) and Killick *et al.* (2017: 1077) studied cardiomyopathies on a group of captive bats, where dilated cardiomyopathy may be a major cause of death (Drane *et al.*, 2017: 89). Rahma *et al.* (2021: 609) [referring to Dickson *et al.* (2016)] mentions that the vertebral heart score (VHS = the number of vertebrae the heart spans) is 8.71 ± 0.93.

Other
For a description of the cranium, teeth, ear and tragus, and wingshape and aspect ratio see Smith and Leslie (2006: 1-2).

SEXUAL DIMORPHISM:
It is not clear if sexual dimorphism occurs in *P. livingstonii* due to insufficient numbers of adult females have been difficult to collect in the wild (Clark *et al.*, 1997; Trewhella *et al.*, 2005; Young *et al.*, 1993; Smith and Leslie, 2006: 2).

ECHOLOCATION:
Not known to echolocate.

MOLECULAR BIOLOGY:
Genetics
See O'Brien *et al.* (2009) and Almeida *et al.* (2014).

Ibouroi *et al.* (2018a: 1425) found a large genetic difference between population from Anjouan and Mohéli, and on Anjouan, Ibouroi *et al.* (2024: 1) reported that there are strong genetic structures between populations from different colonies, which are linked with distance and habitat fragmentation.

HABITAT:
Ibouroi *et al.* (2018b: 2395) reported that the species' habitat is restricted to steep, high-elevation slopes of the Comoro's remaining natural forests.

On Anjouan, Mandl *et al.* (2021: 51) radiotagged two individuals, which had a home range covering 13.1 ± 1.7 km^2, where they frequented 5 to 8 roost sites.

HABITS:
See Smith and Leslie (2006).

Based on wing morphology, Lindhe Norberg *et al.* (2000) classified *P. livingstonii* as a soaring species.

Edwards *et al.* (2022: 1) studied cortisol levels in captive bats and found that animals that linked social groups had higher than average hormone levels and conversely, individuals with high-quality, positive relationships had lower cortisol levels. They also found that in males the vocalisation frequency was correlated with the cortisol concentration. Bats with high cortisol concentrations also showed a higher frequency of self-grooming and scent marking (p. 8).

ROOST:
See Smith and Leslie (2006). Anonymus (2000: 30) indicates that *P. livingstonii* roosts in tall trees in the rain forest, at medium altitude. These nesting trees are, in general, local species. Trewhella *et al.* (2001) indicate that day-roost sites are also shared with *P. s. comorensis*. Daniel *et al.* (2016: 747) indicate that only four tree species were used as roost on Mohéli [M] and 12 on Anjouan [A]: *Ficus exasperata* Vahl (sandpaper tree, forest sandpaper fig, white fig, or sandpaper leaf tree) [M+A], *Gyrostipula comoriensis* J.-F. Leroy [A], *Gambeya* spp. [A], *Ficus lutea* Vahl (giant-leaved fig or Lagos rubbertree) [A], *Nuxia pseudodentata* Gilg [A], *Albizia lebbeck* (L.) Benth. (lebbeck, lebbek tree, flea tree, frywood, koko and woman's tongue tree) [M], *Ocotea comoriensis* Kosterm. [A], *Weinmannia comoriensis* Tul. [A], *Brachylaena ramiflora* (DC.) Humbert [A], *Ficus pirifolia* Lamk.

[A], *Terminalia catappa* L. (country-almond, Indian-almond, Malabar-almond, sea-almond, tropical-almond or false kamani) [M], *Antidesma hildebrandtii* Pax & K. Hoffm. [A], *Albizia glaberrima* (Schumach. & Thonn.) [A], *Khaya comorensis* (Comorian mahogany) [M], *Cryptocarya* spp. [A].

Ibouroi *et al.* (2018b: Suppl.) reported the following roost trees being used on the Comoro Islands: Asteraceae: *Brachylaena ramiflora*; Combretaceae: *Terminalia catappa*; Cunoniaceae: *Weinmannia comorensis*; Gentianaceae: *Anthocleista grandiflora*; Lauraceae: *Ocotea comorensis*; Leeaceae: *Leea guineensis*; Loganiaceae: *Nuxia pseudodenta*; Meliaceae: *Khaya comorensis*; Mimosaceae: *Albizia glaberrima, Albizia lebbeck*; Moraceae: *Ficus antandronarum, Ficus lutea, Ficus pirifolia*; Myrtaceae: *Eugenia comorensis*; Sapotaceae: *Gambeya boiviniana*.

Granek (2000a: 29 - 30) determined the following roost site characteristics:
1) between 500 and 1,100 m in elevation,
2) steeply sloped land,
3) some native forest cover was present,
4) presence of water in the same valley,
5) presence of an east- or south-facing slope
6) the valley was protected by mountains on three sides, forming a 'bowl' (protecting them from the wind and the mid-day sun),
7) presence of the following tree species: *Gambeya* sp. and *Nuxia pseudodentata*.
However, Granek (2002: 95) indicates that there was no significant association between the bat roosts and characteristics 1, 2 and 3.

Mandl *et al.* (2024: 2) reported that the eight known roosts on Mohéli are all above 230 m.

MIGRATION:
Intra-island movement among roosts is likely, but inter-island movement is unknown (Smith and Leslie, 2006: 3).

DIET:
See Smith and Leslie (2006: 3). Kock and Nader (1984: 30 - 31) and Sewall (2004:10) point out that this species almost completely feeds on native trees, and changes tree species according to the season. One of its favourite foods is the fruit of a giant-leaved fig tree (*Ficus lutea*) (Sewall, 2004: 9 - 10). Young *et al.* (1993) [in Carroll and Feistner (1996: 330)] indicate that *R. obliviosus* and *P. livingstonii* were captured at the same kapok and fig feeding sites on Anjouan, which would suggest that their feeding niches might overlap. However, they also indicate that there might be a vertical separation between the two species.
Nectar and fruits of the Moraceae family form an important part of the diet, while pollen is not important Cotterill (1995).

Trewhella *et al.* (2001: 141) reported the following food items (with known items in bold and suspected items in plain text): Aphloiaceae: *Aphloia theaeformis* [= *Aphloia theiformis* (Vahl) Benn.]; Asteraceae: ***Brachylaena ramiflora*** (DC.) Humbert; Clusiaceae: *Rheedia anjouanensis* H. Perrier [= *Garcinia anjouanensis* (H. Perrier) P.W. Sweeney & Z.S. Rogers; Cunoniaceae: *Weinmannia comorensis* Tul.; Gentianaceae: *Anthocleista grandiflora* L. (forest fever tree); Lauraceae: *Ocotea comorensis* ?; Malvaceae: ***Ceiba pentandra*** (L.) Gaertn. (kapok tree); Monimiaceae: ***Tambourissa comorensis*** Lorence; Moraceae: *Artocarpus altilis* (Parkinson) Fosberg (breadfruit), *Artocarpus heterophyllus* Lam. (jackfruit or jack tree), ***Ficus lutea*** Vahl (giant-leaved fig), ***Ficus pirifolia*** ?; Myrtaceae: *Eugenia jambos* L. [= *Syzygium jambos* L. (Alston)] (rose apple); Oxalidaceae: *Averrhoa bilimbi* L. (bilimbi, cucumber tree or tree sorrel); Sapotaceae: ***Gambeya*** sp.; Stilbaceae: *Nuxia pseudodentata* Gilg, 1895.

Courts (1998: 189) reports that captive animals catch and eat insects flying by.

Bell *et al.* (2019: 250) indicate that dominant male bats (in a captive colony) defend small feeding territories within the colony, and are therefore often more sedentary, which might result in these animals being heavier and running a higher risk of cardiomyopathy.

PREDATORS:
See Smith and Leslie (2006).

POPULATION:
Structure and Density
In 2002 there were estimated to be 1,200 bats in 20 roosts, many of which have been recently located as a result of the implementation of a national environmental education programme (Trewhella *et al.*, 2005). Sewall (2009: 3) indicates that the population might count 1,200 - 1,500 animals. Prior to the national environmental education programme there were estimated to be fewer than 200 bats.

During an extensive survey in 2011 - 2012, Daniel *et al.* (2016: 742) estimated the population size to be about 1,260 animals, distributed over 21 roosts on Anjouan and Mohéli. Bi-annual surveys between 2016 and 2023 led Mandl *et al.* (2024: 1) to estimate the population size on

Anjoun to be between 1,200 and 1,500 bats, and on Mohéli between 300 and 400 bats. Over that eight year period, they did not find any significant in- or decreases in the number of bats.

Ibouroi *et al.* (2018b: 2408) observed 1,243 bats divided over 19 locations, with colony sizes ranging from 3 to 349 individuals (average: 65).

Ibouroi *et al.* (2021: 10) calculated and compared the costs for a long-term monitoring program based on conventional Capture-Mark-Recapture (CMR) and on Non-invasive Genetic Sampling (NIGS-CMR), which came to 166 USD/sample and 62 USD/individual respectively.

Also see Smith and Leslie, 2006: 1).

Trend
2016: Decreasing (Sewall *et al.*, 2016). 2008: Decreasing (Mickleburgh *et al.*, 2008t; IUCN, 2009).

Repeated simultaneous surveys of all 23 known roosts during 1998-2006 typically recorded about 1,200 bats (Sewall *et al.*, 2007); many of these roosts were located as a result of the implementation of a national monitoring program (Trewhella *et al.*, 2005). Surveys have been conducted only sporadically since 2007, so it is unclear whether populations have changed recently. However, a survey conducted with sequential visits to all previously known roosts in 2011 and 2012 estimated 1,300 bats across 22 roosts (Anjouan: 940 bats at 16 roosts, Mohéli: 360 bats at 6 roosts) (Daniel *et al. in press*.). Colony size typically ranges from 15 to 150 individuals (Sewall *et al.*, 2007). The largest known roosts have sometimes reached about 250 individuals during the rainy season, but not all of these are mature individuals (Sewall *et al.*, 2011a, 2011b).

Generation length for the wild population of *P. livingstonii* is unknown, but several demographic parameters can be derived from the studbook for captive bats of this species (Glendewar, 2014). Bats of this species can be long-lived in captivity (e.g., one founder captured as an adult in 1992 is still alive and has now lived 22 years in captivity). Females do not reproduce during the first few years of life in captivity (minimum dam age at first reproduction = 3.4 years, mean dam age at first reproduction = 5.9 years), and the average age of females giving birth is elevated (of all dams born in captivity that have since died or are >10 years of age, mean age when giving birth = 8.1 years). Thus, based on studbook data (Glendewar, 2014), this last figure of 8.1 years represents our best estimate of the generation length of the captive population. This estimate may be conservative as most (75%) of these females are still alive and at least some presumably will reproduce again at a later age.

It is unclear to what extent the generation length of the captive population correlates with the generation length of the wild population of *P. livingstonii*. However, the generation length of captive *P. livingstonii* correlates well with the few published generation length values for wild populations of other *Pteropus* species. In a wild population of *P. poliocephalus*, generation length was estimated conservatively as 7.4 years (Tidemann and Nelson, 2011), though the true generation length could be much higher. Further, a generation length of 5.0 years was estimated for a rapidly declining wild population of P. conspicillatus (Fox *et al.*, 2008); however, our calculations using these same data suggest that in a stable population, generation length for *P. conspicillatus* would be about 7.7 years. Thus, generation length values for the captive population of *P. livingstonii* correlate well with the only published generation length values for wild *Pteropus*. Further, an estimate derived from taxonomically adjusted allometric equations for mammals suggests generation length for *P. livingstonii* is 8.1 years (Pacifici *et al.*, 2013). Thus, the captive estimate appears in line with estimates for wild populations, and we conservatively estimate the generation length in the wild population of *P. livingstonii* to be 8.1 years.

True changes in the population size of *P. livingstonii* are currently unknown but are likely to be linked to changes in forest and underplanted forest habitat. Our estimates, derived from the little available data on forest loss rates (FAO, 2010; UNDP, 2013), suggest that habitat decline over the most recent three generation (or 24.3-year) period was 83%. Thus, our best estimate of loss of *P. livingstonii* habitat exceeds the threshold under the A2 criterion for CR status (≥ 80% loss of population, as suspected by habitat change, over a three-generation period, where habitat loss is ongoing).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 15 years.

Segura-Cortijos *et al.* (2022: 149) reported the most common cause of morbidity in a captive colony were wounds (34.9 %) [in patagia and digits of forelimbs], localised inflammation (12.9 %) and fractures (10.8 %). Males ran greater risks than females, and immatures were more prone to suffer wounds than adults and geriatric

animals. Causes of death included early foetal death (18.2 %), heart disease (14.8 %) and conspecific aggression (10.2 %).

ACTIVITY AND BEHAVIOUR:
See Smith and Leslie (2006: 1).

Trewhella *et al.* (2001: 135) indicate that *P. livingstonii* is more diurnally active than the sympatric *P. seychellensis comorensis* and is the dominant species during their encounters.

Sugita (2016: 2) refers to Courts (1996b), who observed zoo-reared males in mutual allogrooming accompanied by licking of erect penises, but could not confirm whether this was homosexual behaviour or some kind of basic social contact.

Also in studying a captive colony, Richdon *et al.* (2022: 7) found a straightforward model of dominance hierarchy in males, with age playing a crucial role in determining the male's rank. They also found that the frequency of aggressive interactions was driven by the bat's own rank and the difference from the
recipient male's rank.

REPRODUCTION AND ONTOGENY:
See Smith and Leslie (2006: 2).

Szekely *et al.* (2015: Suppl.) mention a gestation period of 152 days. At birth, the young weights 137 g (adult weight: 696.5 g).

MATING:
See Smith and Leslie (2006).

Riccucci (2011: 141) reports on same sex sexual behaviour in captive held *P. livingstonii*.

PARASITES:
Fountain *et al.* (2019: 268) examined the captive population at the Jersey Zoo and found them to be infected by the following *Staphylococcus* species (in descending order): *S. xylosus, S. aureus, S. saprophyticus, S. nepalensis, S. simulans, S. sciuri, S. kloosii, S. simiae, S. hominis, S. epidermidis, S. succinus, S. warneri, S. lentus, S. lugdunensis, S. cohnii, S. haemolyticus, S. equorum, S. capitis*. From the same captive population, Fountain *et al.* (2021: 2,) described two new species: *Staphylococcus lloydii* and *S. durrellii*.

Fountain *et al.* (2022: 1) compared the genomes of *Staphylococcus aureus* colonising the bats that are in a captive breeding programme at the Jersey Zoo with those from bats in the endemic founder population in the Comoros Republic, and they found that both groups of bats carried the same two distinctive lineages.

UTILISATION:
Is not hunted for food (Trewhella *et al.*, 2005).

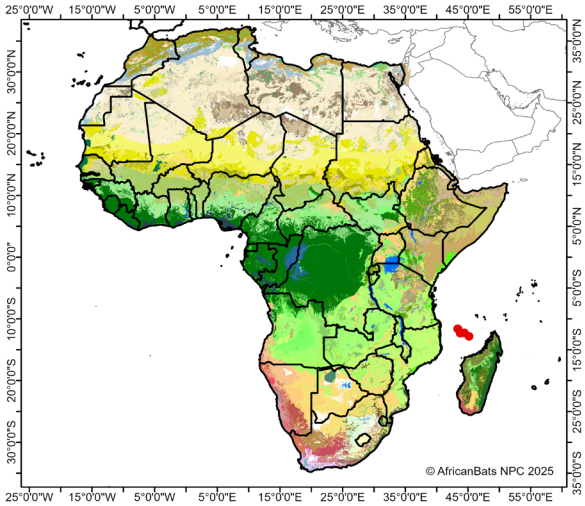

Figure 6. Distribution of *Pteropus livingstonii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros, Mayotte.

Pteropus niger (Kerr, 1792)

*1792. *Vespertilio vampirus niger* Kerr, in: Linnaeus, Animal Kingdom, 1 (1): xvii, 90. Publication date: February 1792. Type locality: Réunion: "Réunion island". - Comments: Andersen (1912b: viii) mentions that the type was once in the ancient Royal Cabinet in Paris but is probably no longer in existence.

1797. *Vespertilio caninus* Blumenbach, Handb. Naturg, 5 ed: 73. - Comments: Pavlinov *et al.* (1995) consider *caninus* to be a synonym of *vampyrus*, but Andersen (1912b: 220) indicates this is a synonym of *niger* Kerr, 1792. The name was originally proposed as a replacement for *V. vampyrus* L., but this includes *vampyrus*, *rufus* and *niger*. Andersen also indicates that Goldfuss' plate of "*V. caninus*" Blumenbach (1809), is a copy of Schreber's plate xiv, which is *Pteropus niger*.

1803. *Pteropus fuscus* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, 46. Type locality: Réunion: Réunion and Madagascar. [Goto Description]. - Comments: Andersen (1912b: 220) mentions that Geoffroy based himself on three specimens "viz., two mounted specimens (wings expanded), sent from Réunion by de la Nux (nos. 86 and 87), and a third 'envoyé de Madagascar, par le citoyen Macé, naturaliste' (no. 88)". Andersen also indicates that specimen 88 (from Madagascar) was probably obtained from a dealer. He was also unable to find any of these specimens.

1804. *V[espertilio] mauritianus* Hermann, Obs. Zool. , 19. Publication date: 31 August 1804. Type locality: Mauritius: "Mauritius". [Goto Description].

1808. *Pteropus rufus:* Tiedemann, Zool, 1808: 535. Type locality: Madagascar: "Madagascar". - Comments: Not of E. Geoffroy Saint-Hilaire, 1803, but see).
1810. *Pteropus vulgaris* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 15: 92. Type locality: Réunion: Réunion and Madagascar: Restricted to Réunion by Andersen (1912b: 221), due to the type locality for Pteropus fuscus is Réunion. Holotype: MNHN ZM-MO-1990-26: ad ♂, mounted skin (skull not removed). Collected by: Etienne Geoffroy-Saint-Hilaire. Additional numbers: A.1.C.18 - 745H - 154. - Comments: A redescription and renaming of *Pteropus fuscus* Geoffroy, 1803 (see Andersen, 1912b: 221).
1871. *Spectrum vulgare* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 100. Publication date: 14 January 1871. Type locality: : Mauritius, Réunion, ? Madagascar. [Goto Description].
1895. *Pteropus pteropus* Merriam, Science, NS 1 (14): 376. Publication date: 5 April 1895. Type locality: Réunion: Réunion and Madagascar. - Comments: Combination introduced into literature by Merriam on the mistaken supposition that Brisson's nomenclature was binomial (see Andersen, 1912b: 223).
? *Pteropus niger:* (Name Combination, Current Combination).

TAXONOMY:
See Bergmans (1991) and Simmons (2005: 341).

O'Brien *et al.* (2009) suggested that *P. aldabrensis*, *P. rufus*, *P. niger* and *P. seychellensis* (including *comorensis*) should be considered geographical forms of a single species *P. giganteus* (Brünnich, 1782) from the Indian subcontinent, Maldives and Andaman archipelagos.

Almeida *et al.* (2014: 85) place *P. niger* in the "*vampyrus*" group.

COMMON NAMES:
Castilian (Spain): Zorro volador negro de Mauricio. Czech: kaloň mauricijský. English: Greater Mascarene Flying Fox, Mascarene Flying-fox, Mauritian Flying Fox. French: Renard volant de l'île de Mascarene, Renard volant de Maurice, Renard volant des Mascaraignes, Roussette noire, grande Roussette des Mascareignes. German: Grosser Maskarenen-Flugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable based on a projected 30% population reduction in the next 21 years (three generations) due to the continuing decline in the extent and quality of a key habitat (forest, which is relied upon for roosting and at certain times of year for foraging); knowledge of impacts of past cyclones on this and other island fruit bats and the likelihood of this happening again on Mauritius within the next few years; and based on current pressures from hunting, which are likely to increase (Hutson and Racey, 2013)..

Conenna *et al.* (2017: Suppl.) mention its status as Vulnerable (VU), but Anthony *et al.* (2018: 12075) indicated that the culling ot the bats in 2015-2016 resulted in upgrading the status to "Endangered" by the IUCN in 2018.

Assessment History
Global
2013: VU A3cd ver 3.1 (2001) (R). 2008: EN B1ab(iii,v) ver 3.1 (2001) (Jenkins *et al.*, 2008k; IUCN, 2009). 1996: VU A1d+2cd ver 2.3 (1994) (Baillie and Groombridge, 1996). 1994: VU A1d+2cd ver 2.3 (1994) (Groombridge, 1994). 1993: VU (World Conservation Monitoring Centre, 1993). 1990: VU (IUCN, 1990). 1988: VU. 1986: Rare (IUCN Conservation Monitoring Centre, 1986). 1981: VU: A1d+2cd. Extinct on Réunion Island (see Cheke and Dahl, 1981).

Regional
None known.

Legal Status
CITES - Appendix II.

MAJOR THREATS:
Like other *Pteropus* species in the region, this species is threatened by cyclones, the loss of roosting and feeding trees, and by persecution and/or hunting (Carroll and Feistner, 1996). Although no major cyclone has affected bats on Mauritius in recent years (Hutson and Racey, 2013), the risk remains high and climate change forecasts suggest that there will be an increase in the frequency and intensity of cyclones in this region. Cyclone damage can result in high levels of starvation and mortality, as well as loss of roost trees. Elsewhere, such cyclones have caused massive declines (up to 99%) in island fruit bat populations. In the previous 10 years six intense tropical cyclones had affected Mauritius (Hutson and Racey, 2013). Note that, for example, a cyclone in the 1970s reduced the population of the endemic fruit bat on the neighbouring island of Rodrigues to less than 1% of its current population (Powell and Wehnelt, 2003).

Forest habitat suitable for roosting and important for feeding, particularly at certain times of year, have seen major decline of what is already a habitat much depleted in both area and quality (15-20% decline in the 10 years to 2005). While the significant holdings by government have

shown little decline in recent years, private holdings have seen the majority of the declines, and that decline is likely to continue (Hutson and Racey, 2013).

Page and D'Argent G. (1997) demonstrated that less than 2% of Mauritius' native forest remained, and this was recognized in the Ministry of Environment and Sustainable Development's 2006 Pocketbook of Environmental Statistics. Forest areas currently occupy about 25% of the total land area, but many of these areas are heavily invaded by exotic vegetation. The report on Economic and Social Indicators, Environment statistics 2009, from the Central Statistics Office (quoted in National Economic and Social Council Report 17, 2011, Maintaining the Green Cover of Mauritius) identifies a loss of forest area amounting to a change of 5.1% of the total land area over the period 1995 to 2005. From the figures given, currently half the forest area is privately owned. The report identified loss to state owned forest of 1.5%, but a loss of 27.6% of privately-owned forest. Very little change was identified for the four following years to 2009. The same report quotes from Digest of Environment Statistics 2009, CSO, giving a loss of forest, shrubs and grazing land of 10,000 ha (17.2%) between 1995 and 2005. The data suggests that the government is maintaining its own holdings, indeed Appendix 3 to this report identified a number of government initiatives for the maintenance, restoration and creation of forest areas, but at present these are mainly new and small initiatives and in no way compensate for the losses to privately owned forest (Hutson and Racey, 2013). Even if foraging area has increased following the wider introduction of fruit farms, especially for litchi, longan and mango, these are only available for a short period of the year and it is believed that there are times of year when the bats would not survive well without forest foraging.

Although protected (Nyhagen, 2004), there is currently a level of control and sport hunting that is likely to be sustainable (Robinson *et al.*, 2010). However, there is increased pressure to reduce populations, through conflict with fruit growers at certain times of year. Any significant increase in the take of fruit bats is likely to have serious impact on the populations and combined with the other major threats described above could threaten the survival of this endemic species.

Hutson and Racey (2013) estimates the existing levels of take for sport or as measures for pest control are given at about 2,000 bats per year. This is between 4 and 10% of the recent population estimates. Any introduction of a cull that would significantly reduce fruit bat damage to fruit (mainly litchi, longan and mango) must similarly impact on the bat population. Since the species is currently listed by IUCN as Vulnerable and is protected under Mauritian law (Wildlife and National Park Act 1993, currently under revision), the introduction of a cull is likely to result in the species being removed from the protected list and would be aimed at making a significant impact on the population, but is also very likely to increase the exploitation for sport and for unmanaged control. Hence, the moment a cull were introduced, it would immediately trigger the need for a re-evaluation of the status of the species. While no full analysis of sustainable take is available for such fruit bats it is widely considered that a take of 10% per year will result in significant population decline (e.g., Pierson and Rainey, 1992).

In October 2006 the government endorsed a culling programme for 2,000 bats because of their perceived role in inflicting serious economic damage on lychees. This is obviously in conflict with the fact that the species is protected under the Wildlife and National Parks Act 1993. Only six bats were officially culled, despite illegal hunting parties being known to kill up to a few hundred bats in one night. The law is currently being revised and it is unknown whether further culling will be supported, although most likely it will be (Jenkins *et al.*, 2008k; IUCN, 2009).
Anthony *et al.* (2018: 12075) reported that in November-December 2015 30,938 bats were culled and in December 2016 yet another 7,380 bats. Florens and Baider (2018: 60) and Jaunky *et al.* (2021: 2) furthermore reported that 12,500-13,000 bats (of an estimated population of 65,000) were planned to be culled in 2018. Jaunky *et al.* (2021: 2) also indicated that by 2019 a total of 51,318 bats were killed and that a new culling campaign occurred from end October 2020 to mid-December.

Olival (2015: 6) reviews why culling is not an effective means to mitigate conflicts between fruit growers and bats, nor to reduce the likelihood of zoonotic disease risk.

Florens (2015: 1325; 2016: 33) indicated that the official population estimates are between 90,000 and 1,000,000 bats. The government set a cull target of 20 %, which resulted in the death of 20,000 bats. However, as the real number of bats accounted for about 50,000 animals, this meant that about half of the population was eradicated.

Hutson and Racey (2013) report that there is no data on specific threats to specific roost sites, but

the threats to bats at roost sites in Mauritius (principally deforestation, hunting and cyclones) can impact a number of roosts at one time and in no particular pattern. In the case of a larger cyclone a very large number of roosts can be damaged at the same time and which roosts are damaged will depend on details of the movement of the cyclone and its strength. These cyclones also affect the foraging of the bats, both around the roost site and elsewhere and there are many examples of where cyclone damage has resulted in high levels of starvation and mortality, in addition to damage to roost trees, in island-dwelling fruit bat species.

Reinegger *et al.* (2021: 428) also point to potential competition for native fruits by the invasive long-tailed macaque (*Macaca fascicularis* Raffles, 1821)

CONSERVATION ACTIONS:
Hutson and Racey (2013) repeats what is stated by Jenkins *et al.* (2008k) [in IUCN (2009)] who report that *P. niger* became a protected species in 1993 on Mauritius (Nyhagen *et al.*, 2005) and is reported to occur in protected areas, including the Black River Gorges National Park (Nyhagen, 2004), nature reserves and mountain reserves. There is a clear need to assess the population size, population dynamics, response to cyclones, assess relative fruit predation, roosting habitat requirements and impact of culling on this species and effectiveness of fruit protection to prevent foraging. Oleksy *et al.* (2018: "5") also suggest to harvest the fruits at an earlier stage to reduce their attractiveness to bats as bats prefer to eat fruits that are to ripe to be sold (see also Krivek *et al.*, 2020). Additionally, they found that 10 % of the lychee losses and up to 50 % (or more) of the mango losses could be attributed to natural falling of fruit, which could also be reduced by early harvesting. Their study also indicated (p."6") that netting of trees could reduce damage caused by bats 12 to 23-fold. Another study concentrating on backyard lychee trees, Tollington *et al.* (2019: 1) suspected that fruit bats were responsible for about 42 % of the total damage to these trees, and that protecting trees with nylon nets could yield 1/3 extra fruits.

Oleksy (2019: 104) suggested that full exclusion netting or the installation of a sound system can decrease the damage caused by bats to the fruits, but he also indicated that it is equally important to restore forest ecosystems to increase native food supply for the bats.

GENERAL DISTRIBUTION:
Historically, *Pteropus niger* is distributed within the Mascarene Islands (Reunion Island, Mauritius Island, subfossil on Rodriquez Island). Since becoming extirpated from La Réunion in the early eighteenth century, this species has been restricted to the western Indian Ocean island of Mauritius. In 2007 a small colony of *P. niger* (up to 6 individuals) was located on La Réunion, though a few individuals have been observed on previous occasions over the past decade, most likely blown over from Mauritius by annual cyclones. Breeding within this small population on La Réunion is suspected but not confirmed.

Caceres (2010: 9) mentions that the original population disappeared from La Réunion between 1772 and 1801.

Native: Mauritius; Réunion.

BIOGEOGRAPHY:
See O'Brien *et al.* (2009) for further details.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
The adult's weight is on average 456.3 g (see Szekely *et al.*, 2015: Suppl.), but Oleksy *et al.* (2019: 5) reported an average weight of 617 (± 76) g for females and 630 (± 96) g for males.

MOLECULAR BIOLOGY:
Genetics
See O'Brien *et al.* (2009).

HABITS:
P. niger is primarily nocturnal, but Nyhagen *et al.* (2005: 492) observed some specimens foraging during the day.

Using solar-powered GSM-tracking, Oleksy *et al.* (2019: 5) found that on average males travelled 9.38 km each night and females 6.06 km. The maximum distance travelled during one night was 92.92 km for a male and 79.19 km for a female. They also found that home ranges of males averaged 74,633 ha, whereas these for females only covered 31,072 ha. The core foraging areas averaged 2,222 ha for males, 1,364 ha for females.

ROOST:
On La Réunion, Caceres (2010: 14) reported that Yellow jade orchid tree (*Michelia champaca,* Chinese fan palm (*Livistona chinensis*), Longan (*Dimocarpus longan*), soft bollygum (*Litsea glutinosa*) and Wampee (*Clausena lansium*) are used as roosting trees. These roost trees can be used for several years, although during the year several roosts on different places of the island can be used.

DIET:
Nyhagen *et al.* (2005: 493) reported that on Mauritius, *P. niger* ate 22 plant species, 20 of which were visited for fruit, two for floral resources and one for leaves (of *Diospyros tessellaria* both fruits and flowers were eaten). Nyhagen (2004: 120) described the characteristics, which fruit eaten by *P. niger* posses: easily accessible (95 %), medium size (47 %), medium size seed (68 %), vivid colours (53 %), sweet smell (58 %), sweet flavour (74 %), and not juicy, i.e. low water content (58 %). Four of the plant species (*Artocarpus heterophyllus, Diospyros tessellaria, Mangifera indica* and *Mimusops petiolaris*) possess five of these seven characteristics. Nyhagen (2004: 122) also mentions that this bat is the only native vertebrate to feed on fruits of *Labourdonnaisia glauca*.

Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *P. niger* these include *Psidium guajava* L. (apple guava - Myrtaceae) and *Syzygium jambos* L. (Alston) (Malabar Plum - Myrtaceae).

Florens *et al.* (2017: 89) provided the following list of fruits eaten by *P. niger*: Aphoiaceae: *Aphloia theiformis* (Vahl) Benn.; Apocynaecae: *Tabernaemontana persicariifolia* Jacq.; Araliaceae: *Polyscias maraisiana* (Marais) Lowry & G.M. Plunkett (Ox tree); Arecaceae: *Dictyosperma album* (Bory) H. Wendl. & Drude ex-Scheff. (princess palm, hurricane palm), *Hyophorbe lagenicaulis* (L.H. Bailey) H.E. Moore (bottle palm, palmiste gargoulette), *Latania loddigesii* Martius (Latanier de l'île Ronde, Latanier de Maurice); Burseraceae: *Protium obtusifolium* (Lam.) Marchand; Calophyllaceae: *Calophyllum tacamahaca* Willd., 1811; Celastraceae: *Cassine orientalis* (Jacq.) Kuntze (bois d'olive); Chrysobalanaceae: *Grangeria borbonica* Lam., 1789; Combretaceae: *Terminalia bentzoe* (L.) L. f.; Ebenaceae: *Diospyros egrettarum* I. Richardson, *Diospyros tessellaria* Poir. (black ebony, Mauritian ebony), *Diospyros melanida* Poir.; Elaeocarpaceae: *Elaeocarpus integrifolius* Lam.; Lecythidaceae: *Foetidia mauritiana* Lam.; Loganiaceae: *Geniostoma borbonicum* (Lam.) Spreng.; Melastomataceae: *Warneckea trinervis* (DC.) Jacq.-Fél.; Moraceae: *Ficus reflexa* Thunb., *Ficus rubra* Vahl, 1805, *Ficus mauritiana* Lam.; Myrtaceae: *Eugenia alletiana* Baider & V. Florens, *Eugenia elliptica* Lam., 1789, *Eugenia pollicina* J. Guého & A.J. Scott, *Eugenia lucida* Lam., *Eugenia tinifolia* Lam., *Syzygium glomeratum* (Lam.) DC., *Syzygium populifolium* (Baker) J. Guého & A.J. Scott, 1980; Pandanaceae: *Pandanus eydouxia* Balf. f., *Pandanus utilis* Bory; Pittosporaceae: *Pittosporum senacia* Putt.; Rubiaceae: *Pyrostria borbonica* (J.F. Gmelin) Razafim. & B. Bremer; Salicaceae: *Ludia mauritiana* J.F. Gmelin, 1791; Sapindaceae: *Stadmania oppositifolia* Lam.; Sapotaceae: *Labourdonnaisia calophylloides* Bojer (Bois de natte à petites feuilles), *Labourdonnaisia glauca* Bojer (Bois de natte à grandes feuilles), *Labourdonnaisia revoluta* Bojer, *Mimusops maxima* (Poir.) R.E. Vaughan (Grand natte), *Mimusops petiolaris* Dubard, 1915 (macaque, makak, bois makak), *Sideroxylon boutonianum* A. DC, *Sideroxylon cinereum* Lam., *Sideroxylon puberulum* C. DC. (Manglier rouge), *Sideroxylon grandiflorum* A. DC. (tambalacoque, dodo tree).

Reinegger *et al.* (2021: Suppl.) mentioned the following species documented to have been eaten by *Pteropus niger*: Aphloiaceae: *Aphloia theiformis* (Vahl) Benn., 1840; Celastraceae: *Cassine orientalis* Jacq.; Combretaceae: *Terminalia bentzoe* L. (L. fil., 1782); Ebenaceae: *Diospyros tessellaria* Poir., 1804; Fabaceae: *Dalbergia latifolia* Roxb., 1799; Lamiaceae: *Vitex glabrata* R.Br., 1810; Lecythidaceae: *Foetidia mauritiana* Lam., 1788; Linaceae: *Hugonia serrata* Lam., 1789; Myrtaceae: *Eugenia* sp. 1, *Eugenia* sp. 2, *Psidium cattleyanum* Afzel. ex Sabine, 1821, *Syzygium glomeratum* (Lam.) DC., 1828; Rubiaceae: *Coffea macrocarpa* A. Rich., 1834; Salicaceae: *Flacourtia indica* (Burm. fil.) Merr., 1917, *Ludia mauritiana* J.F. Gmel., 1791; Sapindaceae: *Hornea mauritiana* (Bojer) Baker, 1877, *Stadmania oppositifolia* Lam. ex Poir.; Sapotaceae: *Mimusops maxima*, *Mimusops petiolaris* (A.DC.) Dubard, 1915, *Labourdonnaisia glauca* Bojer, 1841, *Labourdonnaisia revoluta* Bojer, 1841, *Sideroxylon cinereum*, *Sideroxylon grandiflorum* A. DC, 1844.

POPULATION:
Structure and Density
The present population on Mauritius appears to be stable; 14 roosting sites were reported by Nyhagen (2004), but Robin, 2007) identified 57 roosts. This latter study only looked at 24 of the 57 roosts and calculated a minimum population size of 12,000 - 16,000. It can therefore be assumed that the minimum island wide population is over 25,000 (V. Tatayah *pers. comm.* [in Jenkins *et al.* (2008k) in IUCN, 2009]).

There has been a range of population estimates with the first estimate of 10,000 individuals in 1974 (Cheke and Dahl, 1981). Cheke (*pers. comm.* 2012 in Hutson and Racey (2013)) admits that this was a very crude estimate based on counts of a few colonies and talks with hunters and other anecdotal sources. The Mauritian government states that it has carried out counts

since 2003, and data are available for 2006 and 2010. These give figures of 22-25,000 for 2006 and 49-56,000 for 2010 (Sookhareea, 2011) using a range of techniques depending on circumstances. The population figures given are for all animals: the numbers of mature individuals is estimated to be ca. 65% of the total population, hence 33,000 of an estimated population of 50,000, and 16,000 for a population of 25,000 (based on a 50% mortality in the first year, and a 30% mortality in subsequent years, with a period of at least two years to maturity and a generation time of seven years).

Using evening dispersal counts, Robin (2007) comes to a number of 12,000-16,000 bats for 2007. The counts over the last 10 years have not been carried out in a consistent fashion and may not be directly comparable. Nevertheless, it is likely that there has been an increase in population in that time, although the scale of that increase is uncertain. An increase is likely since there has been no significant cyclone in that period, and major cyclones will result in heavy population losses, which will be slow to recover. The number of known roost sites has also increased from c.14 in 2003 (Nyhagen, 2004) to c. 57 (Robin, 2007; Sookhareea, 2011). A methodology has now been established for counting all known roost sites and it is hoped that regular surveys will provide data to track the population trend. In 2007 a small population (10-20 animals) was identified on Réunion (where the species formerly occurred but has been extinct for well over 100 years). These animals can be assumed to have blown over from Mauritius (as suggested for other stray individual records since 2000). Limited erratic breeding has been demonstrated on Réunion, and so this population has not been considered for the purposes of this assessment.

Anthony *et al.* (2018: 12074) referred to a survey held in October 2016, which yielded a population estimate of about 62,000 individuals.

Trend
2013: Stable (Hutson and Racey, 2013). 2008: Decreasing (Jenkins *et al.*, 2008k; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) report a maximum longevity of 19.4 years.

PARASITES:
Hirst (1923: 980) mentions that the mite *Ancystropus mulleri* Kolenati was collected from *P. vulgaris* [= *P. niger*].

VIRUSES:
Rhabdoviridae
Of the 36 bats from Mauritius tested by Mélade *et al.* (2016a: 6) against *Lagos bat lyssavirus* and *Duvenhage lyssavirus*, two and 13 respectively, displayed a sero reaction. Also one out of 21 specimens tested for *European bat lyssavirus 1* showed this reaction.

UTILISATION:
This species is locally used for sport hunting and as a source of food (R).

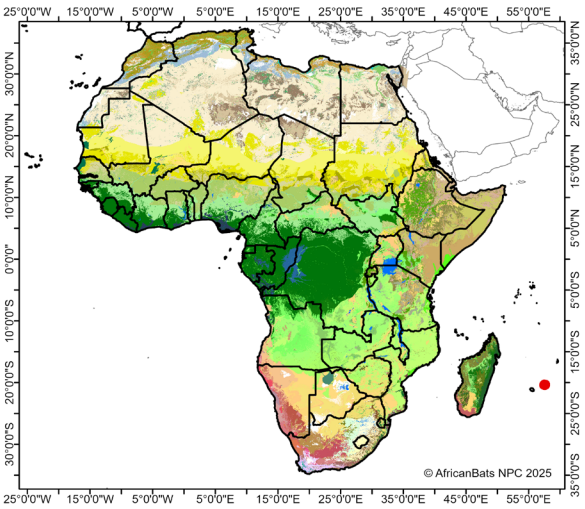

Figure 7. Distribution of *Pteropus niger*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar, Mauritius.

Pteropus rodricensis Dobson, 1878

*1878. *Pteropus rodricensis* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, xxxvii, 20, 36, pl 3, fig 3. Publication date: 15 June 1878. Type locality: "Africa": Mascarene Islands: Rodrigues Island. [Goto Description]. Holotype: NHMUK 1876.3.11.1: ad ♂, skull and alcoholic. Collected by: J. Gulliver. Presented/Donated by: The Royal Society. See Andersen (1912b: 275). Paratype: SMF 44785: juv ♀, skull and alcoholic. Collected by: J. Gulliver. (Current Combination).

1907. *Pteropus mascarinus* Mason, Ann. Mag. nat. Hist., ser 7, 20 (117): 221. Publication date: 1 September 1907. Type locality: Mauritius: 15 mi (=22 km) NE Mauritius: Round island (La Ronde). [Goto Description]. Holotype: NHMUK 1925.8.10.1.

TAXONOMY:
See Bergmans (1991) and Simmons (2005: 343).

Almeida *et al.* (2014: 85) place *P. rodricensis* in the "*vampyrus*" group.

COMMON NAMES:
Castilian (Spain): Zorro volador de la isla Rodrigues. Czech: kaloň rodrigueský, kaloň zlatý. Dutch: Rodriguez vliegende hond. English: Rodriguez Flying Fox, Rodrigues Flying Fox. French: Renard volant de Rodrigues, Renard Volant de l'île de Rodriguez. German: Rodriguez-Flughund, Rodrigues-Flugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (B1ac(iv)+2ac(iv) ver 3.1 (2001)) because the Global population is restricted to a single location (the island of Rodrigues), and has an extent of occurrence (EOO) and area of occupancy (AOO) that are both less than 500 km^2. The population undergoes extreme fluctuations due to severe tropical cyclones, which can cause mortalities of over 50% but the population subsequently recovers at a rate of about 12-15% a year provided there are no further severe cyclones. This fruit bat exploits both native habitats and those dominated by introduced species. Native habitats are highly fragmented.

The mathematical predictor-rich model developed by Welch and Beaulieu (2018: 10) placed *Pteropus rodricensis* in the sixth position of the top ten species at risk of extinction.

Assessment History
Global
2016: EN B1ac(iv)+2ac(iv) ver 3.1 (2001) (Tatayah *et al.*, 2017). 2008: CR B1ab(iii)c(iv) ver 3.1 (2001) (Mickleburgh *et al.*, 2008u; IUCN, 2009). 2004: CR B1ac(iv) ver 3.1 (2001) (Mickleburgh *et al.*, 2004q; IUCN, 2004). 2002: CR: B1+3d (Mickleburgh *et al.*, 2002a: 22), extinct on Round Island. 1996: CR (Baillie and Groombridge, 1996). 1994: EN (Groombridge, 1994). 1993: EN (World Conservation Monitoring Centre, 1993). 1990: EN (IUCN, 1990). 1988: EN (IUCN Conservation Monitoring Centre, 1988). 1986: EN (IUCN Conservation Monitoring Centre, 1986).

Regional
None known.

Legal Status
U.S. ESA - Endangered.
CITES - Appendix II.

MAJOR THREATS:
Tatayah *et al.* (2017) report that deforestation has been a serious threat to the species, especially where mature fruit trees and important roost trees were felled. Because of the deforestation of this forest buffer, any remaining patches of forest (and their roosting bats), were more susceptible to tropical cyclones (Trewhella *et al.*, 2005; Mickleburgh *et al.*, 2008u; Ibouroi *et al.*, 2025: 3). These cyclones can cause significant fluctuations in bat population size and, along with shortage of food and dehydration, are now the major current threat to the species (Powell and Wehnelt, 2003). Tatayah *et al.* (2017) also report that deforestation is no longer occurring since at least 2010.

In the past the species was also hunted for food, however, this is now rare (Trewhella *et al.*, 2005; Mickleburgh *et al.*, 2008u; IUCN, 2009). Due to its habit of raiding fruit trees (mangoes, lychees, papaya etc), there is a human-wildlife conflict (Barnes, 2013; Price, 2013), although Carroll (1981: 26) claimed that local fruit growers did not regard them as pests, but that might have been due to the low population numbers at that time. A new law has been passed for the Republic of Mauritius: the Native Terrestrial Biodiversity and National Parks Act (2015). Whilst the Rodrigues Fruit Bat is still protected under this law, it has provisions for declaring any species as a 'pest' and may allow culling of the species (dispite it being a threatened species). An official cull of nearly 31,000 Mauritius Fruit Bat *Pteropus niger* was sanctioned in 2015 (Tatayah *et al.*, 2017). Whilst the law still protects the Rodrigues Fruit Bat, there are now provisions and a precedent for culling. However, the Rodrigues Regional Assembly is an autonomous administration under the Republic of Mauritius and has the right under the Rodrigues Regional Assembly Act (2001) to pass its own laws and regulations, and it is unlikely to sanction culling of bats in the near future (Tatayah *et al.*, 2017).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008u) [in IUCN (2009)] report a successful captive breeding programme for this species was initiated by the Durrell Wildlife Conservation Trust. In 1995, the International Studbook contained 542 individuals distributed over 18 institutions (Carroll and Feistner, 1996: 334). With breeding populations of this bat now maintained at 46 zoos around the world (David White, studbook keeper, 2016, *pers. comm* in Tatayah *et al.* (2017)). However, Kingston *et al.* (2023: 252) mention that no captive-bred individuals have been released to the wild.

In-situ conservation efforts have concentrated on restoration of the natural habitat, watershed protection and awareness raising among the local people through environmental education

programmes (Powell and Wehnelt, 2003; Trewhella *et al.*, 2005; Tatayah *et al.*, 2017).

GENERAL DISTRIBUTION:
Pteropus rodricensis is confined to the western Indian Ocean island of Rodrigues (Mauritius). It was historically present on the island of Mauritius and Round Island (Mauritius), but is now extinct on these islands. It appears to range up to around 200 m asl.

Native: Mauritius [Mauritius (main island) - Regionally Extinct, Rodrigues].

DETAILED MORPHOLOGY:
Brain
Gardner *et al.* (2007: 196) studied the heart of several *P. rodricensis* specimens kept in captivity, and found it to have a normal cardiac silhouette, comparable to domestic small mammals.

Respiratory
Carter and Adams (2013: 33) postulated that tracheal and primary bronchi calcification will occur in echolocating *Artibeus jamaicensis* but not in non-echolocating *Syconycteris australis* and *Pteropus rodricensis*. The calcification would be needed to counteract the compressive forces executed by the flight muscles on the respiratory tract, as there is a synchronization between wing-beat and respiration, and the latter is linked with the production of echolocation calls. However, to their surprise, they found that the tracheae and primary bronchi of *P. rodricensis* were also heavily calcified.

MOLECULAR BIOLOGY:
Genetics
O'Brien and Hayden (2004: 144) report that, notwithstanding the reduction of the population to less than 70 individuals in the 1970's, the species has still retained some genetic diversity.

DIET:
Carroll (1981: 26) mentioned that these bats eat fruits and flowers of *Mangifera indica* (Mango - Anacardiaceae), *Eucalyptus citriodora* [=*Corymbia citriodora*] (Lemon-scented gum), *Eucalyptus tereticornis* (Forest red gum), *Eugenia jambos* [*Syzygium jambos*] (Myrtaceae), *Styrax benjoin* (Gum benjamin tree - Styracaceae) and *Samanea saman* (Rain tree - Fabaceae). Additionally, fruits of *Ficus* spp. (Moraceae) and *Terminalia catappa* (Indian almond - Combretaceae) are eaten too. Furthermore, seeds and young fruits of *Ravenala madagascariensis* (Traveller's tree - Strelitziaceae) and *Cocos nucifera* (Coconut tree - Arecaceae) might be eaten too, although this is highly unlikely due to the tough outer skin of these.

Courts (1998: 189) reports that captive animals catch insects flying by, and that these were readily eaten. The bats also ate mealworms (*Tenebrio molitor*) and waxmoth larvae (*Galeria mellonella*).
Blood glucose - Heard and Whittier (1997) found blood glucose concentrations within the normal mammalian range.

POPULATION:
Structure and Density
Until around 1916, the species was reported to be abundant on Rodrigues, and even in 1955 large numbers (about 500) still roosted in tamarinds (Mickleburgh *et al.*, 2002a). In 1965 there were fewer bats, but the species was still common. There was a marked decline in the 1970's, and following Cyclone Celine II in 1974-1979, the population was reduced to around 70 bats (Hayes *et al.*, 1996: 21). By 1980 the population had recovered to between 200 and 250 animals (Carroll and Mace, 1988), and at the end of February 1990, the population was estimated to be greater than 1,000 bats (Mickleburgh *et al.*, 2002a), but after a cyclone in February 1991, the number decreased to 485 (Hayes *et al.*, 1996: 22). Afterwards, the population recovered to around 5,076 bats (Powell and Wehnelt, 2003). However, the impact of cyclone Kalunde in March 2003 appears to have reduced the population to around 4,000 animals (Anonymus, 2006), although Caceres (2010: 19) reports that the current population is estimated at about 5,500 individuals.

Price (2013) report that Island-wide bat counts are conducted three times a year at the nine major (‘permanent’, older) roosts and up to nine smaller (‘temporary’, more recent) roosts. In 2016, the population had grown to ca. 20,000 individuals. It is notable that some of the more recent roosts have significantly more bats than the traditional roosts, and this may be an indication of bats recolonizing habitat where they have been extirpated in the past or where vegetation has recovered.

Trend
2016: Increasing (Tatayah *et al.*, 2017; Vincenot *et al.*, 2017). 2008: Increasing (Mickleburgh *et al.*, 2008u; IUCN, 2009).

LIFESPAN:
Hayes *et al.* (1996: 22) indicated that seven of the ten bat's that were part of the founding colony at the Jersey Zoo, were still alive in 1992, making them at least 16 years old.

Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 28 years.

ACTIVITY AND BEHAVIOUR:
For a selection of sounds, check https://search.macaulaylibrary.org.

Riccucci (2016: 94) observed several different behaviours: "play chase" by immature bats flying to one location and rapidly leaving; "play wrestle", which involves close belly contact between individuals, with restrained biting on the neck. He also noticed that pairs or groups of bats (mostly females) wrestle together in long play sessions.

REPRODUCTION AND ONTOGENY:
Kunz *et al.* (1994: 691) report on allomaternal care, or epimeletic (caregiving) behaviour, exhibited by one female toward another, before, during. and after giving birth.

Szekely *et al.* (2015: Suppl.) report a gestation period of 198 days. The young then weights 45 g (adult: 350 g). Drake *et al.* (2021: 239) mention a gestation period of between 4.6 and 6.3 months and an inter-birth interval of 9 months.

Hayes *et al.* (1996: 22) mentioned that the inter-birth interval for wild bats was 12 months, whereas in captive bats, this was reduced to nine months. They also indicated that the bats are monotocous (one young per litter) and that the bats become sexually mature at two years, although it might take up to four years before they actually reproduce.

MATING:
McCracken and Wilkinson (2000: 339) refer to Carroll and Mace (1988), who indicated that *P. rodricensis* forms harem groups consisting of one male and up to eight females.

Riccucci (2011 141) suggests that male-male mounting behaviour is a way to assert dominance.

POSTNATAL DEVELOPMENT:
Carroll (1981: 26) mentioned that in captivity, young of about three weeks were left in the roosts while the mothers feed. In the wild, infants remain much longer with their mothers, which carry them in flight to up to five or six weeks, and were never left in the roosts while the mothers went to feed.

PARASITES:
BACTERIA
Gram-positive bacterium
Heard *et al.* (1979) recorded the following gram-positive bacteria from *Pteropus rodricensis* - *Actinomycetis*, *Bacillus* spp., *Corynebacterium* spp., *Enterococcis* spp., *Lactobacillus* spp., *Staphylococcus aureus*, *Staphylococcus* spp., *Streptococcus* spp. hemolytic, *Streptococcus* sp Group D and *Streptococcus* sp.

Gram-negative bacterium
Heard *et al.* (1979) recorded *Bacteroides* spp., *Escherichia coli*, *Klebsiella oxytoca*, *Klebsiella pneumonia*, *Morganella morganii*, *Proteus mirabilis*, and *Proteus* spp. Helmick *et al.* (2004: 88) reported a *Pasteurella* from one captive bat.

Farina and Lankton (2018: 619) mention that infections by *Yersinia pseudotuberculosis* have been described from captive bats.

FUNGI
Heard *et al.* (1979) recorded an unspecified yeast.

UTILISATION:
In the past the species was also hunted for food, however, this is now rare (Trewhella *et al.*, 2005).

Mahomoodally *et al.* (2019: 6) indicate that fat from *P. rodricensis* has an ethno-pharmacological use: it is melted and applied on the scalp against hair loss.

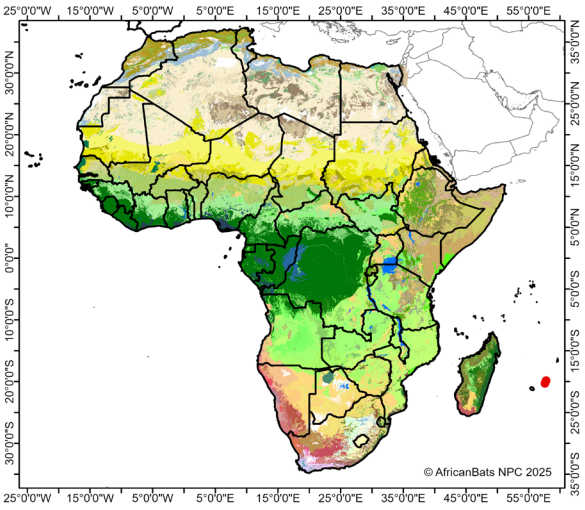

Figure 8. Distribution of *Pteropus rodricensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Mauritius.

Pteropus rufus E. Geoffroy St.-Hilaire, 1803

*1803. *Pteropus rufus* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, 47. Type locality: Madagascar: North and Central Madagascar. [Goto Description]. - Comments: Type

locality originally "Madagascar", restricted to North and Central Madagascar by Andersen (1908b: 367) (See Peterson *et al.*, 1995: 14). Andersen (1912b: viii) indicates that the type was once in the Paris Museum, but is probably no longer in existence. On page 206, he also mentioned that the specimen was sent by "le citoyen Macé, naturaliste" (nr 90 of Geoffroy's catalog). (Current Combination).

1810. *Pteropus Edwardsii* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 15: 92. Type locality: Madagascar: "Madagascar". - Comments: Renaming of *P. rufus* E. Geoffroy Saint-Hilaire, 1803 (see Andersen, 1906c: 206; Allen, 1939a: 60). Mentioned as *edwardii* by Smith (1833: 52) and as *edwarsi* by Koopman (1993a). Description is based on the same specimen as *Pteropus rufus* Geoffroy, 1803.

1816. *Pteropus madagascariensis* Oken, Lehrbuch Naturgeschichte, Jena, 3 (2): 936. Type locality: Madagascar: "Madagascar". - Comments: Renaming of *P. edwardsii* E. Geoffroy Saint-Hilaire, 1810 (see Andersen, 1912b: 207; Allen, 1939a: 60).

1825. *Pteropus phaiops* Temminck, Monogr. Mamm, 1 (5): 178. Publication date: 1825. Type locality: Madagascar: "Madagascar". - Comments: Syntypes: RMNH Jentink Cat. Syst., p. 146 [under *Pt. edwardsi*] c (skull not removed), d (skull removed); Cat. Ost., p. 259, c.

1838. *Pteropus phæops* Oken, Allg. Naturgesch, 7 (2): 990. Type locality: Madagascar.

1878. *[Pteropus] Edvardsii:* Trouessart, Rev. Mag. Zool., sér 3, 6: 202. (Alternate Spelling).

1908. *Pteropus rufus princeps* K. Andersen, Ann. Mag. nat. Hist., ser 8, 2 (10): 367. Publication date: 1 October 1908. Type locality: Madagascar: Tuléar province: Fort Dauphin [25 02 S 47 00 E]. [Goto Description]. Holotype: NHMUK 1891.11.30.10: ad ♂, skull and alcoholic. Collected by: M. Cloisel. See Andersen (1912b: 14), Peterson *et al.* (1995: 14).

? *Pteropus rufus rufus:* (Name Combination).

TAXONOMY:

See Bergmans (1991) and Simmons (2005: 343 - 344). Commonly cited from "E. Geoffroy, 1803. Cat. Mamm. Mus. Nat. Hist. Nat. Paris, p. 47", but this work was never published, which would make this a *nomen nudum*. However, Opinion 2005 (Case 3022) fixed the authorship and date of this name to E. Geoffroy St.-Hilaire (1803) by (see Anonymus, 2002b: 154).

O'Brien *et al.* (2009) suggested that *P. aldabrensis*, *P. rufus*, *P. niger* and *P. seychellensis* (including *comorensis*) should be considered geographical forms of a single species *P. giganteus* (Brünnich, 1782) from the Indian subcontinent, Maldives and Andaman archipelagos.

Almeida *et al.* (2014: 85) place *P. rufus* in the "*vampyrus*" group.

COMMON NAMES:

Castilian (Spain): Zorro volador de Madagascar. Czech: kaloň madagaskarský, upír černolícní. English: Madagascan Flying Fox, Madagascan Flying-fox, Red Flying Fox, Madagascar Fruit Bat, Madagascar Flying Fox. French: Renard volant de Madagascar, Renard volant roux, Roussette rougeâtre, Renard volant malgache. German: Madagaskar-Flugfuchs. Malagasy: Fanihy, Fanihy mena, Fanihy be, Andrehy.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Gunnell *et al.* (2014: 3) refer to Goodman and Junkers (2013), who report on fossil material from the Andrahomana cave in Madagascar.

CONSERVATION STATUS:

Global Justification

This species is listed as Vulnerable (VU A2acd ver 3.1 (2001)) based on the loss of over 30% in the last three generations (18 years; Pacifici *et al.*, 2013). The species can be legally hunted and the reduction can be attributed to the increased level of hunting particularly with the introduction of shotguns and continued loss of its preferred roosting habitats (Andriafidison *et al.*, 2008a; IUCN, 2009; Racey, 2016).

Assessment History

Global

2016: VU A2acd ver 3.1 (2001) (Racey, 2016). 2008: VU A2acd ver 3.1 (2001) (Andriafidison *et al.*, 2008a; IUCN, 2009). 2004: VU A2b+3d ver 3.1 (2001) (Participants of CBSG CAMP Madagascar Mammal Worksh, 2004; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996). 1993: LR/lc (World Conservation Monitoring Centre, 1993).

Regional

None known.

Legal Status

CITES - Appendix II.

On Madagascar, its legal status is "animaux gibiers (game)", which can be hunted between May and August (Andrianaivoarivelo *et al.*, 2022: 1912, 1913).

MAJOR THREATS:

There are numerous threats to this species. It is listed as a game species under Malagasy law and can be legally hunted between the first of May and the first of September (Anonymus, 2007b: 6; Durbin, 2007; Randrianandrianina *et al.*, 2010: 412). Only the few roosts that are in protected areas therefore receive some protection (Racey *et al.*, 2009). *Pteropus rufus* is hunted for food across Madagascar (MacKinnon *et al.*, 2003; Rakotondravony, 2006; Rakotonandrasana and Goodman, 2007; Racey *et al.*, 2009; Randrianandrianina *et al.*, 2010; Andrianaivoarivelo *et al.*, 2022) where it is an

important subsistence food, but also of commercial importance. Although quantitative data on the supply of *P. rufus* for food and the impact of this harvest on colonies/populations is lacking, there is some evidence that the offtake is locally unsustainable (Racey *et al.*, 2009). Hunting occurs at roost sites and where the bats forage, especially when they feed on trees in villages (Jenkins and Racey, 2008). There is evidence that *P. rufus* from Ile Sainte Marie is hunted commercially and frozen shipments are sent to the mainland port of Toamasina (Rakotonandrasana and Goodman, 2007). The conversion of the forest used by roosting bats into agriculture is another threat to *P. rufus* and results in the permanent loss of suitable trees which in many cases have been used for decades. *Pteropus rufus* feeds on several cultivated fruits that have a high economic value in rural Madagascar and is often subjected to persecution.

Randrianandrianina *et al.* (2010: 413) observed that a minimum of five *P. rufus* specimens were caught each night, when they were feeding on kapok (*Ceiba pentandra*) nectar in July. For one roost in Andranomena, Oleksy *et al.* (2015b: 4) reported that six hunters camped for three nights per week for approximately eight months per year and captured about 20 bats per night.

Oleksy *et al.* (2015b: 4), Cardiff and Jenkins (2016: 97) and Andrianaivoarivelo *et al.* (2022: 1912) mention that roost sites are also threatened by fire and agricultural expansion. These roost sites are particularly vulnerable as they are in large trees located in forest fragments in savanna or scrub habitats.

CONSERVATION ACTIONS:
Racey (2016) who support Andriafidison *et al.* (2008a) [in IUCN (2009)] who report that it is listed on CITES Appendix II and is a game species under Malagasy law (Durbin, 2007) but neither of these provide any practical in situ conservation measures (Racey *et al.*, 2009). There are a few roosts in protected areas, notably Parc National Kirindy-Mité, Parc National de Masoala, Parc National de Mananara-nord (MacKinnon *et al.*, 2003) and Berenty Private Reserve (Long, 2002), but many of the existing parks and reserves appear to be without roosting colonies (e.g., Goodman, 1996; 1999; Alonso *et al.*, 2002; Goodman *et al.*, 2005a; Schmid and Alonso, 2005). The ongoing process to triple the surface of protected areas in Madagascar is providing an unprecedented opportunity to include traditional roosts in the new conservation sites. There is also significant scope for local institutions to conserve roosts and this is already occurring in some parts of Madagascar where the bats use sacred forests (Jenkins *et al.*, 2007b) or where communities have created social contracts to protect the bats (Jenkins *et al.*, 2007a).

GENERAL DISTRIBUTION:
Pteropus rufus is endemic to Madagascar. It is one of the most widespread bat species on the island and appears to only be absent from the highly populated central highlands (MacKinnon *et al.*, 2003). The highest density of roost sites is in coastal regions, especially from Morombe in the south-west to Antsiranana in the north (MacKinnon *et al.*, 2003). It has also been recorded from the islands of Nosy Be, Nosy Komba, and Ile Sainte-Marie (Rakotonandrasana and Goodman, 2007: 6).

Michielsen *et al.* (2023: 3) indicate that *P. rufus* is the most recent colonist of Madagascar, arriving about 0.32 (0.08 - 0.65) Myr ago.

González-Gutiérrez *et al.* (2025: Suppl.) calculated that the distribution area of this species covers 591,490.80 km^2.

Native: Madagascar (Bollen and Van Elsacker, 2002; MacKinnon *et al.*, 2003; Simmons, 2005: 344; Rakotonandrasana and Goodman, 2007: 6; Long and Racey, 2007; Jenkins and Racey, 2008).

BIOGEOGRAPHY:
See O'Brien *et al.* (2009) for further details.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Pteropus rufus is the largest bat on Madagascar: total length 23.0 - 31.8 cm, forearm: 14.0 - 17.8 cm, wingspan: 100 - 125 cm and weight: 245 - 749 g (Andrianaivoarivelo *et al.*, 2022: 1912).

DETAILED MORPHOLOGY:
Brain
Tambusso and Fariña (2015: Suppl.) mention a brain mass of 7.30 g for an average body mass of 374.86 g.

Baculum
Rakotondramanana and Goodman (2017: 54) described the baculum having a distal tip forming an arch-shaped structure and a basal portion which is lobed with a distinct central prolongation; length: 3.22, 3.86 mm, width: 3.53, 4.15 mm. In subadults, the bones are notably reduced in length and width.

Skeleton
Sánchez-Villagra *et al.* (2007a: 6) mention that Pteropus rufus has 12 thoracal and 5 lumbar

vertebrae giving a total of 17, whereas 19 is the rule in bats.

MOLECULAR BIOLOGY:
Karyotype
2*n* = 38 and FN = 68, containing 11 pairs of metacentrics, 6 submetacentrics, 1 pair of acrocentrics; X: large submetacentric, Y: small acrocentric (see Richards *et al.*, 2016d: 187, 189).

Genetics
See O'Brien *et al.* (2009).

Wang *et al.* (2025b: 7) report that the total length of the genome is 2.09 Gb.

HABITAT:
MacKinnon *et al.* (2003) failed to locate any roost sites within the endemic spiny forests of south-west Madagascar. Long and Racey (2007) did not find any evidence to show that *P. rufus* uses the endemic plants of the spiny forest in the Mandrare region of Madagascar.

Jenkins *et al.* (2007b: 212) indicate that *P. rufus* is generally found in forest fragments or linear patches of vegetation along water.

HABITS:
Jenkins and Racey (2008) indicate that day roosts and night feeding areas are often spatially distinct, and are up to over 40 km apart. Garbutt (2022: 75) mention that their average flight speed is about 32 km/h, with bursts of over 60 km/h.

ROOST:
P. rufus roost in foliage (Jenkins and Racey, 2008), preferring the outermost branches (probably to avoid predators) (Garbutt, 2022: 75).

In their 2005 survey, Jenkins *et al.* (2007b: 213) have found six roosting sites, with colony sizes ranging from 40 to over 1,000 animals. Three of these were protected by local taboos or ancestral traditions.

Ravelomanantsoa *et al.* (2019: 110) indicate that *P. rufus* uses large trees (e.g., *Cocos nucifera* - Arecaceae) as roost.

Andrianaivoarivelo *et al.* (2022: 1912) report that roosts are generally found in lowlands within 100 km of the coast as well as on offshore island, but sometimes also in the Central Highlands. These roost can contain between 10 and 10,000 individuals, with an average of 250 bats. About 45 % of the original roosts were abandoned between 2001 and 2006. However, in the Central Highlands, 70 % (5 out of 7) of the roosts were abandoned.

DIET:
Bollen and Van Elsacker (2002: 37) found that *P. rufus* at Ste. Luce, ate the fruits of 40 endemic species, and that typically one seed species was found in a dropping. Oleksy and Jones (2013: 113) reported that 110 plant species were found in its diet, of which 59 (55 %) were endemic. However, Long (2002) and Long and Racey (2007) found *P. rufus* at Berenty in south-east Madagascar to have a narrow dietary breadth, consisting of only 14 plant species. The single most important food source for *Petropus rufus* in south-east Madagascar, is the pollen of *Agave sisalana* a commercial introduced species, while they also eat other locally cultivated and introduced fruits (*Mangifera indica*, *Psidium* cf. *cattleianum*, *Sclerocarya caffra*, *Cordia sinensis* and *Hylocereus* sp.) and native and endemic forest species (*Tamarindus indica* (leaves), *Celtis philippensis*, *Ficus megapoda*, *F. grevei*, *F. pachyclada* and *Grewia* sp.) (Long, 2002; Long and Racey, 2007). Jenkins *et al.* (2007b: 212) indicate that the most important food plants include *Ficus guatteriifolia*, *Syzigium* sp., *Terminalia fatrea*, *Uapaca thouarsii* and *U. littoralis*.

Raheriarisena (2005: 255) mentions that this species' diet is composed of fruits (59.0 - 65.1%), flowers (17.3 - 35.0%), and leaves (6.0 - 18.0%), but also that the percentages of these elements vary with the seasonal variations of plant phenology and the species' activity, especially its reproduction status.

Bollen *et al.* (2004a: 603) found that *P. rufus* preferred to consume multi-seeded fruits.

Bollen (2007: 140) lists the following food plants consumed by *P. rufus*: Annonaceae: *Polyalthia madagascariensis* Cavaco & Keraudren, 1957; Araliaceae: *Polyscias* sp.; Areceae: *Dypsis nodifera* Mart., 1849, *Dypsis prestoniana* Beentje, 1995; Bignoniaceae: *Ophiocolea delphinensis* H. Perrier, 1938; Canellaceae: *Cinnamosma madagascariensis* var. *namoronensis* H. Perrier, 1948; Combretaceae: *Terminalia fatraea* (Poir.) DC., 1828; Ericaceae: *Vaccinium emirnense* Hook, 1837; Euphorbiaceae: *Uapaca ferruginea* Baillon, 1858, *Uapaca littoralis* Denis, 1927, *Uapaca thouarsii* Baillon, 1858; Flacourtiaceae: *Ludia antanosarum* Capuron & Sleumer, 1972, *Scolopia orientalis* Sleumer, 1972; Grossulariaceae: *Brexia* sp.; Lauraceae: *Beilschmiedia madagascariensis* (Baillon) Kostermans, 1952, *Ocotea* sp.; Liliaceae: *Dracaena reflexa* var. *nervosa* H. Perrier, 1936;

Loganiaceae: *Anthocleista longifolia* (Lam.) Boiteau, 1973, *Anthocleista madagascariensis*, Baker, 1882, *Bakerella ambongoensis* Balle, 1964, *Bakerella* sp.; Monimiaceae: *Tambourissa purpurea* (Tul.) A. DC, 1868; Moraceae: *Ficus baroni* Baker, 1883, *Ficus guatteriifolia* Baker, 1890, *Ficus pyrifolia* Burm. f., 1768; Myrtaceae: *Syzygium* sp.2; Rubiaceae: *Canthium variistipula* (Arènes ex Cavaco), *Ixora* sp., *Mapouria aegialodes* Bremekamp, 1963, *Mapouria* sp., *Hyperacanthus mandenensis* Rakotonas. & A.P. Davis, 2004, *Tricalysia* cf. *cryptocalyx* Baker, 1882, *Vepris elliotii* (Radlk.) I. Verdoorn, 1926; Sapotaceae: *Sideroxylon beguei* var. *saboureani*, *Sarcolaena multiflora* Thouars, 1805.

Ravelomanantsoa *et al.* (2019: 110) reported that fruits of *Ziziphus jujuba* Mill.(Jujube, Red dade, chinese dade - Rhamnaceae) are consumed.

Oleksy *et al.* (2015a: 678) followed 15 radio-tracked animals (nine ♂♂ and six ♀♀ females) between July and September 2012 and found that females had larger home ranges and core foraging areas, which might be explained by the higher energy requirements of the females during the gestation period. The bats showed a strong preference for overgrown sisal (*Agave sisalana*) plantations, and also ate large quantities of figs (*Ficus grevei*).

Oleksy *et al.* (2017: 1) found seeds of *Ficus polita*, *F. grevei* and *F. lutea* in bat faeces. They found that the seeds that passed through the bat's digestive track had an increased germination success. Hending *et al.* (2021b: 2) observed these bats feeding on *Ceiba pentandra* (kapok).

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Pteropus rufus*: *Anthocleista longifolia* (Lam.) Boiteau, 1973, *Anthocleista madagascarensis* Baker, 1882, *Bakerella ambongoensis* Balle, 1964, *Bakerella clavata* (Desr.) Balle, 1964, *Beilschmiedia madagascariensis* (Baill.) Kosterm., 1952, *Brexia* sp, *Canephora axillaris* Willd., 1798, *Canthium* sp, *Cinnamosma madagascariensis* Danguy, 1910, *Dracaena reflexa* Lamarck, *Dypsis nodifera* Mart., *Dypsis prestoniana* Beentje, *Ficus baronii* Baker, 1883, *Ficus guatteriifolia* Baker, 1890, *Ficus pyrifolia* Salisb., 1796, *Ixora* sp, *Ludia antanosarum* Capuron and Sleumer, 1972, *Ocotea* sp, *Ophiocolea delphinensis* H. Perrier, 1938, *Polyalthia madagascariensis* Cavaco and Keraudren, *Polyscias* sp, *Psychotria aegialodes* (Bremek.) A.P.Davis and Govaerts, 2007, *Rothmannia mandemensis*, *Sarcolaena multiflora* Thouars, 1805, *Scolopia orientalis* Sleumer, 1972, *Sideroxylon beguei* Capuron ex Aubrév., 1974, *Syzygium* sp, *Tambourissa purpurea* (Tul.) A.DC., 1868, *Tricalysia cryptocalyx* Baker, 1882, *Uapaca ferruginea* Baill., 1858, *Uapaca littoralis* Denis, 1927, *Uapaca thouarsii* Baillon, 1858, *Vaccinium eminense*, *Vepris eliottii* (Radlk.) Verd., 1926.

Based on stable isotope analyses, Reuter *et al.* (2016c) found that *Pteropus rufus*, *Eidolon dupreanum* and *Rousettus madagascariensis* have broadly overlapping diets, although there are differences between *P. rufus* and *E. dupreanum*. Furthermore, they found that the diet shifted when these two species occurred sympatrically.

Raharimihaja *et al.* (2016: 9512) tested a number of methods to deter *P. rufus* from feeding on commercial fruits (*Litchi chinensis*). They found that an organic product made from dried blood and vegetable oil (Plantskydd®) with a taste and odour aimed at deterring mammal feeding, gave the best results.

Predators:

Mikula *et al.* (2016: Supplemental data) and Goodman *et al.* (2022: 1900) mention the Madagascar harrier-hawk (*Polyboroides radiates* (Scopoli, 1786)) as diurnal avian predator, although probably not very frequent.

Population:

Structure and Density

Roosts are conspicuous and noisy, but the bats are often tightly clustered making abundance estimates at the larger sites difficult. MacKinnon *et al.* (2003) reported that colony size ranged from 10 to 5,000 animals with a median of 400. They found that nationally 17.5% of 154 roosts had been abandoned in the last ten years and desertion rates were much higher (70%) in the central highlands. The estimated national population size in 2000 was 300,000 (MacKinnon *et al.*, 2003). In December 2005, Rahaingodrahety *et al.* (2008) recorded colony sizes of 900 at Berenty Private Reserve, 412 at Amborabao and 54 at Sainte Luce. Andrianaivoarivelo *et al.* (2022: 1913) reported that their surveys resulted in a count of 100,000 animals in an area that covers about one half of the suitable habitat, which led them to a total population size of about 200,000 bats.

Based on tooth-derived estimated of adult survival, Brook *et al.* (2019a: 165) showed that even with a perfect juvenile annual survival (100 %) stable population trajectories for *P. rufus* are not possible.

Trend
2016: Decreasing (Racey, 2016). 2008: Decreasing (Andriafidison *et al.*, 2008a; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
For a selection of sounds, check https://search.macaulaylibrary.org.

REPRODUCTION AND ONTOGENY:
Kaudern (1914: 11 - 12) reported that he was unable to shoot any pregnant female or females with young during his travels on Madagascar, which took place in the dry season (May to September), so he assumed they had their reproductive season in Spring or Summer [as *P. edwardsi*].

Rand (1935) [in Fox *et al.* (2009: 272)] found two large foetuses in each of the three female specimens that were available to him.

Andrianaivoarivelo *et al.* (2022: 1912) mention that young are born in October and November.

MATING:
This bat's mating season peaks in April and May (Chen *et al.*, 2023: 1912). During that season, males were obsd urinating on chest and neck and rub it in with feet and forearms (Garbutt, 2022: 75).

PARASITES:
BACTERIA
Gram-positive bacterium
Reviewed in McCoy (1974), who listed *Enterococcus* spp. and *Staphylococcus* spp.

Gram-negative bacterium
Mayoux *et al.* (1971: 29) and McCoy (1974) listed *Citrobacter* sp., *Enterobacter* sp., *Escherichia coli*, *Salmonella typhi*, *S. typhimurium*, *Salmonella* spp., and *Shigella flexneri*.

Gomard *et al.* (2016: 5) added *Leptospira* to this list (see also Dietrich *et al.*, 2018a: 3).

PROTOZOA
Ranaivoson *et al.* (2019: 1) were the first to report *Babesia* sp. (order Piroplasmida; family Babesiidae), an erythrocythic protozoan) from Madagascan bats (and the first Pteropodid infection). They examined 203 *P. rufus*, of which nine (all males) were positive for babesial infection, whereas none of the 203 bats carried any ectoparasites.

Ranaivoson *et al.* (2015: 76) reported the presence of (*Hepatocystis* spp. (Haemosporida). As this parasites prevalence in this tree-roosting bat was higher than in the cave-roosting *Eidolon dupreanum*, this seems to suggest that a mosquito might be the vector for this parasite.

VIRUSES:
Astroviridae - Astroviruses
Horigan *et al.* (2024: 2.) reported the presence of astroviruses in Malagasy *Pteropus rufus*.

Coronaviridae - Coronaviruses
Thirteen novel strains of betacoronaviruses were identified in Madagascar in 2010 (Razanajatovo *et al.*, 2015).

Kettenburg *et al.* (2022) discovered a new virus belonging to the genus *Betacoronavirus* and subgenus *Nobecovirus*.

Filoviridae
Ebola virus
Brook *et al.* (2019b: 1004) reported the presence of reliable reactive antibodies to tested antigens in serum from *P. rufus*. However, they also mention (p. 1010) that no filoviruses (nor henipaviruses) have been identified from Madagascan bats (either via live viruses or RNA).

Flaviviridae
Coulanges *et al.* (1974) [in Fontenille *et al.* (1989: 239)] found antibodies against West-Nile virus in 11.4 % of the 94 bats from the Anjiro region they examined.

Paramyxoviridae
3 out of 20 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

Henipavirus
Nipah (NiV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found an overall contamination of 2.3%.

Hendra (HeV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found an overall contamination of 2.3%. Brook *et al.* (2019b: 1004) reported the presence of reliable reactive antibodies to tested antigens for HeV in serum.

Tioman (TiV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found an overall contamination of 2.3%.

Rhabdoviridae – Rabies like viruses
Lyssavirus - Rabies related viruses
Andriamandimby *et al.* (2013: 3) reported on one *P. rufus* from Madagascar, which tested positive to antibodies for European Bat Lyssavirus type 1 (EBLV-1). Of the 11 bats tested by Mélade *et al.*

(2016a: 6) for *Duvenhage lyssavirus*, five showed a positive reaction.

UTILISATION:
Pteropus rufus being the largest bat is the main source of bat bushmeat in Madagascar (Jenkins and Racey, 2008). In many regions nets are erected inside or on the periphery of roosts to intercept flying bats (Jenkins *et al.*, 2007b; Jenkins and Racey, 2008). In southern Madagascar *P. rufus* is netted when it feeds on sisal (*Agave sisalana*) plants at night and at least some of the bats are sold locally (Rahaingodrahety, 2007). Firearms (shotguns) are also used to hunt *P. rufus* in many areas (Jenkins and Racey, 2008). In eastern Madagascar individual trees with roosting bats are felled by hunters who club the fallen animals with sticks (MacKinnon *et al.*, 2003).

Pteropus rufus is hunted in the Daraina area in northeastern Madagascar (Rakotondravony, 2006) where roosts of over 1,000 individuals have been reported from littoral forest (Jenkins and Racey, 2008). Although the people living around the forests refrain from eating the bats, the colonies are reportedly subject to frequent hunting by local immigrants (Rakotondravony, 2006). In Makira, *P. rufus* is eaten widely by local communities and at $1.5 US/kg was the most expensive meat (Golden, 2005). In the Mahavavy-Kinkony area of western Madagascar, regular hunting at a *P. rufus* roost was reported by Rakotoarivelo and Randrianandrianina (2007); hunting teams of up to eight men visited the roost on a regular basis and caught up to 100 bats on each occasion. These were sold around villages and to local restaurants for $0.5 US each. On Nosy Boraha, *P. rufus* is regularly exploited from at least one roost and is served seasonally in restaurants in the main town on the island (Rakotonandrasana and Goodman, 2007). One hunter also reported that frozen shipments of *P. rufus* are sent to the mainland port of Toamasina (Rakotonandrasana and Goodman, 2007). At a small restaurant near Mahajanga in 2000, at least 30 *P. rufus* were reportedly sold daily, although it is not clear whether this figure is monthly average estimate or reflects a seasonal peak in availability (Racey *et al.*, 2009). In the sisal plantations surrounding Berenty Private Reserve, hunters can expect to catch 8 - 12 individuals per week between September and May and 25 - 30 between June and August, where they are sold discretely in villages around the reserve for $ 0.7 - 1.0 US (Rahaingodrahety, 2007) therefore a single hunter could catch between 164 and 192 bats per year.

Pteropus rufus and *Eidolon dupreanum* appear to be the only species sold in restaurants, where they are either served individually, complete with head and wings, jointed, or are diced up into small pieces and accompanied by rice (Jenkins and Racey, 2008).

Rakotondravony (2006) considered hunting of *P. rufus* a minor threat in northern Madagascar, while Golden (2005) reported large annual harvests in the Makira forest and Maroantsetra were unsustainable.

See also Goodman *et al.* (2008d).

Golden and Comaroff (2015: 5) indicate that flying foxes and other fruit bats (including *P. rufus*) are frequently the subject of food taboos, which they link to the fact that these bats are carriers of virulent zoonotic diseases.

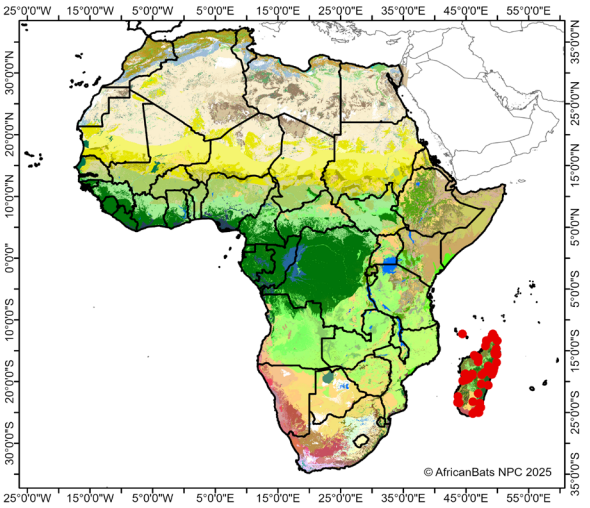

Figure 9. Distribution of *Pteropus rufus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Comoros, Madagascar, Seychelles.

Pteropus seychellensis A. Milne-Edwards, 1877

*1877. *Pteropus seychellensis* A. Milne-Edwards, Bull. Sci. Soc. Philom. Paris, sér 7, 2: 221. Type locality: Seychelles: Mahe Island. Lectotype: MNHN ZM-MO-1878-1110: ad ♂, mounted skin and skull. Collected by: Auguste Lantz. Rode (1941: 230) mentions numbers "157", "35A" and "1878-1110". Paralectotype: MNHN ZM-MO-1878-1106: Collected by: Auguste Lantz. Rode (1941: 230) mentions numbers "157b,c,d", "35C" and "1878-1106,1108, 1109". Paralectotype: MNHN ZM-MO-1878-1107: ♂, mounted skin and skull. Collected by: Auguste Lantz. Rode (1941: 230) mentions numbers "157a", "35B" and "1878-1107". Paralectotype: MNHN ZM-MO-1878-1108: Collected by: Auguste Lantz. Rode (1941: 230) mentions numbers "157b,c,d", "35C" and "1878-1106,1108, 1109". Paralectotype: MNHN ZM-MO-1878-1109: Collected by: Auguste Lantz. Rode

(1941: 230) mentions numbers "157b,c,d", "35C" and "1878-1106,1108, 1109". Paralectotype: MNHN ZM-MO-1878-1111: ad ♀, skin and skull. Collected by: Auguste Lantz. Paralectotype: MNHN ZM-MO-1878-1112: ad ♀, skin and skull. Collected by: Auguste Lantz. - Comments: Bergmans (1991: 151) indicated that the lectotype (MNHN CG 1878-1110), as well as most of the other specimens on which Milne-Edwards based his description, were in fact collected by Lantz on Marianne Island, and not on Mahé Island. (Current Combination).

1880. *Pteropus comorensis* Wallace, Island Life, 400. Type locality: Comoros: "Comoro Islands". - Comments: Allen (1939a: 60) and Simmons (2005) mention J.M. Nicoll, 1908 as author, since the original description by Wallace (1880) is actually a nomen nudum.

1908. *Pteropus comorensis* Nicoll, Three voyages of a naturalist being an account of many little-known islands in three oceans visited by the "Valhalla" R.Y.S. - Witherby & Co. London, 87. Type locality: Mayotte: Buzi Island. [Goto Description]. Paratype: SMF 44784: ♂, skull and alcoholic. Collected by: Michael John Nicoll; collection date: 1906. Syntype: NHMUK 1906.6.3.14: ad ♂, skin and skull. Collected by: Michael John Nicoll; collection date: 2 March 1906. Presented/Donated by: Earl of Crawford. Syntype: NHMUK 1906.6.3.15: ad ♂, skin and skull. Collected by: Michael John Nicoll; collection date: 2 March 1906. Presented/Donated by: Earl of Crawford. Syntype: NHMUK 1906.6.3.16: ad ♂, skin and skull. Collected by: Michael John Nicoll; collection date: 25 February 1906. Presented/Donated by: Earl of Crawford. - Comments: Nicoll (1908: 88) mentions that the bats were shot in the evening when returning to the ship, and before (p. 87) he mentioned that every evening the bats were flying from the little island (= "Buzi Island") to the main island (= Mayotte).

2016. *Pteropus seychellensis comoroensis:* Amador, Moyers Arévalo, Almeida, Catalano and Giannini, J. mamm. Evolut., 25 (1): Suppl (for 2018). Publication date: 24 November 2016. (Lapsus).

2025. *P[teropus] comoroensis:* Almeida, Helgen, Simmons, and Giannini, Proc. R. Soc. Lond., B 292 (2051): 20250743 (Suppl). Publication date: 16 July 2025. (Lapsus).

? *Pteropus seychellensis comorensis:* (Name Combination).

? *Pteropus seychellensis seychellensis:* (Name Combination).

TAXONOMY:
Hill (1971a: 574) included *aldabrensis*, but we follow Bergmans (1991) and Simmons (2005: 344) who considers this to be a separate species.

It seems probable that the two recognized subspecies *Pteropus seychellensis seychellensis* (from the Seychelles) and *Pteropus seychellensis comorensis* (from the Comoros Islands and Mafia Island) represent distinct taxa at the species level. In addition, the population of *Pteropus seychellensis comorensis* from Mafia island (Tanzania) might represent a species distinct from the populations of this bat recorded from the Comoros Islands (Mickleburgh *et al.*, 2008di; IUCN, 2009).

O'Brien *et al.* (2009) suggested that *P. aldabrensis*, *P. rufus*, *P. niger* and *P. seychellensis* (including *comorensis*) should be considered geographical forms of a single species *P. giganteus* (Brünnich, 1782) from the Indian subcontinent, Maldives and Andaman archipelagos. O'Brien *et al.* (2009) show that *P. s. seychellensis* is more closely related to *P. niger* from Mauritius, than to *P. s. comorensis*. Further, based on cytochrome *b* and 12S results, there appears to be no notable genetic differentiation in populations of *P. s. comorensis* from Grande Comore and Mayotte, suggesting genetic exchange.

Chan *et al.* (2011: 7) found that *P. s. comorensis* and *P. rufus* alleles differed by as few as two base-pairs. Based on this mitochondrial haplotype network, *P. s. seychellensis* was more closely related to *P. niger* and these two were more closely related to *P. rufus* than to *P. s. comorensis*.

Almeida *et al.* (2014: 85) place *P. seychellensis* in the "*vampyrus*" group.

The analyses by Almeida *et al.* (2025: Suppl.) indicate that *P. s. seychellensis* groups with *Pteropus niger*, whereas *P. s. comorensis* groups with *P. aldabrensis* and *P. rufus*, but all five taxa are closely related and form a clade of West Indian Ocean islands species. They also suggest to raise comorensis to full species rank.

COMMON NAMES:
Castilian (Spain): Zorro volador de las Seychelles. Comorian: ndema, ndrema. Czech: kaloň seychelský. English: Seychelles Flying Fox, Seychelles Fruit Bat. French: Renard volant des Seychelles, Roussette des Seychelles. German: Seychellen-Flugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008di; IUCN, 2009; Goodman, 2017k).

Assessment History
Global
2016: LC ver 3.1 (2001) (Bergmans *et al.*, 2017b). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008di; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cs; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

1993: LR/lc (World Conservation Monitoring Centre, 1993); VU [assessed as *P. s. aldabrensis*] (World Conservation Monitoring Centre, 1993). 1990: VU [assessed as *P. s. aldabrensis*] (IUCN, 1990). 1988: VU [assessed as *P. s. aldabrensis*] (IUCN Conservation Monitoring Centre, 1988).

Regional
None known.

Legal Status
CITES - Appendix II.

MAJOR THREATS:
Overall, there currently appear to be no major threats to the species. There is some limited hunting for food on a few islands in the species range (e.g., Mahé and Praslin in the Seychelles) however, this does not appear to be significantly impacting the population at present. Additional localised threats include mortality through collision with power lines, and possible persecution as a pest of fruit crops (Mickleburgh *et al.*, 2008di; IUCN, 2009; Bergmans *et al.*, 2017b). However, Sagot and Chaverri (2015: 1670) mention the following threats: Roost loss or disturbance, habitat degradation or loss, introduced predators.

Ibouroi *et al.* (2025: 1, 2) reported that the second largest colony of *Pteropus seychellensis comorensis* in the Comoros underwent an dramatic decline after the passage of cyclone Chido in December 2024 (from 5,700 to 113 individuals).

Based on the numerous amount of bats around Mutsamudu (Anjouan, Coromo islands), Middleton and Hume (2010: 132) report that this bat is not a part of the people's diet.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008di) [in IUCN (2009)] report that a large population (2,000 to 3,000 bats) of this species is present in the Morne Seychellois National Park on Mahé, Seychelles (Nicoll and Racey, 1981). There is a general need to continue monitoring activities for this species in order to detect any possible declines and to determine if there are any movements between populations. Studies are underway to better determine the taxonomic status of the population of bats from Mafia Island (*Pteropus seychellensis comorensis*) largely to understand if this population should be recognised at the species level distinct from *P. seychellensis*. The population of Mafia Island may be threatened, and an assessment of the situation on this island and of the possibilities for the species' protection there is highly desirable (Mickleburgh *et al.*, 2002a).

Based on their study of mitochondrial and microsatellite markers, Ibouroi *et al.* (2018a: 1425) conclude that the populations of *P. seychellensis* occurring on the Comoro Islands can be treated as one management unit for conservation purposes (contrary to what they found for *P. livingstonii*).

GENERAL DISTRIBUTION:
Pteropus seychellensis has been recorded from the Seychelles, the Union of the Comoro and Tanzania. In the Seychelles it is present on a number of islands including Mahé, Praslin, La Digue, and Silhouette. Gerlach (2004) mentions that it has recently been recorded roosting on several islands where its presence was previously unconfirmed. In the Comoros it is known from the islands of Anjouan, Grand Comore and Moheli. In Tanzania, it is restricted to Mafia island, possibly Zanzibar, although Simmons (2005) considers this record extremely dubious.

Ibouroi *et al.* (2018b: 2395) indicated that its distribution is negatively correlated to natural forest across the entire area on the Comoro Islands, but that its foraging areas were positively correlated with natural forests and high-elevation areas.

Cheke (2011: 59) argues this species (as *P. comorensis*) was introduced on Mafia island by Comorians, rather than having arrived on the island by itself, which he supports by indicating that the bat was not noticed (perhaps not present) until the 1930s, and that no bones were found in middens (p. 65).

Known across an elevational range on Grand Comore from sea level to 1,000 m, on Anjouan from sea level to 760 m, on Mohéli from sea level to 500 m, and Mayotte from sea level to 250 m (Cheke and Dahl, 1981; Mickleburgh *et al.*, 1992; Trewhella *et al.*, 2001; Goodman *et al.*, 2010c: 123).

Native: Comoros (Goodman *et al.*, 2010c: 123 as *P. s. comorensis*); Mayotte; Seychelles; Tanzania.

BIOGEOGRAPHY:
See O'Brien *et al.* (2009) and Goodman *et al.* (2010c: 123) for further details.

DENTAL FORMULA:
None of the 27 skulls examined by Esquivel *et al.* (2021: Suppl.) had an anomalous number of teeth.

MOLECULAR BIOLOGY:
Genetics
See O'Brien *et al.* (2009).

HABITAT:
Goodman *et al.* (2010c: 123) indicate that *P. s. comorensis* is adapted to the anthropogenic transformation of the former natural habitats of the different islands, including the widespread plantations of fruit trees. They occur in a variety of habitats from urban settings, agricultural zones, to remnant forest patches.

HABITS:
See Cheke and Dahl (1981); Trewhella *et al.* (1995); Trewhella *et al.* (2001) and Louette (2004).

Gerlach (2003: 79) reports on *P. seychellensis* specimens flying low over the sea surface and dipping their belly fur in the water. He postulates that this is possibly a strategy to remove parasites. The risk of falling in sea was minimised as the bats only dipped in exceptionally calm weather.

Based on wing morphology, Lindhe Norberg *et al.* (2000) classified this species (as *P. seychellensis comorensis*) as "non-soaring".

ROOST:
Racey and Nicoll (1984) [in O'Brien (2011: 262)] indicate that *P. seychellensis* roosts in tall trees (*Casuarina* or *Albizzia*).

Ibouroi *et al.* (2018b: Suppl.) reported the following roost trees being used by *P. seychellensis comorensis* on the Comoro Islands: Anacardiaceae: *Mangifera indica, Brachylaena ramiflora*; Bombacaceae: *Adansonia digitata, Ceiba pentandra*; Caesalpiniaceae: *Tamarindus indica* Combretaceae: *Terminalia catappa* Fabaceae: *Pterocarpus indicus*; Lauraceae: *Ocotea comorensis*; Leeaceae: *Leea guineensis*; Loganiaceae: *Nuxia pseudodenta*; Mimosaceae: *Albizia glaberrima, Albizia lebbeck*; Moraceae: *Artocarpus heterophyllus, Ficus antandronarum, Ficus lutea, Ficus pirifolia*; Myrtaceae: *Eucalyptus* sp., *Eugenia jambolana*; Sapindaceae: *Litchi chinensis*.

DIET:
Pteropus seychellensis eats 27 species of plant, including 17 fruits (Racey and Nicoll, 1984).

Trewhella *et al.* (2001: 141) reported the following food items (with known items in bold and suspected in plain text): Anacardiaceae: *Anacardium occidentale* L. (cashew), ***Mangifera indica*** L. (mango); Annonaceae: *Annona muricata* L. (soursop), *Annona reticulata* L. (custard apple), *Annona squamosa* L. (sugar apple or sweetops); Aphloiaceae: *Aphloia theaeformis* [= *Aphloia theiformis* (Vahl) Benn.]; Arecaceae: *Cocos nucifera* L. (coconut tree); Cannabaceae: *Trema orientalis* (L.) Blume (charcoal-tree, Indian charcoal-tree,pigeon wood or Oriental trema); Caricaceae: ***Carica papaya*** L. (papaya); Combretaceae: ***Terminalia catappa*** L. (Indian-almond); Fabaceae: ***Erythrina*** sp. (coral trees); Gentianaceae: *Anthocleista grandiflora* L. (forest fever tree); Lamiaceae: ***Vitex*** sp. (chaste tree); Loganiaceae: *Strychnos spinosa* Lam. (Natal orange, spiny orange or green monkey orange); Malvaceae: ***Adansonia digitata*** L. (baobab), ***Adansonia madagascariensis*** Baill. (baobab), ***Ceiba pentandra*** (L.) Gaertn. (kapok tree); Monimiaceae: *Tambourissa anjouanensis*, *Tambourissa leptophylla* (Tul.) A. DC., *Tambourissa mohelienses* Lorence, *Tambourissa paradoxa* Perkins; Moraceae: *Artocarpus altilis* (Parkinson) Fosberg (breadfruit), *Artocarpus heterophyllus* Lam. (jackfruit or jack tree), ***Ficus*** sp.; Musaceae: *Musa sapientum* L. (banana or plantane); Myrtaceae: *Eugenia jambos* L. [= *Syzygium jambos* L. (Alston)] (rose apple), *Psidium cattleyanum* Sabine (Cattley guava, strawberry guava or cherry guava), *Psidium guajava* L. (common guava), ***Syzygium cuminii*** (L.) Skeels (Java plum); Oxalidaceae: *Averrhoa bilimbi* L. (bilimbi, cucumber tree or tree sorrel); Rubiaceae: *Psychotria* aff. *aledjoensis* De Wild. [= *Psychotria mannii* Hiern, 1877]; Rutaceae: *Citrus* x *aurantifolia* (Christm.) Swingle (key lime), *Citrus* x *aurantium* L. (bitter orange, seville orange, sour orange, bigarade orange, or marmalade orange), *Citrus reticulata* Blanco, 1837 (mandarine orange), *Citrus* x *sinensis* (L.) Osbeck (orange).

POPULATION:
Structure
O'Brien *et al.* (2009), based on cytochrome *b* and 12S results, indicated that there appeared to be no notable genetic differentiation in populations of *P. s. comorensis* from Grande Comore and Mayotte, suggesting genetic exchange.

Density
This species is widespread throughout the Seychelles, with some colonies consisting of up to 300 individuals. It is very common in villages and towns (Goodman, 2007). The population was estimated to be around 10,000 individuals on the Seychelles in 1979, and was believed to be

close to this level in 2004 although adequate censuses have not been completed for all islands (Gerlach, 2004).

On the Comoro Islands, Ibouroi *et al.* (2018b: 2406) observed 11,898 bats at 59 different sites, with colony sizes varying between 11 and 742 individuals (average: 184).

Trend
2016: Stable (Bergmans *et al.*, 2017b). 2008: Stable (Mickleburgh *et al.*, 2008di; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Riccucci (2016: 93) reported on play behaviour on Praslin Island, which included play-fighting, tussle, and play-chasing. He indicated that this behaviour was not limited to young bats but saw this also among adults.

Trewhella *et al.* (2001: 135) indicate that the sympatric *P. livingstonii* is more diurnally active (leaving their roosts at 11 a.m.) than *P. seychellensis comorensis* (leaving its roosts not before 3 p.m.), and is the dominant species during their encounters.

REPRODUCTION AND ONTOGENY:
See Trewhella *et al.* (1995) and Reinhardt and Jacobs (2006).

MATING:
McCracken and Wilkinson (2000: 339) indicate that Cheke and Dahl (1981) reported that *P. seychellensis* forms harem groups.

PARASITES:
BACTERIA
Dietrich *et al.* (2018a: 3) reported the presence of bacteria of the genus *Leptospira*.

VIRUSES:
Astroviridae
Hoarau *et al.* (2018: 1) tested 21 bats from the Comoros, but none of them tested positive for this group of viruses.

Rhabdoviridae
Four of 40 tested bats from Mayé showed a seroreaction against *Lagos bat lyssavirus* (LBV) (Mélade *et al.*, 2016a: 6). Six against *Duvenhage lyssavirus* (DUVV), and one out of 17 tested, against *European bat lyssavirus 1* (EBL-1). For the 19 specimens tested from Mayotte, two were positive for LBV and one for DUVV.

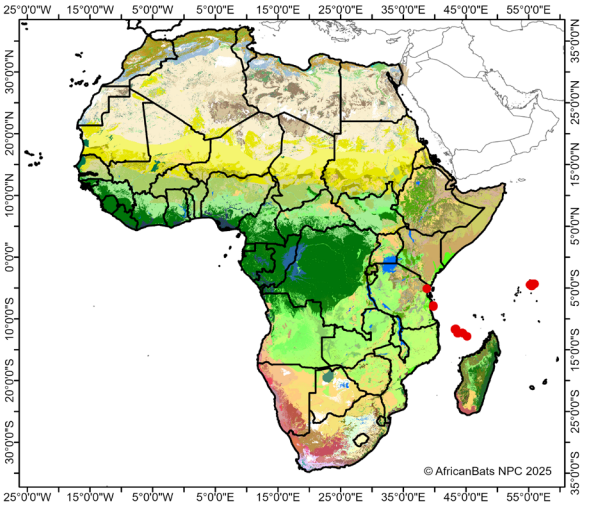

Figure 10. Distribution of *Pteropus seychellensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Comoros, Mayotte, Seychelles, Tanzania.

Pteropus subniger (Kerr, 1792)

*1792. *Vespertilio vampyrus subniger* Kerr, in: Linnaeus, Animal Kingdom, 1 (1): xvii, 91. Publication date: February 1792. Type locality: Réunion: "Réunion island". - Comments: Andersen (1912b: viii) mentions that the type was originally in the Cabinet Réaumur, but is probably no longer in existence.

1802. *Spectrum rubidum* Daudin, in: Buffon, Histoire Naturelle des Quadrupèdes, Didot ed, 14: 188. Type locality: Réunion: Reunion. - Comments: Type locality fixed by Andersen (1912b: 169) since the name was proposed for Buffon's Rougette, which was based on a specimen sent by de la Nux from Reunion. The year of publication might not be correct (see Allen, 1939a: 61).

1803. *Pteropus fuscus:* Desmarest, Nouveau Dictionnaire d'Histoire Naturelle, 19: 544. Type locality: Réunion: "Réunion Island". - Comments: Not of E. Geoffroy Saint-Hillaire, 1803, see Allen (1939a: 61).

1803. *Pteropus ruber* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, 48. Type locality: Réunion: Réunion. [Goto Description]. - Comments: Originally "Madagascar", but corrected to Réunion by Andersen (1912b: 169). Andersen also indicates that the type specimen is not in the Paris Museum.

1810. *Pteropus rubricollis* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 15: 93. Type locality: Réunion: "Réunion Island". - Comments: One specimen sent by Mr. de la Nux: see Geoffroy Saint-Hilaire (1810a: 94). Andersen (1912b: 169) indicates that this is the same specimen as used by Brisson (1756) for his description of "*Pteropus collo rubro*" and by Buffon (1763) for his "*Rougette*".

1814. *Pteropus torquatus* G. Fischer, Zoognosia, 3: 553. - Comments: This is a renaming and redescription of Brisson's "*Pt. collo rubro*" (see Andersen, 1912b: 169).

1815. *Pteropus collaris* Illiger, Abh. K. Preuss. Akad. Wiss. Berlin, 78, 84. Type locality: Réunion: Réunion: Type locality originally "E. African Islands", but restricted to Réunion by Andersen (1912b: 169). - Comments:

"According to Andersen (1912b: 169), it looks like the publication was part of series dated 1804-1811, but actually appeared in 1815 in the section on E. African Islands." Simmons (*pers. comm.*).
1837. *Pteropus vulgaris* Temminck, Monogr. Mamm, 2 (11): 74, pl 38. Publication date: 1837.
? *Pteropus subniger:* (Name Combination, Current Combination).

TAXONOMY:
See Bergmans (1991) and Simmons (2005: 344).

Almeida *et al.* (2014: 83) indicate that *P. subniger* could not be tested, but tentatively placed in an "*incertae sedis*" group.

COMMON NAMES:
Castilian (Spain): Zorro volador oscuro de Mauricio. Czech: kaloň maskarénský, upír obecný, upír červenokrký, kaloň obojkový. English: Dark Flying Fox, Lesser Mascarene Flying Fox, Lesser Mascarene Flying-fox. French: Petit Renard volant de Mascareignes, Roussette foncée, Rougette, Petit renard volant de Mascarene, Roussette à collet rouge. German: Kleiner Maskarenen-Flugfuchs.

CONSERVATION STATUS:
Global Justification
The last authentic record of this species on Mauritius was in 1859, but it is believed to have died out between 1864 and 1873. On Réunion, no new records appeared after 1862 and it seems probable that it became extinct in the 1860s (Mickleburgh *et al.*, 2008de; IUCN, 2009; Mickleburgh *et al.*, 2020c).

Assessment History
Global
2019: Ex ver 3.1 (2001) (Mickleburgh *et al.*, 2020c). 2008: Ex ver 3.1 (2001) (Mickleburgh *et al.*, 2008de; IUCN, 2009). 2004: Ex ver 3.1 (2001) (Mickleburgh *et al.*, 2004cu; IUCN, 2004). 1996: Ex (Baillie and Groombridge, 1996). 1994: Ex (Groombridge, 1994). 1993: Ex (World Conservation Monitoring Centre, 1993). 1990: Ex (IUCN. 1990). 1988: Ex (IUCN Conservation Monitoring Centre, 1988). 1981: probably extinct (Cheke and Dahl, 1981).

Legal Status
CITES - Appendix II.

MAJOR THREATS:
Both deforestation and local hunting are thought to have contributed to the extinction of this species. It was thought to have lived in hollow trees (Mickleburgh *et al.*, 2008de; IUCN, 2009).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008de) [in IUCN (2009)] and Mickleburgh *et al.* (2020c) report that this is no longer applicable.

GENERAL DISTRIBUTION:
Pteropus subniger was previously known from the Mascarenes Islands (Mauritius and Réunion). It was restricted to elevations of between 1,200 and 1,600 m asl.

O'Brien (2011: 286) reports it from the Tanzanian island of Mafia.

Regionally extinct: Mauritius; Réunion.

DENTAL FORMULA:
None of the eight skulls examined by Esquivel *et al.* (2021: Suppl.) had an aberrant number of teeth.

POPULATION:
Structure and Density
This species is now extinct. It is believed to have become extinct on Mauritius between 1864 and 1873. It is likely to have disappeared from Réunion in the 1860s. It may have lasted a little longer but is now certain to be extinct. In the 1730s it was common enough to consider for the bat oil trade (Mickleburgh *et al.*, 2008de; IUCN, 2009; Mickleburgh *et al.*, 2020c).

UTILISATION:
Caceres (2010: 9) indicates that in the 1730s its population (on La Réunion) was large enough to trade its fat.

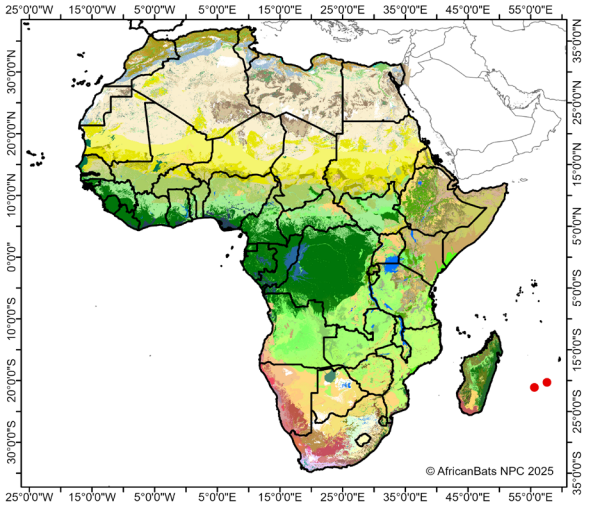

Figure 11. Distribution of *Pteropus subniger*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Mauritius, Réunion.

Pteropus voeltzkowi Matschie, 1909

*1909. *Pteropus (Spectrum) voeltzkowi* Matschie, Sber. Ges. naturf. Freunde Berlin, 486. Publication date: October 1909. Type locality: Tanzania: Pemba Island: Fufuni [ca. 07 31 S 38 25 E]. Holotype: ZMB 88677: ad ♂, skin and skull. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 13 March 1903. Paratype: ZMB |TS555|: ad ♀. See Turni and Kock (2008). Paratype: ZMB 88678: ad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 13 March 1903. See Turni and Kock (2008). Paratype: ZMB 88679: ad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 12 March 1903. See Turni and Kock (2008). Paratype: ZMB 88680: ad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 13 March 1903. See Turni and Kock (2008). Paratype: ZMB 88681: ad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 13 March 1903. See Turni and Kock (2008).

2010. *P[teropus] voletzkowi:* Goodman, Weyeneth, Ibrahim, Saïd and Ruedi, Acta Chiropt., 12 (1): 133. (Lapsus).

? *Pteropus voeltzkowi:* (Name Combination, Current Combination).

TAXONOMY:
See Bergmans (1991) and Simmons (2005: 346).

P. voeltzkowi together with *P. livingstonii* form the most distinct and ancient lineage of the western Indian Ocean *Pteropus* spp. (O'Brien *et al.*, 2009). The phylogenetic analyses performed by Chan *et al.* (2011: 7) suggest that both are sister species. This is supported by Almeida *et al.* (2014: 85), who place this species in the "*livingstonii*" group.

COMMON NAMES:
Castilian (Spain): Zorro volador de Voeltzkow. Czech: kaloň pembánský, kaloň pembský. Dutch: Pemba vliegende hond. English: Pemba Flying-fox, Pemba Flying Fox. French: Renard volant de Pemba. German: Pemba-Flugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (VU D2 ver 3.1 (2001)) because it is known from only a single location (Pemba Island), where ongoing active conservation activities have significantly reduced the plausibility of future declines of this species (Mickleburgh *et al.*, 2008df; IUCN, 2009; Entwistle and Juma, 2016). Entwistle and Juma (2016) report that hunting has been reduced but not stopped, human disturbance at roost sites and conflict with local fruit growers are plausible threats increasing that could drive the species to a higher threatened status.

The mathematical taxon-rich model developed by Welch and Beaulieu (2018: 10) placed *Pteropus voeltzkowi* on the tenth position of the top ten bat species at risk of extinction worldwide.

Assessment History
Global
2016: VU D2 ver 3.1 (2001) (Entwistle and Juma, 2016). 2008: VU D2 ver 3.1 (2001) (Mickleburgh *et al.*, 2008df; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Mickleburgh *et al.*, 2004cw; IUCN, 2004). 2002: CR C2a (Mickleburgh *et al.*, 2002a: 22). 1996: CR (Baillie and Groombridge, 1996). 1994: EN (Groombridge, 1994). 1993: EN (World Conservation Monitoring Centre, 1993). 1990: EN (IUCN, 1990). 1988: VU (IUCN Conservation Monitoring Centre, 1988).

Regional
None known.

Legal Status
CITES - Appendix II.

MAJOR THREATS:
Much of the natural forest habitat of this bat has been cleared or severely fragmented. The species has been hunted for food with the use of shotguns replacing traditional methods, resulting in an unsustainable use (Seehausen, 1991; Entwistle and Corp, 1997a). As of 2005, hunting had been reduced but not stopped on Pemba (Trewhella *et al.*, 2005). An additional threat is posed by the collision of bats with overhead electric cables (Mickleburgh *et al.*, 2008df; IUCN, 2009).

In addition human disturbance at roost sites appears to have a significant impact on colony sizes (Robinson *et al.*, 2010). A potential emerging threat may include increasing conflict with local fruit growers, given the species' growing population and tendency to eat cultivated fruit (Robinson *et al.*, 2010).

CONSERVATION ACTIONS:
Entwistle and Juma (2016) supports Mickleburgh *et al.* (2008df) [in IUCN (2009)] who report that ongoing awareness raising on the importance and uniqueness of the endemic fruit bat, and the need for sustainable hunting, has been undertaken through environmental education programmes (Trewhella *et al.*, 2005; Juma, 2007). Income for the local community is being generated through bat related ecotourism activities (Juma, 2007). It has been reported from the recently gazetted Ngezi-Vumawimbi Nature Forest Reserve and Msitu Kuu Forest (Pakenham, 1984; Juma, 2007). Illegal logging and the invasive umbrella tree (*Maesopsis eminii*), that degrades the habitat of this bat, are

being controlled within the Nature Forest Reserve (Juma, 2007).

A captive breeding program was set up in 1994, starting with 18 specimens, of which 12 were housed in the Phoenix Zoo (USA), but only 4 ♂♂ and 1 ♀ survived, and Carroll and Feistner (1996: 334) were not yet able to provide information about the program's success.

GENERAL DISTRIBUTION:
Pteropus voeltzkowi is endemic to the island of Pemba in Tanzania, where it occurs at elevations from sea level to 45 m asl. The entire distribution area of this species cover 1,031.27 km^2 (González-Gutiérrez *et al.*, 2025: Suppl.).

Native: Tanzania.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
P. voeltzkowi is the largest bat occurring on Pemba Island, with a weight up to 600 g and a wingspan of about one meter (Amman *et al.*, 2021: 2).

MOLECULAR BIOLOGY:
Genetics
See O'Brien *et al.* (2009).

ROOST:
Entwistle and Corp (1997a: 137) reported roosts to be found in primary forest (n = 5), secondary forest (overgrown clove plantations) (n = 6), traditional graveyards (n = 4), mangroves (n = 1), and isolated trees (n = 3).
The tree species included: *Uapaca guineensis, Mangifera indica, Ficus natalensis, Ficus lutea, Syzygium jambolanum, Terminalia catappa, Adansonia digitata, Antiaris toxicaria, Erythrophleum suaveolens, Afzelia quanzensis, Parinari curatellifolia*, and *Blighia unijugata*.

Mwinyi and Nnko (2022: 7, 8) found these bats roosting in *Afzelia quazensis, Antiaris toxicaria, Bombax rhodognaphalon, Calophyllum inophyallum, Chrysalidocarpus pembanus, Erythrophleum suaveolens, Ficus carica, Ficus lutea, Mangifera indica, Manikara sulcata, Pterocarpus angolensis, Quassia indica, Quassia undulata, Synsepalum brevipes, Syzygium cordatum, Tamarindus indica, Terminalia catappa* and *Vitex doniana*, with a large preference for *Terminalia catappa*, where almost three times as many bats were roosting as the next tree species.

DIET:
Pakenham (1984: 26) reported these bats feeding on mangos (*Mangifera indica* L.), mzambarau (*Syzygium jambolanum* DC), blossoms of mlangilangi (*Cananga odorata* Hook f. & Thomas) and kapok (*Ceiba pentandra* Gaertn), and leaves of pawpaw (*Carica papaya* L).

Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *P. voeltzkowi* this includes *Ficus sur* Forssk. (Broom cluster fig - Moraceae).

Entwistle and Corp (1997b: 357) analysed faecal pellets, ejecta and dropped fruits, as well as information obtained from villagers and students, and provided the following overview of the bat's diet: *Mangifera indica* L. (mango - Anacardiaceae [fruit]), *Artocarpus altilis* (Parkinson) Fosberg (breadfruit - Moraceae [fruit]), *Ficus* spp. (figs - Moraceae [fruit]), *Carica papaya* L. (papaya - Caricaceae [fruit]), *Ceiba pentandra* (L.) Gaertn. (kapok - Malvaceae [flowers/pollen]), *Anacardium occidentale* L. (cashew apple - Anacardiaceae [fruit]), *Musa spp.* (banana or plantain - Musaceae [fruit and flowers/pollen]), *Psidium guajava* L. (guava - Myrtaceae [fruit]), *Terminalia catappa* L. ('kungu' or Indian-almond - Combretaceae [fruit]), *Parinari curatellaefolia* Planch. ex Benth. (mupundu or mobola plum - Chrysobalanaceae), *Cocus nucifera* L. (coconut - Arecaceae [leaves]), *Eugenia aromatica* (L.) Baill. [= *Syzygium aromaticum* (L.) Merrill & Perry (clove - Myrtaceae [fruit]), *Calophyllum inophyllum* L. (Alexandrian laurel - Callophyllaceae), *Syzygium jambolanum* Lam. [= *Syzygium cumini*] (L.) Skeels. (jambolana or Java plum - Myrtaceae [flowers/pollen]). They also indicated (p. 359) that cultivated species are prominently present in the diet during the months of June and July.

Mwinyi and Nnko (2022: 9) reported 14 plant species consumed by *P. voeltzkowi*: Anacardiaceae (*Mangifera indica, Anacardium occidentale* - fruit), Bombacaceae (*Ceiba pentandra* - flowers), Caricaceae (*Carica papaya* - fruit), Combretaceae (*Terminalia catappa* - fruit), Lamiaceae (*Vitex doniana* - fruit), Moraceae (*Ficus carica* - fruit, *Artocarpus altilis* - fruit/flowers), Musaceae (*Musa paradisiaca* - fruit/flowers), Myrtaceae (*Psidium guajava* - fruit/leaves, *Syzygium cuminii* fruit/flowers), Phyllanthacceae (*Uapaca guineensis* - fruit), Sapindaceae (*Litchi chinensis* - fruit) and Amaranthaceae (*Celosia trigyna* - leaves).

POPULATION:
Structure and Density
In the early 1990s the population of this species appears to have been reduced to a few hundred animals (Seehausen, 1991; Mickleburgh *et al.*, 1992), with an estimate of 2,800 to 3,600 individuals in 1992, the majority being found at just two roost sites (O. Seehausen, unpubl.). In

1995 Entwistle and Corp (1997a) estimated a population of of 4,600 to 5,500 individuals, with 94% of bats found at 10 roosts (of 41 in total). Over the subsequent years surveys conducted by local teams on the island reported increasing population counts (Entwistle, 2001; Trewhella *et al.*, 2005; Carter, 2005; Juma, 2007). Entwistle (2001: 356) reported that more recent local participation in survey work had helped to give a more accurate population estimate of ca. 6,900 bats (Trewhella *et al.*, 2005). The population of bats has continued to increase and by the end of 2006 there were ca. 19,000 animals (Juma, 2007). A full survey in 2008 provided a population estimate between 18,200 and 22,100 individuals (Robinson *et al.*, 2010) distributed across 44 active roost sites, with up to 87% of the population found at just four roost sites. Roosts ranged from solitary individuals to colonies of up to 5,040 bats. An unpublished report indicates a more recent population count of over 28,700 in 2011, with evidence of year-on-year increases over the intervening period (DCCFF, 2013).

Trend
2016: Increasing (Entwistle and Juma, 2016; Vincenot *et al.*, 2017). 2008: Increasing (Mickleburgh *et al.*, 2008df; IUCN, 2009).

PARASITES:
Pakenham (1984: 26) referred to Voeltzkow, who reported numerous *Cyclopodia greeffi* flies (Nycteribiidae) occurring on these bats. Dick *et al.* (2023: 71) mentioned these as *Cyclopodia greeffi greeffi* Karsch, 1884.

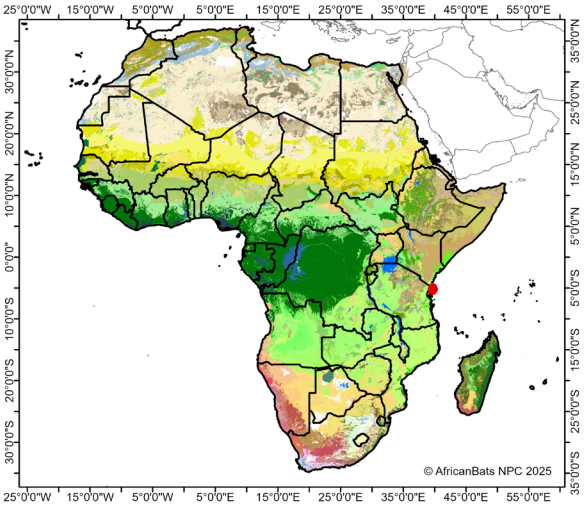

Figure 12. Distribution of *Pteropus voeltzkowi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Tanzania.

Subfamily Rousettinae Andersen, 1912

1912. *Epomophorinae* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, liii. Publication date: 23 March 1912. - Comments: Considered as a valid subfamily by Bergmans (1997: 69) who includes the tribes Epomophorini Gray, 1866 (*Epomophorus, Micropteropus, Hypsignathus, Epomops, Nanonycteris*), Myonycterini Lawrence and Novick, 1963 (*Myonycteris, Lissonycteris, Megaloglossus*), Scotonycterini Bergmans, 1997 [new tribe] (*Scotonycteris, Casinycteris*), Plerotini Bergmans, 1997 [new tribe] (*Plerotes*)? However, Almeida *et al.* (2016: 83) included the Epomophorine genera in the Rousettinae.
Although Andersen (1912b: liii: 67) was the first to explicitly use Epomophorinae as name for the subfamily, ICZN article 50.3.1 states "The authorship of the name of a nominal taxon within the family group, genus group or species group is not affected by the rank at which it is used.", therefore Knut Andersen is to be considered the author.

1912. *Rousettinae* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, xxx. Publication date: 23 March 1912. - Comments: Bergmans (1997: 69) recognizes the Rousettinae as a separate subfamily in which he included the tribes Rousettini Andersen, 1912 (*Rousettus, Eonycteris, Eidolon*) and Dobsoniini Andersen, 1912 (*Dobsonia, Aproteles*). Almeida *et al.* (2016: 83), however, provided an entirely different arrangement.

1970. *Rousettina* Koopman and J.K. Jones Jr., Classification of Bats. - Comments: Not included in Simmons (2005) since it was not proposed as family name, but as a subdivision within the Pteropodidiae (Simmons, pers. comm.).

TAXONOMY:
The subfamily was already recognized by Bergmans (1997: 69) and confirmed by the phylogenetic study by Almeida *et al.* (2016: 83), although their content differs. Bergmans (1997: 69) considered the Epomophorinae to be a valid separate subfamily, whereas Almeida *et al.* (2016: 83) included them in the Rousettinae.

Currently recognized tribes and genera of Rousettinae (Almeida *et al.*, 2020: 11): Rousettini Andersen, 1912 (***Rousettus*** Gray, 1821), Eonycterini Almeida *et al.*, 2016 (*Eonycteris* Dobson, 1873), Epomophorini Gray, 1866 (***Epomophorus*** Bennett, 1836, ***Epomops*** Gray, 1870, ***Hypsignathus*** H. Allen, 1861, ***Nanonycteris*** Matschie, 1899), Myonycterini Lawrence and Novick, 1963 (***Megaloglossus*** Pagenstecher, 1885, ***Myonycteris*** Matschie, 1899), Stenonycterini Nesi *et al.*, 2013 (***Stenonycteris*** Gray, 1870), Scotonycterini Bergmans, 1997 (***Casinycteris*** Thomas, 1910, ***Scotonycteris*** Matschie, 1894), Plerotini Bergmans, 1997 (***Plerotes*** K. Andersen, 1910).

The recently distinguished genus *Pilonycteris* Nesi et al., 2021 has not been assigned to any of these tribes (Nesi *et al.*, 2021: 1083).

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Burundi, Cameroon, Congo (Democratic Republic of the), Kenya, Liberia.

TRIBE Epomophorini J. E. Gray, 1866

*1866. *Epomophorini* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (v): 65. Publication date: May 1866.

TAXONOMY:
Includes the genera ***Epomophorus*** Bennett, 1836, ***Epomops*** Gray, 1870, ***Hypsignathus*** H. Allen, 1861, and ***Nanonycteris*** Matschie, 1899 (Almeida *et al.*, 2020: 11).

Genus ***Epomophorus*** Bennett, 1836

1835. *Pteropus:* Ogilby, Proc. zool. Soc. Lond., 1835, III (xxxi): 100. Publication date: 9 October 1835. - Comments: Preoccupied by *Pteropus* Brisson, 1762.
*1836. *Epomophorus* Bennett, Proc. zool. Soc. Lond., 1835, III (xxxiv): 149. Publication date: 12 February 1836. - Comments: Type species: *Pteropus whitei* var. *epomophorus* Bennett, 1836 (= *Pteropus gambianus* Ogilby, 1835). - Etymology: From the Greek "*ἐπι*", meaning upon, "*ωμος*", meaning shoulder, and "*φόρος*", meaning bearing, refering to the conspicuous tufts of hair on the shoulders of the males (see Palmer, 1904: 268; Boulay and Robbins, 1989: 4). (Current Combination).
1853. *Pachysoma* Temminck, Esq. zool. Côte de Guiné, 64. - Comments: Preoccupied by *Pachysoma* MacLeay, 1821, a genus of Coleoptera: see Boulay and Robbins (1989: 1). Not *Pachysoma* I. Geoffroy Saint-Hilaire, 1828. Andersen (1912b: 514) indicates that *Pachysoma* Temminck includes both *Epomophorus* and *Cynopterus*.
1975. *Epomorphus:* Höhne, Loose and Seeliger, Ann. Microbiol. (Inst. Pasteur), 126 A: 503. (Lapsus).
1978. *Epomophevus:* Arata and Johnson, in: Pattijn, Ebola Virus Haemorrhagic Fever, 135. (Lapsus).
2014. *Epimorphosis:* Walldorf and Mehlhorn, Parasitology Research Monographs, 5 - Springer Verlag - Berlin Heidelberg: 13. (Lapsus).
2016. *Epomorphorus:* Pancer, Gut and Litwińska, Post. Mikrobiol., 55 (2): 208. (Lapsus).
2017. *Epomophorous:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 5. Publication date: 6 April 2017. (Lapsus).
2024. *Microptreopus:* de Souza, Gaye, Ndiaye, Morgan, Daouda Sylla, Amadou SY, Diallo and Weaver, Emerg. Inf. Dis., 30 (7): 1491. Publication date: July 2024. (Lapsus).
2025. *Microteropus:* Ngene, Okwuonu, Ogbonna, Ukwueze and Ejere, Caryologia, 78 (1): 3. Publication date: 1 October 2025. (Lapsus).
? *Epomophorus sp.:*

TAXONOMY:
Revised by Bergmans (1988), who transferred *Micropteropus grandis* to this genus. A key to this genus is presented in Boulay and Robbins (1989) and Claessen and De Vree (1991). See Simmons (2005: 322).

Almeida *et al.* (2016: 83) found *Epomophorus* to be paraphyletic not only because they transferred *dobsonii* from the genus *Epomops*, but also because *Micropteropus pusillus* seems highly related. However, they suggest further investigation of rapidly evolving nuclear loci and additional species of both genera to decide whether *Micropteropus* and *Epomophorus* are synonyms.

Included in the Epomophorinii tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Hassanin *et al.* (2020: 5) include it in the Epomophorina subtribe of the Epomophorini tribe.

Almeida *et al.* (2020: 16) considered *Micropteropus* Matschie, 1899 to be a synonym of *Epomophorus*. They also provisionally considered *minimus* Claessen and De Vree, 1991 to be a synonym of *E. minor* Dobson, 1879.

Currently (Simmons and Cirranello, 2024a) recognized species of *Epomophorus* (Almeida *et al.*, 2020: 16): ***angolensis*** Gray, 1870; ***anselli*** Bergmans and Van Strien, 2004; ***crypturus*** Peters, 1852; ***dobsonii*** Bocage, 1889; ***gambianus*** (Ogilby, 1835); ***grandis*** (Sanborn, 1950); ***intermedius*** (Hayman, 1963); ***labiatus*** (Temminck, 1837); ***minor*** Dobson, 1880; ***pusillus*** Peters, 1867; ***wahlbergi*** (Sundevall, 1846).

COMMON NAMES:
Afrikaans: Witkol-vrugtevlermis. Czech: výložkoví kaloni. English: Epauletted Fruit-bats. French: Epomophores, Chauves-souris à épaulettes. German: Epaulettenflughund, Epaulettenflughunde. Italian: Epomòfori. Kiluba (DRC): Mulima.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Fenton (1992: 49) suggests that the white ear spots present disruptive patterns, which contribute to the cryptic appearance of these bats when resting in foliage.

DETAILED MORPHOLOGY:
The region of the shoulder pouches was morphologically, anatomically and histologically investigated by Püscher (1972), who found special muscles to move the dermal pouch, but no special cutaneous glands.

DIET:
Mphethe *et al.* (2023: 8) investigated the diet of *Epomophorus crypturus* and *E. wahlbergi* in litchi orchards in the Limpopo province (RSA) and found that these bat's diet consisted of about 98 % of non-commercial fruits (primarily *Ficus* sp.) and only 2 % of litchis. They also found similar numbers in quinine orchards.

PREDATORS:
Steyn (1964: 257) reported an Epauletted Fruit Bat of 6 inches being eaten by a small Python of 2 feet 7 inches.

Mikula *et al.* (2016: Supplemental data) mention *Epomophorus* sp. to be preyed upon by African goshawk (*Accipiter tachiro* (Daudin, 1800)) [possibly either *E. crypturus* or *E. wahlbergi*], Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850).

PARASITES:
BACTERIA
Bartonellae
Kamani *et al.* (2014: 628) tested 30 Nigerian *Epomophorus* sp., and found at least 16 of them testing positive for *Bartonella* DNA.

HAEMOSPORIDA
Perkins and Schaer (2016: Suppl.) mention the presence of *Hepatocystis epomophori* Rodhain, 1926 in *Epomophorus* sp. bats. Of the 138 South Sudanese *Epomophorus* sp. bats examined by Schaer *et al.* (2017: 2), 130 (94 %) were infected by *Hepatocystis*. In the Amurum forest reserve (Nigeria), Atama *et al.* (2019: 1550) found *Hepatocystis* parasites in 25 % of the examined *Epomophorus* bats.

HEMIPTERA
Cimicidae
Haeselbarth *et al.* (1966: 8) recorded *Afrocimex constrictus* Ferris & Usinger 1957 associated with *Epomorphorus* sp. from Kiambu, near Nairobi, Kenya.

DIPTERA
Nycteribiidae
Cyclopodia greeffi Karsch 1884 found in a belt across central Africa, between lat. 10° south and north, while in West Africa it occurs further north up to lat. 20° (Haeselbarth *et al.*, 1966: 117; Stuckey *et al.*, 2017: 22).

Dick *et al.* (2023) mentioned the following nycteribiid flies have already been found on *Epomophorus* sp.: *Cyclopodia greeffi greeffi* Karsch, 1884 and *Dipseliopoda biannulata* (Oldroyd, 1953),

VIRUSES:
Coronaviridae
Joffrin *et al.* (2020: 7) reported Beta-D coronaviruses from *Epomophorus* sp. from Tanzania.

Filoviruses
Lacroix *et al.* (2021: 7) examined 187 bats from the DRC for antibodies against Ebola and found 0 to 22 of them to be positive.

Flaviviridae
Andral *et al.* (1968: 855) reported on the isolation of yellow fever virus in Ethiopia from either *Epomophorus anurus*, "*Epomophorus monstruosus*" or "*Epomophorus limbatus*".

Paramyxoviridae
Orthorubulavirus
Krüger *et al.* (2018: 318) state that broad geographic distribution of the genus *Epomophorus* in Sub-Saharan Africa makes it conceivable that Bat Mumpsvirus (batMuV) is widely dispersed in the region. This virus is closely related to the human Mumpsvirus of which in 2016 100,576 cases were reported in Africa, and which is serologically not distinguishable from the human virus.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Kenya, Liberia, Mozambique, Namibia, Nigeria, Rwanda, Senegal, South Africa, South Sudan, Tanzania, Togo, Uganda, Zambia.

Epomophorus angolensis J. E. Gray, 1871

*1871. *[Epomophorus macrocephalus] var. angolensis* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 125. Publication date: 14 January 1871. Type locality:

Angola: Benguela [12 34 S 13 24 E, 160 m]. [Goto Description]. Holotype: NHMUK 1864.8.16.1: juv ♂. - Etymology: Named from a specimen taken at Benguela, Angola (see Smithers, 1983: 56; Taylor, 2005).
? *Epomophorus angolensis:* (Current Combination).

TAXONOMY:
Member of the *gambianus* species group Simmons (2005: 322). See also Bergmans (1988).

COMMON NAMES:
Afrikaans: Angola-witkolvrugtevlermuis. Czech: kaloň angolský. English: Angolan Epauletted Fruit-bat, Angolan Epauletted Fruit Bat. French: Epomophore d'Angola, Roussette à épaulettes d'Angola. German: Angola-Epaulettenflughund.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened. Almost qualifies as threatened under criterion A2c because it is suspected to be experiencing a significant decline at a rate of 20-25% over three generations (12 years; Pacifici *et al.*, 2013) because of the loss of riverine roosting and fruit trees. (Mickleburgh *et al.*, 2008d; IUCN, 2009; Mildenstein, 2016a).

This is a precautionary listing, as it is possible that the species has a less restricted habitat, and as such should be listed as Least Concern (Mickleburgh *et al.*, 2008d; IUCN, 2009; Mildenstein, 2016a).

Assessment History
Global
2016: NT ver 3.1 (2001) (Mildenstein, 2016a). 2008: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2008d; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004b; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996). 1994: Rare (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
This species is threatened by the removal of roost trees, often for use as fuel. Griffin (1998) indicates that the removal of riverine trees is a particular threat to species of *Epomophorus* in Namibia, with relatively little suitable habitat remaining; presumably this is similar problem in Angola. It may have been threatened by the availability of firearms during the long civil war in Angola, although this requires confirmation (Mildenstein, 2016a).

CONSERVATION ACTIONS:
Current conservation efforts
Although there appear to be no direct conservation measures in place for this species it has been recorded from Mupa National Park and Bikuar National Park in Angola (Mickleburgh *et al.*, 2008d; IUCN, 2009; Mildenstein, 2016a).

Conservation needs/priorities
There is a need to conserve remaining areas of suitable roosting and feeding sites for this species (Mickleburgh *et al.*, 2008d; IUCN, 2009).

Studies are needed on the species' population sizes, distribution, and extent of occurrence throughout its range. Monitoring of population sizes and locations over time are also important to establish whether these are stable or experiencing trends of decline (Mildenstein, 2016a).

The threats to these bats are poorly understood. Studies are needed on the species' habitat requirements and on the effects of forest loss and degradation on the species' population sizes/distribution. Research is also needed on the amount of hunting and the level of bushmeat trade, and the effects of that hunting on population sizes and persistence (Mildenstein, 2016a).

Effective roost site protection efforts are needed to minimize disturbance and protect colonies. Similar to most threatened flying foxes, local capacity building for conservation managers and education and awareness within local communities are greatly needed to support conservation efforts (Mildenstein, 2016a).

GENERAL DISTRIBUTION:
Epomophorus angolensis is present in Angola and adjacent parts of northern Namibia. It is largely a lowland species but may range into more montane areas. In Angola it is present west and south of the Mosaic of Guineo-Congolian lowland rain forest and secondary grassland (Bergmans, 1988). In eastern Angola the range seems to be halted by the extensive mosaic region of *Brachystegia bakerana* thicket and edaphic grassland (Bergmans, 1988). Palmeirim *et al.* (2023: 313) called this species in Angola a near-endemic, occurring from the southern part of the Northern Escarpment to the northern part of the Southern Escarpment, only marginally extending into Namibia.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 339,737 km^2.

Native: Angola (Bergmans, 1988; Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 551; Taylor *et al.*, 2018b: 60); Namibia (Monadjem *et al.*, 2010d: 551).

DENTAL FORMULA:
Esquivel *et al.* (2021: Suppl.) examined nine skulls for dental anomalies, but found none.

HABITAT:
Bergmans (1988; 1999) reports that the species is present in wetter Zambezian miombo woodland, north Zambezian woodland; *Colophospermum mopane* woodland and scrub woodland. Skinner and Chimimba (2005) suggest that the species may be largely confined to riverine forest and other evergreen forest with fruit-bearing trees.

Arumoogum *et al.* (2019: 188) simulated the role of biotic and a-biotic factors in view of climate change and found that the current suitable habitat for *E. angolensis* is primarily mediated by abiotic variables associated with productivity, but under extreme future climate change scenarios, the most significant factor would be the distribution of freestanding fig trees.

HABITS:
Shortridge (1934) reported on animals hanging singly from bare branches of large Acacia trees near the Cunene River, however, loose colonies of up to 200 have also been found.

POPULATION:
Structure and Density
The abundance of this species is poorly known, with very little recent information (Mickleburgh *et al.*, 2008d; IUCN, 2009; Mildenstein, 2016a).

Trend
2016: Decreasing (Mildenstein, 2016a). 2008: Decreasing (Mickleburgh *et al.*, 2008d; IUCN, 2009).

UTILISATION:
The species may be hunted for the bushmeat trade (Mildenstein, 2016a).

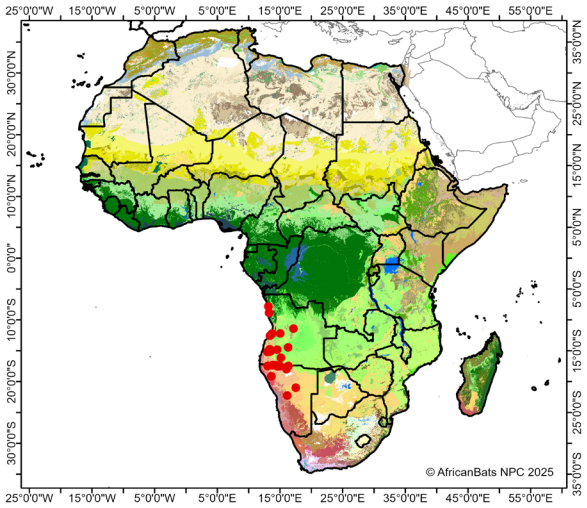

Figure 13. Distribution of *Epomophorus angolensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Namibia.

Epomophorus anselli Bergmans and Van Strien, 2004

*2004. *Epomophorus anselli* Bergmans and Van Strien, Acta Chiropt., 6 (2): 258. Type locality: Malawi: Kasungu National Park: Lisanthu [13 00 S 33 10 E, 1 000 m]. Holotype: ZMA MAM.21693b: ad ♂, skull and alcoholic. Collected by: Hugo Jachmann; collection date: 19 March 1982; original number: #25. See Bergmans and Van Strien (2004: 258 - 259). Paratype: ZMA MAM.26105: sad ♀, skin and skull. Collected by: Nico[laas] Jan Van Strien; collection date: 19 May 1988; original number: #162. Locality: Lifupa Camp - 13.05 S 3005E, 1050 m; see Bergmans and Van Strien (2004: 258 - 259). - Comments: Publication date: The volume is for "September 2004", but the paper has been accepted on 16 October 2004. - Etymology: In honour of Mr. William Frank Harding Ansell for his important contributions to the mammalogy of Malawi and other African countries (see Bergmans and Van Strien, 2004: 262). (Current Combination).

2020. *Epomophorus sp1:* Hassanin, Bonillo, Tshikung, Pongombo Shongo, Pourrut, Kadjo, Nakouné, Tu, Prié and Goodman, J. Zool. Syst. Evol. Res., 4. Publication date: 20 February 2020. (Name Combination).

TAXONOMY:
See Bergmans and Van Strien (2004).

COMMON NAMES:
Czech: kaloň Ansellův. French: Epomophore d'Ansell. German: Ansells Epaulettenflughund. Malawian: Lichinji, Mleme.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since it has only recently been described, and there is still very little information on its extent of occurrence, status, threats and ecological requirements (Bergmans and van Strien, 2008; IUCN, 2009; Mildenstein, 2016b).

Assessment History
Global
2016: DD ver 3.1 (2001) (Mildenstein, 2016b). 2008: DD ver 3.1 (2001) (Bergmans and van Strien, 2008; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Bergmans and Van Strien (2004) note that they "have no reason to believe that the species is in any danger but at the same time the available data are few and between 43 and 16 years old".

CONSERVATION ACTIONS:
Current conservation efforts
Bergmans and van Strien (2008) [in IUCN (2009)] reported that this species has been recorded from the Kasungu National Park in Malawi, and further field surveys are needed to better understand the distribution range, threats and conservation status of this species.

Conservation needs/priorities
Studies are needed on the species' population sizes, distribution, and extent of occurrence throughout its range. Monitoring of population sizes and locations over time are also important to establish whether these are stable or experiencing trends of decline (Mildenstein, 2016b).

The threats to these bats are poorly understood. Studies are needed on the species' habitat requirements and on the effects of forest loss and degradation on the species' population sizes/distribution. Research is also needed on the amount of hunting and the level of bushmeat trade, and the effects of that hunting on population sizes and persistence (Mildenstein, 2016b).

Effective roost site protection efforts are needed to minimize disturbance and protect colonies. Like most threatened flying foxes, local capacity building for conservation managers and education and awareness within local communities are greatly needed to support conservation efforts (Mildenstein, 2016b).

GENERAL DISTRIBUTION:
Epomophorus anselli is currently only known from Malawi, where it has been collected in the Kasungu National Park (collected in 1982 and 1988) and (most probably) the Karonga area (collected in 1961) (Bergmans and Van Strien, 2004).

Native: Malawi (Bergmans and Van Strien, 2004; Monadjem *et al.*, 2010d: 551).

HABITAT:
Bergmans and Van Strien (2004) record that 'the type specimen was mist netted in Miombo woodland at an elevation of 1,000 m, over a stream between two water berry trees, *Syzygium cordatum* Hochst., in fruit (Bergmans and Jachmann, 1983).' Furthermore, they state that 'the vegetation of Lifupa Camp, the locality where the female paratype was collected (exact elevation unknown, but between 1,000 and 1,100 m) is Miombo woodland with *Brachystegia* and *Julbernardia* (Bergmans and Jachmann, 1983)'.

POPULATION:
Structure and Density
It is only known from a few specimens (Bergmans and van Strien, 2008; IUCN, 2009; Mildenstein, 2016b).

Trend
2016: Unknown (Mildenstein, 2016b). 2008: Unknown (Bergmans and van Strien, 2008; IUCN, 2009).

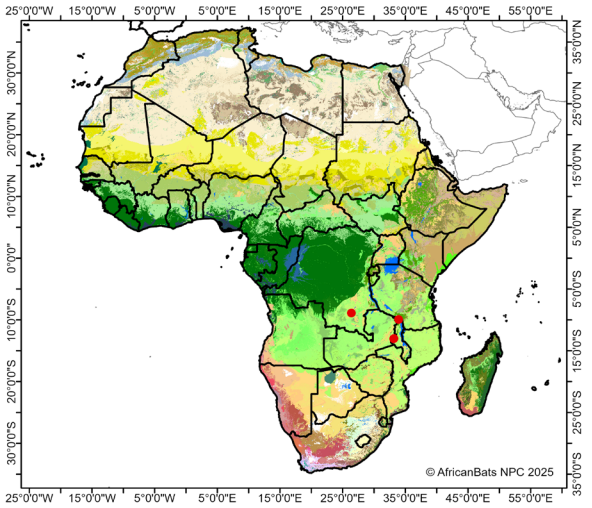

Figure 14. Distribution of *Epomophorus anselli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Malawi.

Epomophorus crypturus Peters, 1852

*1852. *Epomophorus crypturus* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 26, pl 5, pl 13, fig 1 - 6. Type locality: Mozambique: Lower Zambezi River: Tete [16 10 S 33 35 E, 230 m]. [Goto Description]. Lectotype: ZMB 10080: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. Lectotype designated by Andersen (1912b: 537); formerly

ZMB 553; see Turni and Kock (2008). Paralectotype: ZMB 10018: ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Andersen (1912b) and Turni and Kock (2008: 8). Paralectotype: ZMB 10019: ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Andersen (1912b) and Turni and Kock (2008: 8). Paralectotype: ZMB 10020: ♂, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Andersen (1912b) and Turni and Kock (2008: 8). Paralectotype: ZMB 10078: skull only. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Andersen (1912b) and Turni and Kock (2008: 8). Paralectotype: ZMB 10081: skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. Formerly ZMB 355. See Andersen (1912b) and Turni and Kock (2008: 8). Andersen (1912b: 537) also mentions that most of the paratypes are immature specimens, and that Peters' adult male is in fact an immature. (Current Combination).

1855. *Pt[eropus] crypturus:* Giebel, Die Säugethiere, 1002. (Name Combination).

1960. *Epomophorus gambianus parvus* Ansell, Rev. Zool. Bot. afr., 61: 160. Type locality: Zambia: Zambezi district: Chingi [13 01 S 22 44 E]. Holotype: NHMUK 1959.610: ad ♂. - Comments: Type locality originally Balovale [=Zambezi] district, restricted to Chingi by Ansell (1978: 17).

1986. *Epomophorus crypturus parvus:* Meester, Rautenbach, Dippenaar and Baker, Transv. Mus. Monogr., 5: 27. (Name Combination).

1988. *Epomophorus gambianus crypturus:* Bergmans, Beaufortia, 38 (5): 93. (Name Combination).

2020. *Epomophorus sp2:* Hassanin, Bonillo, Tshikung, Pongombo Shongo, Pourrut, Kadjo, Nakouné, Tu, Prié and Goodman, J. Zool. Syst. Evol. Res., 4. Publication date: 20 February 2020. (Name Combination).

? *Epomophorus angolensis:* - Comments: Not of Gray, 1870.

? *Epomophorus crypturus crypturus:* (Name Combination).

? *Epomophorus gambianus:* - Comments: Not of Ogilby, 1835.

Taxonomy:

Bronner *et al.* (2003) state that *Epomophorus crypturus* was previously afforded full species status (Corbet and Hill, 1980; Swanepoel *et al.*, 1980; Koopman, 1982; Meester *et al.*, 1986; Claessen and De Vree, 1990, 1991; 2005).

Meester *et al.* (1986) states that Koopman (1966) considers the possibility that the extralimital *E. anurus* Heuglin, 1864, may be conspecific with *crypturus*. This would extend the range of *crypturus* to Uganda, Rwanda, southern Sudan, Ethiopia, Eritrea and westwards to Nigeria. However, Kock (1969a) and Koopman (1975) regard *anurus* instead as a synonym of the extralimital *E. labiatus* (Temminck, 1837), while Hayman and Hill (1971) retain it as a separate species, so that a close relationship with *crypturus* does not seem to be indicated. Further uncertainty surrounds the status of *E. gambianus parvus*. Ansell (1978), while treating *parvus* as a subspecies of *gambianus*, expresses doubt whether *parvus* can be distinguished at species level from *crypturus*, and suggests that *crypturus* and *gambianus* are conspecific, with *parvus* as an intermediate subspecies or a stage in a cline running between them. Koopman (1982) retains *gambianus* as a separate species, but includes *parvus* in *crypturus*, without specifying whether or not he regards it as sub specifically distinct. While acknowledging that this problem remains to be solved we shall provisionally treat *parvus* as a taxon of *crypturus*.

Common Names:

Afrikaans: Peters se witkolvrugtevlermuis, Peters-witkolvrugtevlermuis, Klein Vrugtevlermuis. Czech: kaloň mosambický. English: Peters's Epauletted Fruit Bat, Smaller Epauletted fruit bat. French: Epomophore de Peters, Roussette à épaulettes de Peters. German: Peters' Epaulettenflughund. Malawian: Lichinji, Mleme [in Nyanja]. Portuguese: Morcego frugivoro de Peters. Tshokwe (Angola): Tshingunzu.

Etymology of common name:

In honour of Wilhelm Carl Hartwig Peters who, in 1852, published a monumental work on zoological material collected mainly in the Tete District of Mozambique (Smithers, 1983: 58).

Similar Species:

Taylor and Monadjem (2008: 24) provided data which enabled them to separate *E. crypturus* from *E. wahlbergi*. In the first species, the maxillary width is always smaller than in the latter (♂♂: < 14 mm; ♀♀: < 13 mm).

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008e; IUCN, 2009; Taylor, 2016c).

Assessment History

Global

2016: LC ver 3.1 (2001) (Taylor, 2016c). 2008: LC ver 3.1 (2001) assessed as *E. crypturus* (Mickleburgh *et al.*, 2008e; IUCN, 2009). 2004: LC ver 3.1 (2001) assessed as *E. crypturus* (Mickleburgh *et al.*, 2004c; IUCN, 2004).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016x). 2004: DD ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species as a whole. Some populations may be impacted by general persecution as crop pests (Mickleburgh *et al.*, 2008e; IUCN, 2009; Taylor, 2016c).

CONSERVATION ACTIONS:
Taylor (2016c) agrees with Mickleburgh *et al.* (2008e) [in IUCN (2009)] who state that this species has been recorded from many protected areas, and no direct conservation measures are needed for this widespread and adaptable species as a whole.

GENERAL DISTRIBUTION:
E. crypturus is a widespread southern African species distributed from southern parts of the Democratic Republic of the Congo and southern Tanzania, to the eastern coastline of South Africa. It ranges from eastern Angola and northern Botswana to the southeastern African coastline. It has been recorded at elevations of up to 2,185 m asl, although it has mostly been collected between 500 and 1,500 m asl (Mickleburgh *et al.*, 2008e; IUCN, 2009). For South Africa, Babiker Salata (2012: 49) found that its distribution is stongly associated with the mean temperature of the coldest quarter.

Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,213,597 km^2.

Native: Angola (Bergmans, 1988; Monadjem *et al.*, 2010d: 551); Botswana (Bergmans, 1988; Monadjem *et al.*, 2010d: 551); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 551); Eswatini (Monadjem *et al.*, 2010d: 552; Monadjem *et al.*, 2021: 5); Malawi (Happold *et al.*, 1988; Bergmans, 1988; Happold and Happold, 1997b: 813; Monadjem *et al.*, 2010d: 551); Mozambique (Smithers and Lobão Tello, 1976; Bergmans, 1988; Monadjem *et al.*, 2010d: 551; 2010c: 376); Namibia (Monadjem *et al.*, 2010d: 552); South Africa (Monadjem *et al.*, 2010d: 552);Tanzania; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 552); Zimbabwe (Monadjem *et al.*, 2010d).

DENTAL FORMULA:
None of the 18 skulls examined by Esquivel *et al.* (2021: Suppl.) had anomalies in the number of teeth.

MOLECULAR BIOLOGY:
Karyotype
In Zimbabwe, Peterson and Nagorsen (1975: 4) recorded the following: 2*n* = 35 for a male, and 2*n* = 36 for a female (XO/XX; see also Nesi *et al.*, 2011: 552).

HABITAT:
This species is generally associated with dry savanna and riverine forest with fruit bearing trees (Mickleburgh *et al.*, 2008e).

ROOST:
Colonies often roost under the canopy of trees, in thick foliage (Mickleburgh *et al.*, 2008e). In Zimbabwe, they were generally observed roosting in wild fig trees and sausage trees (*Kigelia africana*) (Happold and Happold, 2023: 61).

MIGRATION:
Populations exhibit considerable movements in search of food and may come into towns and feed on crops and fruit trees (Mickleburgh *et al.*, 2008e).

DIET:
Bonaccorso *et al.* (2014: 41) studied the foraging movements of *E. crypturus* in the Kruger National Park (RSA) in relation to the distribution of sycamore figs *Ficus sycomorus*. They also performed germination trials on 20 intact seeds that had passed through the gastro-entero tract of the bats and found 100 % germination. They also found (p. 48) that during a very dry period, the bats flew between 4 and 14 km from their roosting site to fruiting *F. sycomorus*. In normal circumstances, they only flew 400 - 2,000 m. The bats visited up to four fig trees per night.

POPULATION:
Structure and Density
It is a quite common species, sometimes forming loose colonies of hundreds of bats (Mickleburgh *et al.*, 2008e; IUCN, 2009; Taylor, 2016c).

It is a quite common species, sometimes forming loose colonies of hundreds of bats.

Trend
2016: Unknown (Taylor, 2016c). 2008: Unknown (Mickleburgh *et al.*, 2008e; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In the Kruger Park, Pienaar (1964: 8) reported single young attached to their mothers in December and January.

In Malawi, Happold and Happold (1990b: 564) found lactating females in November, March and May, suggesting aseasonal reproduction.

MATING:
McCracken and Wilkinson (2000: 349) suggest that *E. crypturus* uses nocturnal display sites where females visit males for mating. Males call from roosts in trees that are spaced about 50 m apart along rivers.

At Shingwedzi (Kruger National Park), Adams and Snode (2015: 4) found the following values for the male mating calls: mean fundamental frequency: 15.71 ± 0.07 kHz (first harmonic), only in one case followed by multiple harmonics at 16, 48, 64, 96, and 112 kHz.

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in four individuals from Limpopo Province, none tested positive (0/4) and six individuals from Mpumalanga Province, South Africa, none tested positive (0/6).

Hantaviridae
In Zambia, Sarii *et al.* (2024: 14) found *Epomophorus crypturus* to be seropositive for Brno virus.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Congo (Democratic Republic of the), Eswatini, Kenya, Malawi, Mozambique, Namibia, South Africa, South Sudan, Tanzania, Zambia, Zimbabwe.

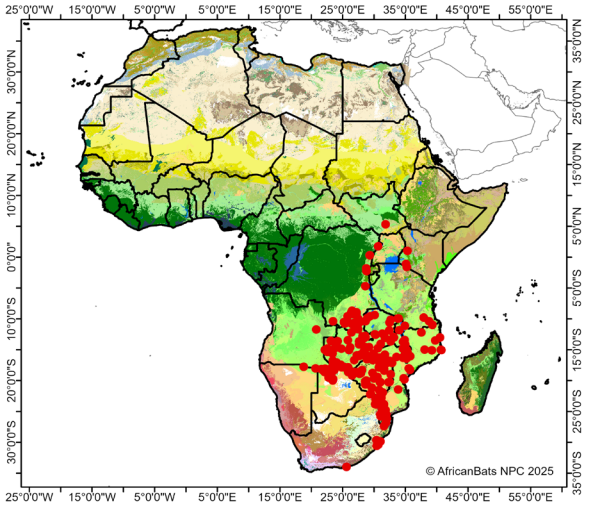

Figure 15. Distribution of *Epomophorus crypturus*.

Epomophorus dobsonii Bocage, 1889

*1889. *Epomophorus Dobsonii* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (1): 1, Fig 1. Publication date: March 1889. Type locality: Angola: Benguela district: Quindumbo. [Goto Description]. Neotype: AMNH 88068: ♂, skin and skull. Collected by: the Phipps-Bradley Expedition; collection date: 27 February 1933; original number: 902. At Chitau, 4930 ft. Designated by Bergmans (1989) (see AMNH website). - Comments: Andersen (1912b: 501) mentions that the original type was an adult male in the Lisbon museum. Frequently mentioned as *dobsoni*. - Etymology: Named after George Edward Dobson who, among his many other papers on bats, published a Catalogue of the Chiroptera in the collection of the British Museum in 1878 (see Taylor, 2005). (Current Combination).
1899. *Epomophorus (Epomops) dobsoni:* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 57. (Name Combination).
1912. *Epomops dobsoni:* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, lvi, 500. Publication date: 23 March 1912. (Name Combination, Alternate Spelling).
1939. *Epomops dobsonii:* G.M. Allen, Bull. Mus. comp. Zool., 83: 57. Publication date: February 1939. (Name Combination).
2016. *E. dobosonii:* Calderon, Guzman, Salazar-Bravo, Figueiredo, Mattar and Arrieta, Manter, Suppl 6: 7. Publication date: 30 September 2016. (Lapsus).
? *Epomophorus dobsoni:* (Alternate Spelling).
? *Epomophorus dobsonii:* (Current Spelling).

TAXONOMY:
See Bergmans (1979b; 1989) and Simmons (2005: 323).

The phylogenetic analyses by Almeida *et al.* (2016: 83) suggest that *dobsonii* is closely related to *Epomophorus wahlbergi* and they transferred the species to the latter genus.

COMMON NAMES:
Afrikaans: Dobson se vrugtevlermuis, Dobson-vrugtevlermuis. Czech: kaloň Dobsonův. English: Dobson's Fruit Bat, Dobson's Epauletted Fruit Bat, Dobson's Epauletted Bat, Singing Fruit Bat. French: Epomophore de Dobson, Roussette de Dobson. German: Dobsons Epaulettenflughund. Malawian: Lichinji, Mleme. Tshokwe (Angola): Tshingunzu.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be

declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bx; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bx; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cj; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species (Mickleburgh *et al.*, 2008bx; IUCN, 2009).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bx) [in IUCN (2009)] report that it has been recorded from Kasungu National Park in Malawi and from Parc National de l'Upemba in the Democratic Republic of the Congo. There is a need for additional studies into the natural history of this species and into any possible future threats to the species (Mickleburgh *et al.*, 1992).

GENERAL DISTRIBUTION:
Epomophorus dobsonii is distributed in East Africa, Central Africa and southern Africa. It has been recorded from Angola, Namibia, Zambia, southern Democratic Republic of the Congo, Malawi and Mozambique, being found as far north as Tanzania and possibly Rwanda. It has been recorded at elevations of up to 1,500 m asl (in Malawi) and at 1,890 m asl at Kibwele, Tanzania.

For southern Africa (south of 8° S), Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 503,585 km^2.

Native: Angola (Crawford-Cabral, 1989; Bergmans, 1989; Monadjem *et al.*, 2010d: 553; Taylor *et al.*, 2018b: 60); Botswana (Monadjem *et al.*, 2010d: 554); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 554); Malawi (Bergmans, 1989; Monadjem *et al.*, 2010d: 554); Mozambique; Namibia; Tanzania; Zambia (Ansell, 1973; Bergmans, 1989; Monadjem *et al.*, 2010d: 554); Zimbabwe.

Presence uncertain: Namibia (see Cotterill, 2004a: 260); Rwanda.

DENTAL FORMULA:
None of the three skulls examined by Esquivel *et al.* (2021: Suppl.) had an aberrant number of teeth.

POPULATION:
Structure and Density
It does not appear to be an especially rare species in Malawi. There is little information on the abundance of the species over the rest of its range, but it is presumed to be reasonably common (Mickleburgh *et al.*, 2008bx; IUCN, 2009).

Trend
2008: Stable (Mickleburgh *et al.*, 2008bx; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Hill (1941) [in Fox *et al.* (2009: 272) reported that "*E. dobsoni*" gave birth to two young, but Fox *et al.* (2009: 272) indicate that this statement was based on translated field notes, and it is not clear whether they refer to twins or to two birthing seasons each year.

VIRUSES:
Rhabdoviridae
Lyssavirus - Rabies related viruses
de Jong *et al.* (2011: 9) and Willoughby *et al.* (2017: Suppl.) report Lagos Bat Virus from *E. dobsonii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Congo (Democratic Republic of the), Malawi, Rwanda, Tanzania, Zambia, Zimbabwe.

Epomophorus gambianus Ogilby, 1835

*1835. *Pteropus Gambianus* Ogilby, Proc. zool. Soc. Lond., 1835, III (xxxi): 100. Publication date: 9 October 1835. Type locality: The Gambia: Banjul. [Goto Description]. Holotype: NHMUK 1907.1.1.233: ad ♀, skin and skull. Collected by: Dr. Percy John Rendall. Formerly in Tomes collection. Paratype: NHMUK 1874.a-c: 2 sad FF, 1 imm F, skin and skull. Collected by Liet. Rendall. Paratype: NHMUK 1874.a = 124b: imm ♀. Paratype: NHMUK 1874.b = 124c: ad ♀. Collected by: Dr. Percy John Rendall. Paratype: NHMUK 1874.c = 124d: imm ♀. Paratype: NHMUK 1907.1.1.231: sad ♀, skin and skull. Collected by: Dr. Percy John Rendall. Formerly in Tomes collection. - Comments: Type locality restricted by Kock *et al.* (2002b: 80). - Etymology: Named as the species was described from a specimen from Gambia in West Africa (see Taylor, 2005).

1898. *Epomophorus guineensis* Bocage, J. Sci. mat. phys. nat., ser 2, 5 (19): 136, fig 3. Publication date: June 1898. Type locality: Guinea-Bissau: Bolama [11 35 N 15 30 W]. [Goto Description]. Holotype: MLZA T118: ♂, mounted skin and skull. Collected by: D. da Costa; collection date: 1883. Bergmans (1988: 86) mentions this specimen as "probable holotype". - Comments: Andersen (1912b: 541) mentions the type specimen as being a mounted ad ♂, skull extracted, coll. Sr. Damasceno da Costa, and in the Lisbon Museum.

*1950. *Epomophorus reii* Aellen, Rev. suisse Zool., 57 (3): 559, fig 1. Publication date: July 1950. Type locality: Cameroon: Rei Bouba [08 40 00 N 14 11 00 E, 224 m]. [Goto Description]. Holotype: MHNC 32-8-970: ad ♀. Collected by: MSS Cameroun; collection date: 13 September 1947. Paratype: MHNC 32-8-969: imm ♀. Collected by: MSS Cameroun; collection date: 13 September 1947. Paratype: MHNG 1326.001: juv ♂, alcoholic (skull not removed). Collected by: Dr. Villy Aellen; collection date: 13 September 1947; original number: 1438.

2017. *Epomorphus giambianus:* Banyard and Fooks, Microbiol. Aust., 38 (1): 18. Publication date: March 2017. (Lapsus).

2019. *E[pomophorus] gambiansus:* Mbu'u, Mbacham, Gontao, Kamdem, Nlôga, Groschup, Wade, Fischer and Balkema-Buschmann, Vector-Borne Zoon. Dis., xxx: "6". Publication date: 13 April 2019. (Lapsus).

? *Epomophorus gambianus:* (Current Combination).

TAXONOMY:

See Boulay and Robbins (1989), Claessen and De Vree (1990) and Simmons (2005: 322).

Two subspecies are currently recognized: *E. g. gambianus* (Ogilby, 1835) and *E. g. pousarguesi* Trouessart, 1904.

COMMON NAMES:

Afrikaans: Gambiaanse witkolvrugtevlermuis. Czech: kaloň výložkový, kaloň větší. English: Gambian Epauletted Fruit bat, Gambian Epauleted Bat. Ewe (Ghana): Aguto. French: Epomophore de Gambie, Chauve-souris à épaulettes de Gambie. German: Gambia Epaulettenflughund. Tanoboase (Ghana): sreso ampane [= "original or normal bat"], ampane kronfo [= "thief or criminal bat"] (see Ohemeng *et al.*, 2017: 184).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001) assessed as full species in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008f; IUCN, 2009; Tanshi and Fahr, 2016).

Assessment History

Global

2016: LC ver 3.1 (2001) (Tanshi and Fahr, 2016). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008f; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004l; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

There are no major threats to this species as a whole. In parts of its range it is locally threatened by overhunting for food and habitat loss through logging and conversion of land to agricultural use (Mickleburgh *et al.*, 2008f; IUCN, 2009) and climate change (Tanshi and Fahr, 2016).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008f) [in IUCN (2009)] state that the species has a wide range, and is presumably present in many protected areas.

GENERAL DISTRIBUTION:

Senegal, Gambia over Guinea (Fahr and Ebigbo, 2003: 128), Mali (Meinig, 2000: 104), Benin (Capo-Chichi *et al.*, 2004: 161), Cameroon (Bakwo Fils *et al.*, 2014: 3), Central African Republic (Morvan *et al.*, 1999: 1195) to W Ethiopia, south to South Sudan.

Simmons (2005: 322) includes Malawi and Botswana, these records may be associated with *crypturus* and need to be verified.

González-Gutiérrez *et al.* (2025: Suppl.) calculated that the entire distribution area of this species cover 4,007,338 km^2.

E. g. gambianus - west Africa.
E. g. pousarguesi - east Africa.

Native: Benin (Capo-Chichi *et al.*, 2004: 161), Burkina Faso (Kangoyé *et al.*, 2015a: 605), Cameroon (Bakwo Fils *et al.*, 2014: 3), Central African Republic (Morvan *et al.*, 1999: 1195), Chad, Congo (Tolovou and Lenga, 2025: 52), Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Guinea (Fahr and Ebigbo, 2003: 128; Decher *et al.*, 2016: 261), Guinea-Bissau (Bocage, 1889a:2; Seabra, 1898b; Monard, 1939; Veiga-Ferreira, 1948; Bergmans, 1988; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 22), Liberia, Mali (Meinig, 2000: 104), Niger, Nigeria, Senegal, Sierra Leone, South Sudan, Sudan, The Gambia, Togo.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on both the dorsal and ventral sides of the proximal arm and on the dorsal side of the distal arm and forearm. It is moderate on the ventral side of the distal arm and forearm as well as on both the dorsal and ventral sides of the plagiopatagium and propatagium.

DENTAL FORMULA:
Esquivel *et al.* (2021: Suppl.) examined 51 skulls and found three of them (5.9 %) to have extra teeth (polyodontia).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 27.0 Pa, aspect ratio 5.9 for a wingspan of 58 cm and a wing area of 575 cm^2 and a body mass of 158 g.

SEXUAL DIMORPHISM:
Dobson (1873: 247) quotes Tomes' description of the male as: "The conspicuous shoulder-tufts of *E. macrocephalus* are here very fully developed. They consist of a very slight warty excrescence clothed with fur, which differs from that which surrounds it only in being of a dirty white colour."

In Ghana, the overall sex ratio (female to male ratio) was male-dominated (0.69, 95% CI = 0.64 to 0.75), but female-biased for adults (62% female). This ratio showed temporal and age-specific variations.

MOLECULAR BIOLOGY:
Karyotype
Ngene *et al.* (2025: 11) mention *2n* = 36 and FN = 70 for a Nigerian bat (although the erroneously mention FN = 79 on p. 6).

Genetics
Riesle-Sbarbaro *et al.* (2016: 447) reported on the complete mitochondrial genome of this species, which consists of 16,702 bases.

Riesle-Sbarbaro *et al.* (2018: "13") examined mitochondrial and nuclear DNA and found that connectivity and free mixing occurred between the colonies sampled over most of its distribution area. Their data also indicated that male dispersal occurs more often and/or over longer distances than females. The Ethiopian colonies seem to form an exception as the genetic differences indicate that they apparently diverged about 1.6 Mya from the bats from the more western part of the distribution area. Also, the populations from southern Ghana (Accra and Ve-Golokwati) show some genetic differentiation. Riesle-Sbarbaro *et al.* (2018: "14") suggest that the geographical barriers (e.g., mountains and water bodies such as rivers and lakes) and other environmental developments (e.g., urbanization of megacities) are the likely drivers for the regional divergences.

HABITAT:
This species is present in a variety of tropical moist and dry forest, savanna, bushland and mosaic habitats, and has additionally been reported from mangroves and swamp forests (Mickleburgh *et al.*, 2008f). It can persist in areas of partially degraded forest.

HABITS:
Anonymus (2002a: 103) mentions that in some areas of Benin, *E. gambianus* might be causing large trees to die, as they swarm in large numbers on a restricted surface.

ROOST:
Roosting usually takes place as individuals or small groups in dense vegetation (Happold, 1987). *E. gambianus* forms roosting colonies in crowns of trees, containing a few to 50 - 100 individuals (Kunz, 1996: 44). Ayensu (1974: 716) indicates that in Ghana, *Azadirachta indica* or the Neem Tree is a favorite roosting haven. Lawson *et al.* (2018: 110) found them also roosting in Mango (*Mangifera* sp.) and Fig (*Ficus* sp.) trees around schools, churches, marketplaces and people's homes. Ayeh *et al.* (2025: 1) showed that these bats prefer older, large, shady exotic teak (*Tectona grandis* L.f.), mango, and the West African legume *Millettia thonningii* (Schumach.) Baker as roost trees.

Amponsah-Mensah *et al.* (2022: 8) found that roost site selection is non-random: roost trees are generally larger and closer to buildings than non-roost trees. They also are selected in relatively open and less mature areas. Lactating bats also choose roost trees where more bats are present, possibly to reduce predator risk or enhance other social co-operation benefits. Amponsah-Mensah *et al.* (2022; 1) also found that that males more frequently switched roosts as compared with females. Preferrred roosting trees included *Azadirachta indica* A. Juss., 1830 (Neem), *Ficus* spp, *Mangifera indica* Linnaeus (Mango), *Polyalthia longifolia* Sonn. B. Xue & R.M.K. Saunders (False Ashoka), and *Spathodea campanulata* P. Beauv. (African Tulip Tree).

MIGRATION:
Isotopic data collected by Omatsu *et al.* (2008: 21 - 22) suggest that *E. gambianus* has an East-West migratory behaviour inside its distribution range, which is even more pronounced than the migration displayed by *Eidolon helvum*. Six specimens that were captured in February in Mali were most probably originating from some 3,000 km to the east.

DIET:
Ayensu (1974) reports that in West Africa, *E. gambianus* visits *Parkia clappertoniana* (Dawadawa), *Ceiba pentandra* (Silk-Cotton Tree or Kapop Tree), *Mangifera indica* (Mango Tree),

Anacardium occidentale (Cashew Tree), *Psidium guajava* (Guava Tree), *Carica papaya* (Papaya or Pawpaw), and *Azadirachta indica* (Neem Tree) when foraging. Bachirou *et al.* (2011: 2) indicate that *E. gambianus* is the most important seed disperser for the Neem Tree in Cameroon.

Kangoyé *et al.* (2010: 291) show a picture of *E. gambianus* pollinating *Ceiba pentandra* flowers and also indicate that this species was found transporting Shea fruits (*Vitellaria paradoxa*) or figs (*Ficus* sp.), whereas others were found in cashew fields (*Anacardium occidentale*).

Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *E. gambianus* these include *Rauvolfia caffra* Sond. (Quinine Tree - Apocynaceae) and *Psidium guajava* L. (Apple Guava - Myrtaceae).

Based on faecal pellets and ejecta, Amponsah-Mensah *et al.* (2019: 5687) found the following fruits (FR) and flowers (FL) in the diet of bats from Ghana: Anacardiaceae: *Anacardium occidentale* L. (Cashew) FR), *Mangifera indica* L. (Mango - FR), *Spondias mombin* L. (Yellow Mombin - FR); Annonaceae: *Annona muricata* L. (Soursop - FR), *Polyalthia longifolia* Sonn. (Indian Mast Tree, False Ashoka - FR); Bignoniaceae: *Spathodea campanulata* P. Beauv. (African Tulip Tree - FL); Bombacaceae: *Bombax buonopozense* P. Beauv. (Gold Coast Bombax, Red-flowered Silk-cotton - FL), *Ceiba pentandra* (L.) Gaertn. (Kapok, Silk Cotton - FL); Caricaceae: *Carica papaya* L. (Papaya, Pawpaw - FR); Combretaceae: *Terminalia catappa* L. (Indian Almond - FR); Cucurbitaceae: *Melothria* sp. (Mouse Melon - FR); Fabaceae: *Daniellia oliveri* (Rolfe) Hutch. & Dalziel (African Copaiba Balsam - FL), *Parkia biglobosa* (Jacq.) R. Br. ex G. Don (African Locust Bean - FL); Gentianaceae: *Anthocleista vogelii* Planch. (Cabbage Tree - FR, FL); Malvaceae: *Adansonia digitata* L. (Baobab - FL), *Sterculia rhinopetala* K. Schum. (Brown Sterculia, Red Sterculia - FR); Meliaceae: *Azadirachta indica* A. Juss (Neem - FR, FL); Moraceae: *Antiaris toxicaria* Lesch. (False Iroko, Antiaris - FR), *Ficus* spp. (five species Figs - FR), *Milicia excelsa* (Welw.) C.C. Berg (Iroko, Odum - FR); Musaceae: *Musa* sp. (Banana - FR, FL); Myrtaceae: *Psidium guajava* L. (Guava - FR), *Syzygium* sp. (Woodland Waterberry - FR); Solanaceae: *Solanum* sp. (Potato Tree - FR); Verbenaceae: *Vitex doniana* Sweet (Black Plum - FR). *Ficus* sp. was present in over a third of all the samples and were eaten in all months. Other fruits that played a vital role, and were preferred over other available fruits, include *Vitex doniana* and *Anthocleista vogelii*. The main reason was probably the higher protein content of these fruits. They were also highly available in the period of late pregnancy (March and September) and parturition (April/May and October/November) (p. 5689). Amponsah-Mensah *et al.* (2019: 5690) could not confirm whether *E. gambianus* were actively eating pollen, nectar, or both, even when they observed bats visiting flowering trees and being covered in pollen.

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Epomophorus gambianus*: *Annona senegalensis* Persoon, *Lannea microcarpa* Engl. and K. Krause, *Sarcocephalus latifolius* (Sm.) E.A. Bruce, 1947, *Vitellaria paradoxa* C.F. Gaertn., *Vitex doniana* Sweet, 1826.

On the University of Ghana campus, Ayeh *et al.* (2025: 1) found that E. gambianus preferred *Bridelia micrantha* (Hochst.) Baill. (Coastal Golden-leaf) and mangoes for foraging.

Clare and Oelbaum (2024: 242) remark that *Epomophorus gambianus* has a seasonally variable diet that shifts from frugivorous to nectarivorous.

Predators:

Mikula *et al.* (2016: Supplemental data) mention the Bat Hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator, as well as the Pied Crow (*Corvus albus* Statius Muller, 1776). Ayivor *et al.* (2017: 6) indicate that the latter targets young, just weaned *E. gambianus*.

Population:

Structure and Density

This is a common species in the western parts of its range. It is gregarious and form colonies of several hundreds individuals or less (Mickleburgh *et al.*, 2008f; Tanshi and Fahr, 2016) .

Trend

2016: Unknown (Tanshi and Fahr, 2016). 2008: Unknown (Mickleburgh *et al.*, 2008f; IUCN, 2009).

Lifespan:

Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 7.8 years.

Reproduction and ontogeny:

Szekely *et al.* (2015: Suppl.) report that the gestation period lasts for 150 days, and that the young's weight at birth is 10 g (the adult weights 80 g).

In Ghana, Amponsah-Mensah *et al.* (2024: 1, 2) found the reproduction to be seasonal bimodal polyestry, with births (one young) in March/April and August/September. The estimated birth rate was 0.89 (95% CI = 0.85 to 0.92) per reproductive season. The overall sex ratio (female to male ratio) was male-dominated (0.69, 95% CI = 0.64 to 0.75), but female-biased for adults (62% female). This ratio showed temporal and age-specific variations.

MATING:
Nesi *et al.* (2011: 552) indicate that the male's courting call has a frequency of 1,750 Hz.

The mating system is polygynous (Webber *et al.*, 2017: Suppl.).

Grimmberger (2004: 407) describe the courtship behaviour as "largely following the Lek system".

PARASITES:
BACTERIA
Höhne *et al.* (1975: 505) found *Listeria monocytogenes* bacteria in one out of two *E. gambianus* specimens from Lomé, Togo.

HAEMOSPORIDA
Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Hepatocystis* in one investigated bat (see also Arnuphapprasert *et al.*, 2020: Suppl.). Miltgen *et al.* (1977: 595) pointed out that the first reports of gametocytes from this parasite were made by the Léger(s) from Niger in 1914. Thiombiano *et al.* (2023: 4) provided the first report of *Hepatocystis* from bats from Burkina Faso. Additionally, they also reported the presence of *Trypanosoma* cf. *dionisii*.

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Lagos bat lyssavirus, Nipah henipavirus, Reston ebolavirus, Zaire ebolavirus.

Coronaviridae
Five out of 87 (5.7 %) Guinean *E. gambianus* specimens tested positive (Lacroix *et al.*, 2020: 7).

Joffrin *et al.* (2020: 7) reported Beta-D coronaviruses from bats from Cameroon. Motayo *et al.* (2020: 4) assigned these viruses to the subgenus *Nobecovirus*.

From Ghana, Suu-Ire *et al.* (2022: 5, 6) reported that samples collected during the rainy season were significantly more likely (up to five times) to be positive for coronavirus RNA, probably due to the higher numbers of young susceptible individuals being present in the population. The coronaviruses involved were Kenya bat coronavirus/BtKY56/BtKY55, Eidolon bat coronavirus and PREDICT_CoV-102.

Filoviridae - Filoviruses
Ebolavirus
Hayman *et al.* (2012d: 1208) examined 37 bats from the Greater Accra region, Ghana, and found 14 to be positive for EBOV antibodies.

Paramyxoviridae
Paramyxoviruses
Hayman *et al.* (2008a: 926; 2008b: 2) detected antibodies to Nipah virus in one bat collected in Ghana in 2007.

Drexler *et al.* (2012a: Suppl. Table S1) found three bats out of 54 (5.4 %) testing positive for *Henipavirus* in the Democratic Republic of the Congo and Ghana.

Rhabdoviridae
Lyssavirus - Rabies related viruses
2006 in Nigeria, Dzikwi *et al.* (2010: 269) tested 12 brains by direct fluorescent antibody (DFA) and mouse inoculation test (MIT) which tested negative for lyssavirus antigens.

Lagos bat virus (LBV)
Hayman *et al.* (2008a) detected antibodies in Ghana. In 2006, 12 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), where 3 tested positive (25%) for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Mokola virus (MOKV)
In 2006, 12 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), none tested positive for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Togaviridae
de Souza *et al.* (2024: 1490) reported 13.7% (63/461) infected *Epomophorus gambianus* bats in Senegal.

In their overview table, Maganga *et al.* (2014a: 8) reported that the following viruses were already found in *E. gambianus*: Lagos bat virus (LBV), Nipah virus (NPHV), Zaire Ebola virus (ZEBOV), Reston Ebola virus.

Raulino *et al.* (2022: 256) found antibodies against Dengue virus and O'nyong nyong virus.

UTILISATION:
In some localities in Benin, specimens of this species are eaten, but always in small numbers

(Anonymus, 2002a: 102). Dougnon *et al.* (2012: 85) reported that the carcasses have an average weight of 40.52 ± 5.08 g (about 43 % of the body mass). They also evaluated the quality of the meat (for 100 g): total mineral matter: 14.1 g, lipids: 13.36 g, protein: 58.4 g, Calcium: 44 mg, Sodium: 48 mg, Phosphor: 80 mg and Potassium: 88 mg.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

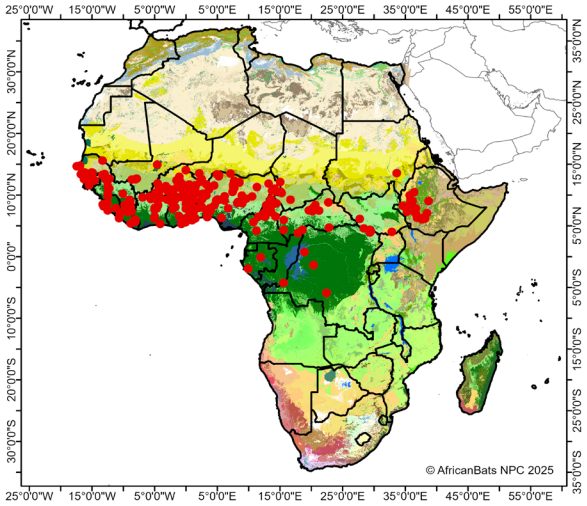

Figure 16. Distribution of *Epomophorus gambianus*.

Epomophorus gambianus gambianus (Ogilby, 1835)

*1835. *Pteropus Gambianus* Ogilby, Proc. zool. Soc. Lond., 1835, III (xxxi): 100. Publication date: 9 October 1835. Type locality: The Gambia: Banjul. [Goto Description]. Holotype: NHMUK 1907.1.1.233: ad ♀, skin and skull. Collected by: Dr. Percy John Rendall. Formerly in Tomes collection. Paratype: NHMUK 1874.a-c: 2 sad FF, 1 imm F, skin and skull. Collected by Liet. Rendall. Paratype: NHMUK 1874.a = 124b: imm ♀. Paratype: NHMUK 1874.b = 124c: ad ♀. Collected by: Dr. Percy John Rendall. Paratype: NHMUK 1874.c = 124d: imm ♀. Paratype: NHMUK 1907.1.1.231: sad ♀, skin and skull. Collected by: Dr. Percy John Rendall. Formerly in Tomes collection. - Comments: Type locality restricted by Kock *et al.* (2002b: 80). - Etymology: Named as the species was described from a specimen from Gambia in West Africa (see Taylor, 2005).

1835. *Pteropus macrocephalus* Ogilby, Proc. zool. Soc. Lond., 1835, III (xxxi): 101. Publication date: 9 October 1835. Type locality: The Gambia: "Gambia". [Goto Description]. - Comments: collected by Rendall.

1835. *Pteropus megacephalus* Swainson, Natural History and Classification of Quadrupeds, 91, 92, 356, figs 31, 154. Type locality: The Gambia. - Comments: Type locality originally as West Africa, but Andersen (1912b: 539) mentions "Gambia" as type locality.

1836. *Pteropus epomophorus* Bennett, Proc. zool. Soc. Lond., 1835, III (xxxiv): 149. Publication date: 12 February 1836. Type locality: The Gambia: "Gambia". Holotype: NHMUK 1907.1.1.232: ad ♂, skin only. Collected by: Dr. Percy John Rendall. (Type for both *Pteropus epomophorus* and *Pteropus whitei*). Ex Tomes collection: see Andersen (1912b: 542).

1836. *Pteropus Whitei* Bennett, Trans. Linn. Soc. Lond., 2 (1): 37, pl 6, pl 7. Publication date: 2 October 1836. Type locality: The Gambia: "Gambia". [Goto Description].

1838. *Epomophorus whitii:* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 504. Publication date: 1 February 1838. - Comments: Also incorrect subsequent spelling, see Boulay and Robbins (1989: 1). (Name Combination).

1898. *Epomophorus guineensis* Bocage, J. Sci. mat. phys. nat., ser 2, 5 (19): 136, fig 3. Publication date: June 1898. Type locality: Guinea-Bissau: Bolama [11 35 N 15 30 W]. [Goto Description]. Holotype: MLZA T118: ♂, mounted skin and skull. Collected by: D. da Costa; collection date: 1883. Bergmans (1988: 86) mentions this specimen as "probable holotype". - Comments: Andersen (1912b: 541) mentions the type specimen as being a mounted ad ♂, skull extracted, coll. Sr. Damasceno da Costa, and in the Lisbon Museum.

1899. *Ep[omophorus (Epomophorus)] zechi* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 46, pl 10, fig 3 a-c. Type locality: Benin: Togoland: Kunjuruma. [Goto Description]. Lectotype: ZMB 10170/17171: ad ♂, skin and skull. Collected by: Baumann; collection date: 1894. Lectotype designated by Andersen (1912b: 541); see Turni and Kock (2008) [skin: ZMB 10170 - skull: ZMB 17171]. Paralectotype: ZMB 10009: ad ♂, skin and skull. Collected by: Baumann; collection date: 1894. Kunjuruma. Paralectotype: ZMB 10011: juv ♂, skull only. Collected by: Bloess. Gross-Popo. Paralectotype: ZMB 10065: ad ♀, skull and alcoholic. Collected by: Anton Reichenow. Accra, Ghana. Paralectotype: ZMB 3413: ad ♂, skull and alcoholic. Lagos, Nigeria, acquired from Salmin. Paralectotype: ZMB 356: ad ♂, skin and skull. Collection date: 1855. West Africa acquired from Salmin. Paralectotype: ZMB 3654: ad ♂, skull and alcoholic. Collected by: Unger. Accra, Ghana. Paralectotype: ZMB 4784: ad ♂, skull and alcoholic. Collected by: Anton Reichenow. Accra, Ghana. - Comments: Kunjuruma is the location from lectotype: see Allen (1939a: 56). Boulay and Robbins (1989: 1) mention "Accra, Goldkuste [=Ghana], Gross-Popo, Misahoho in Togoland, Lagos [Nigeria], restricted to Kunjuruma, Togoland [=Benin] by Andersen (1912b)". Turni and Kock (2008: 10) mention "Matschie (1899b: 46) gave the locality of the specimens collected by Baumann as 'Misahöhe, Togoland' (= Missahoe, Togo); however, according to the entry book the locality is Kunjuruma." Preface by Matschie is dated 14 May 1899.

? *Epomophorus anurus:* - Comments: Not of Heuglin, 1864.

? *Epomophorus gambianus gambianus:* (Current Combination).

? *Epomophorus sp.:*

TAXONOMY:
Simmons (2005:322) does not include *crypturus*.

GENERAL DISTRIBUTION:
This subspecies ranges from Senegal in the west, through much of West Africa and parts of Central Africa. It is typically a lowland species occurring below 500 m asl.

Native: Benin; Burkina Faso; Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the); Côte d'Ivoire; Gambia; Ghana; Guinea; Guinea-Bissau (Bocage, 1889a:2; Seabra, 1898b; Monard, 1939; Veiga-Ferreira, 1948; Bergmans, 1988; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 22); Liberia; Mali; Nigeria; Senegal; Sierra Leone; Togo.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Côte d'Ivoire, Ethiopia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Niger, Nigeria, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, The Gambia, Togo, Zambia, Zimbabwe.

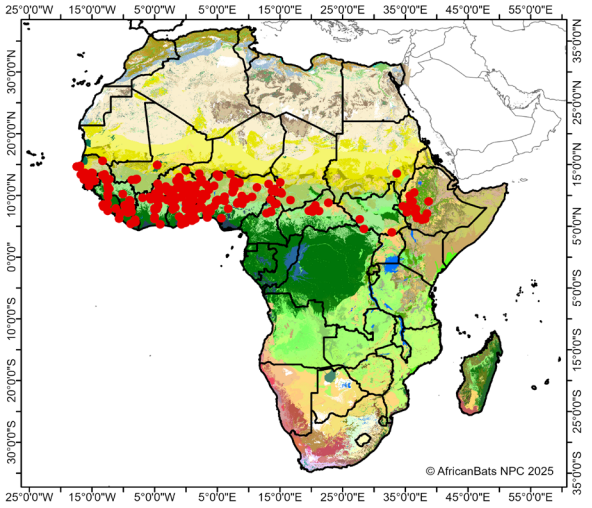

Figure 17. Distribution of *Epomophorus gambianus gambianus*.

Epomophorus gambianus pousarguesi Trouessart, 1904

*1904. *Epomophorus pousarguesi* Trouessart, Catalogus Mammalium tam viventium quam fossilium, supplement, 55. Type locality: Central African Republic: Grande Brousse between Yabanda and Mpoko. Holotype: MNHN ZM-MO-1892-1020: Collected by: Jean Dybowski; collection date: 1-11 December 1891. Bergmans (1978a: 682, 683) mentions two different numbers for this specimen. In the table on pag 682, he mentions 1899-1020 and on page 683 he mentions 1892-1020. - Comments: Boulay and Robbins (1989: 1) mention "Africa Occ.-Centrali, a fl. Chari (Inter Yabanda et Mpoko), reg. Lac. Chad. Central African Republic as type locality; restricted to 'along the track between Mpoko (near Makorou) and Yabanda' by Bergmans (1978b)". The type locality is sometimes given as "Eastern Congo, Shari region". Description based on *E. macrocephalus* Pousargues (not Ogilby) see Allen (1939a: 56).
? *Epomophorus gambianus pousarguesi:* (Current Combination).
? *Epomophorus gambianus:* - Comments: Not of Ogilby, 1835.

TAXONOMY:
Recognized as a subspecies (Simmons, 2005: 322).

GENERAL DISTRIBUTION:
In Ethiopia populations may be found up to 2,000 m asl.

Native: Ethiopia, South Sudan, Sudan.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Gabon.

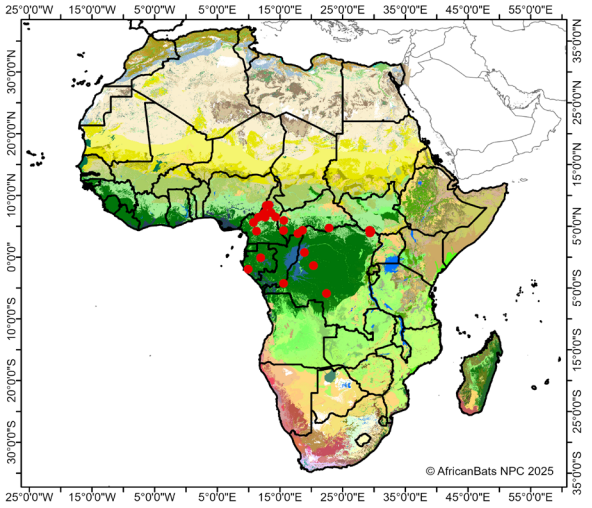

Figure 18. Distribution of *Epomophorus gambianus pousarguesi*.

Epomophorus grandis (Sanborn, 1950)

*1950. *Micropteropus grandis* Sanborn, Publ. Cult. Comp. Diamantes Angola, Lisboa, 10: 55, figs 2 - 3. Publication date: 29 November 1950. Type locality: Angola: Lunda: Dundo [07 22 S 20 50 E]. Holotype: FMNH 66433: ad

♀, skull and alcoholic. Collected by: António A. de Barros Machados; collection date: September 1948; original number: 2015.

1988. *Epomophorus grandis:* Bergmans, Beaufortia, 38 (5): 136. (Current Combination).

TAXONOMY:
Transferred from *Micropteropus* to *Epomophorus* by Bergmans (1988). See Simmons (2005: 322).

COMMON NAMES:
Czech: kaloň Sanbornův. English: Sanborn's Epauletted Fruit-bat, Lesser Angolan Epauletted Fruit Bat. French: Epomophore de Sanborn, Petit Epomophore frugivore d'Angola. German: Sanborns Epaulettenflughund. Tshokwe (Angola): Tshingunzu.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Mickleburgh *et al.*, 2008h; IUCN, 2009, Fahr and Mildenstein, 2016).

Assessment History
Global
2016: DD ver 3.1 (2001) (Fahr and Mildenstein, 2016). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008h; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004e; IUCN, 2004). 2000: DD (Hilton-Taylor, 2000). 1996: EN (Baillie and Groombridge, 1996). 1994: Rare (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known. There is deforestation taking place in parts of the species range. However, it is not known how adaptable this species is to habitat modification (Mickleburgh *et al.*, 2008h; IUCN, 2009; Fahr and Mildenstein, 2016).

CONSERVATION ACTIONS:
Current conservation efforts
It is not known if the species is present in any protected areas. The area where it occurs has been inaccessible for many years ((Mickleburgh *et al.*, 2008h) in IUCN (2009, Fahr and Mildenstein, 2016) .

Conservation needs/priorities
Studies are needed on the species' population sizes, distribution, and extent of occurrence throughout its range ((Mickleburgh *et al.*, 2008h) in IUCN (2009, Fahr and Mildenstein, 2016). Monitoring of population sizes and locations over time are also important to establish whether these are stable or experiencing trends of decline.

The threats to these bats are poorly understood. Studies are needed on the species' natural history and habitat requirements and on the effects of forest loss and degradation on the species' population sizes/distribution. Research is also needed whether the species is hunted, and if so, on the amount of hunting and the level of bushmeat trade, and the effects of that hunting on population sizes and persistence (Fahr and Mildenstein, 2016).

Effective roost site protection efforts are needed to minimize hunting mortality and disturbance to nontarget individuals. Similar to most threatened flying foxes, local capacity building for conservation managers and education and awareness within local communities are greatly needed to support conservation efforts.

GENERAL DISTRIBUTION:
Epomophorus grandis is a poorly known as it has only been recorded at the type locality of Dundo in northeast Angola (Sanborn, 1950), and from Pointe Noire on the coast of Congo (Bergmans, 1988).

Native: Angola (Bergmans, 1988; Sanborn, 1950; Monadjem *et al.*, 2010d: 552); Congo (Bergmans, 1988; Monadjem *et al.*, 2010d: 552; Bates *et al.*, 2013: 333).

HABITAT:
Although the natural history of this species is poorly known, it seems to be primarily a savanna species that may range into tropical moist forest (Mickleburgh *et al.*, 2008h; IUCN, 2009).

POPULATION:
Structure and Density
It is only known from a few specimens (Mickleburgh *et al.*, 2008h; IUCN, 2009; Fahr and Mildenstein, 2016).

Trend
2016: Unknown (Fahr and Mildenstein, 2016). 2008: Unknown (Mickleburgh *et al.*, 2008h; IUCN, 2009).

UTILISATION:
It is not known if this species is hunted for the bushmeat trade (Fahr and Mildenstein, 2016).

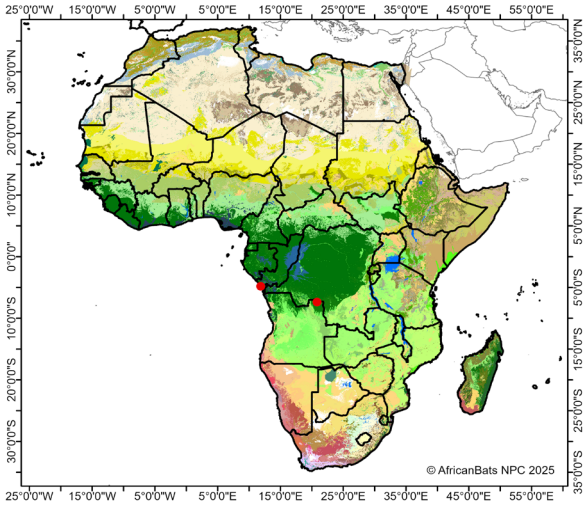

Figure 19. Distribution of *Epomophorus grandis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Congo.

Epomophorus intermedius (Hayman, 1963)

1889. *Epomophorus pusillus:* Noack, Zool. Jb. Syst., 4: 206. - Comments: Not of Peters, 1868. Partim. See Kock (1987b: 220).
1953. *Micropteropus grandis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 49. - Comments: Not of Sanborn, 1950. In part. See Kock (1987b: 220).
1956. *Micropterus grandis:* Leleup, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., 46: 76. - Comments: Not of Sanborn, 1950. (Lapsus).
*1963. *Micropteropus intermedius* Hayman, Publ. Cult. Comp. Diamantes Angola, Lisboa, 66: 100, fig 8. Type locality: Angola: Lunda: Dundo [07 22 S 20 50 E]. [Goto Description]. Holotype: NHMUK 1962.2073: ad ♀, skull and alcoholic. Collected by: Dr. António A. de Barros Machado; collection date: June - July 1953.
1969. *Micropteropus pusillus:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 24. - Comments: Not of Peters, 1868. In Part. See Kock (1987b: 220).
2019. *Epomophorus intermedius:* Van Cakenberghe, in: Wilson and Mittermeier, Handbook Mammals of the World. Vol. 9, 101. (Current Combination).
2025. *Epomophorus intermedus:* Tolovou and Lenga, Biod. J., 16 (1): 51). Publication date: 30 March 2025. (Lapsus).
? *Micropterus (sic) intermedius:* (Name Combination, Lapsus).
? *Micropterus intermedius:* (Emendation).

TAXONOMY:
See Bergmans (1989) and Simmons (2005: 327).

COMMON NAMES:
Czech: kaloň Haymannův. English: Hayman's Lesser Fruit-bat, Hayman's Lesser Fruit Bat, Hayman's Dwarf Epauletted Fruit Bat, Hayman's Epauletted Fruit Bat. French: Microptère de Hayman, Roussette naine de Hayman. German: Haymans Kleiner Epaulettenflughund. Tshokwe (Angola): Tshingunzu.

CONSERVATION STATUS:
Global Justification
Assessed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Mickleburgh *et al.*, 2008ba; IUCN, 2009; Mickleburgh *et al.*, 2020b).

Assessment History
Global
2020: DD ver 3.1 (2001) [assessed as "*Micropteropus intermedius*"] (Mickleburgh *et al.*, 2020b). 2008: DD ver 3.1 (2001) [assessed as "*Micropteropus intermedius*"] (Mickleburgh *et al.*, 2008ba; IUCN, 2009). 2004: DD ver 3.1 (2001) [assessed as "*Micropteropus intermedius*"] (Mickleburgh *et al.*, 2004t; IUCN, 2004). 2000: DD (Hilton-Taylor, 2000). 1996: VU (Baillie and Groombridge, 1996). 1994: Rare (Groombridge, 1994).

MAJOR THREATS:
The threats to this species are not well known, but may include general habitat loss through ongoing deforestation (Mickleburgh *et al.*, 2008ba; IUCN, 2009; Mickleburgh *et al.*, 2020b).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ba) [in IUCN (2009)] and Mickleburgh *et al.* (2020b) report that there appear to be no direct conservation measures in

place. It is not known if the species is present in any protected areas. Further surveys are needed to locate populations of this species, and to record additional details on natural history and possible threats.

GENERAL DISTRIBUTION:
This species has only been recorded from four localities in northern Angola (the type locality of Dundo) and southern Democratic Republic of the Congo (Luluabourg, Banana/Netonna, and Thysville).

Native: Angola (Bergmans, 1989; Monadjem *et al.*, 2010d: 554); Congo (Tolovou and Lenga, 2025: 50); Congo (The Democratic Republic of the) (Bergmans, 1989; Monadjem *et al.*, 2010d: 554).

POPULATION:
Structure and Density
It is currently only known from four specimens. Some of these records are old, and the species does not appear to have been recorded since the 1950s (Mickleburgh *et al.*, 2008ba; IUCN, 2009; Mickleburgh *et al.*, 2020b).

Trend
2020: Unknown (Mickleburgh *et al.*, 2020b).
2008: Unknown (Mickleburgh *et al.*, 2008ba; IUCN, 2009).

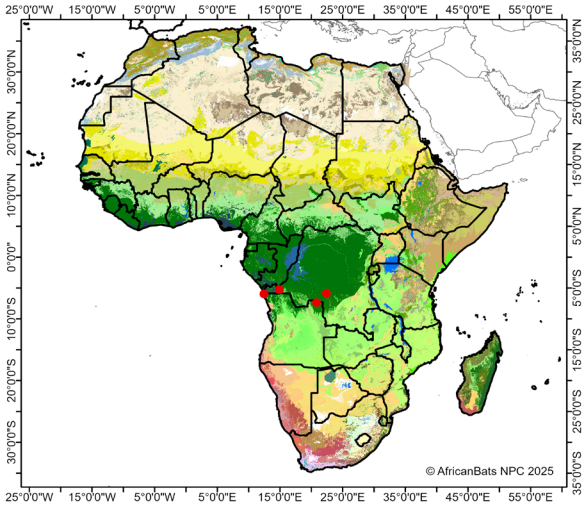

Figure 20. Distribution of *Epomophorus intermedius*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Congo (Democratic Republic of the).

Epomophorus labiatus (Temminck, 1837)

*1837. *Pteropus labiatus* Temminck, Monogr. Mamm, 2 (11): 83, pl 39, figs 1 - 3. Publication date: 1837. Type locality: Sudan: Blue Nile province: Sennaar [15 35 N 33 38 E, 425 m]. [Goto Description]. Lectotype: RMNH MAM.27342: juv ♀, mounted skin and skull. Collected by: Dr. Paolo Emilio Botta; collection date: 1830 - 1833. See Kock (1969a: 18).
The RMNH catalog mentions two numbers: 27342.a (skull + loose bones) and 27342.b (mounted skin). - Comments: Type locality originally given as "Abyssinia"; see Horáček *et al.* (2000: 96). Andersen (1912b: 530) mentions that Temminck (1835-1841) had two specimens, one obtained in London without any indication about the country of origin, and a second from Paris, originating from the collections of M. Botta, the latter is the only one presently in the RMNH. - Etymology: From the Latin "*labiatus*" for lipped.

1842. *Pteropus Schoënsis* Rüppell, Mus. Senckenberg., 3 (2): 131. Type locality: Ethiopia: Shoa province: Shoa province [ca. 09 00 N 39 00 E]. [Goto Description]. Holotype: SMF 4370: juv ♂, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1841. Old catalog II.A.13a; see Kock (1969a: 18); Mertens (1925: 20) mentions it as a juv ♀. - Comments: Andersen (1912b: 531) already mentioned that the mounted specimen is of doubtfull sex.

1860. *Epomophorus labiatus:* Tomes, Proc. zool. Soc. Lond., 28: 55 - 56. (Current Combination).

1864. *Epomophorus anurus* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 31 (7): 12. Type locality: South Sudan: Bahr-el-Ghazal province: Bongo [07 14 00 N 28 42 00 E, 414 m]. Syntype: SMNS 1090: imm ♂, mounted skin and skull. Collected by: Martin Theodor von Heuglin; collection date: 1855. Dieterlen *et al.* (2013: 293) indicate that this specimen was collected in “Bellegas-Tal” [= Belegaz/Belghe], Abyssinia. Syntype: SMNS 1091: ad ♀, mounted skin and skull. Collected by: Martin Theodor von Heuglin; collection date: 1863/1864. Dieterlen *et al.* (2013: 293) indicate that this animal was collected in Bongo [= country of Bongo, southern part of the province of Bahr-el-Ghazal in the south of Sudan]. Syntype: SMNS 609/661: ad ♂, mounted skin and skull. Dieterlen *et al.* (2013: 293) mention the skull bears number 609, and that the mounted specimen has 661 as additional number. - Comments: Thorn *et al.* (2009: 20) mention 06 40 N 29 40 E. Type locality originally given as "Gebied zw. Wau am Djur River und dem Getti River im Westen", see Kock (1969a: 18). Two syntypes: SMNS 1090 (♂, imm) and SMNS 1091 (♀, ad).

1877. *Pteropus (Epomophorus) anurus:* Heuglin, Reise in Nordost Afrika, 2: 16 - 17. (Name Combination).

1877. *Pteropus (Epomophorus) labiatus:* Heuglin, Reise in Nordost Afrika, 2: 15 - 16. (Name Combination).

1877. *Pteropus (Epomophorus) schovanus:* Heuglin, Reise in Nordost Afrika, 2: 18. - Comments: Emendation of *schoënsis* (see Andersen, 1912b: 530; Allen, 1939a: 56; Kock, 1969a: 18). (Emendation).

1899. *Ep[omophorus (Epomophorus)] doriae* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 54. Type locality: Eritrea: Bogos country [=Keren region] [ca. 15 45 N 38 20 E]. [Goto Description]. Holotype: ZMB 10079: Collected by: Gerrard.

1936. *Epomophorus labiatus minor:* G.M. Allen and Lawrence, Bull. Mus. comp. Zool., 79 (3): 45. - Comments: (Locality suggestive of *labiatus* rather than *Epomophorus minor* Dobson, 1880). (Name Combination).

1960. *Epomophorus labiatus anurus:* Harrison, J. East Afr. Nat. Hist. Soc., 23 (7) (104): 287. Publication date: December 1960. (Name Combination).

1966. *Epomophorus crypturus:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 23. - Comments: (in part: specimen IRSN 10677 from "Kilwezi"- label reads Kilubwezi). Not of Peters, 1852.
1971. *Epomophorus sp.* Hill and Morris, 29.
1974. *Epomophorus labiatus labiatus:* Largen, Kock and Yalden, Mon. Zool. ital., (NS) 16 (Suppl 5): 221, 226. (Name Combination).
1978. *Epomophevus anupus:* Arata and Johnson, in: Pattijn, Ebola Virus Haemorrhagic Fever, 135. (Lapsus).
1988. *Epomophorus gambianus gambianus:* Bergmans, Beaufortia, 38 (5): 84.
1996. *Epomophorus anarus:* Kityo and Kerbis, J. East Afr. Nat. Hist., 85: 58. (Lapsus).
2019. *Epomophorus labiatuc:* Banerjee, Kulcsar, Misra, Frieman and Mossman, Viruses, 11 (1) 41: 6. Publication date: 9 January 2019. (Lapsus).
? *Epomophorus cf. labiatus:*

TAXONOMY:

Includes *anurus* and *minor*; see Claessen and De Vree (1991), but see also Bergmans (1988) and Simmons (2005: 322 - 323). Middle Eastern forms reviewed by Horáček *et al.* (2000).

COMMON NAMES:

Azande (DRC): Ndima. Chinese: 小颈囊果蝠. Czech: kaloň sudánský. English: Little Epauletted Fruit-bat, Ethiopian Epauletted Fruit-bat, Ethiopian Epauletted Fruit Bat. French: Petit épomophore, Epomophore d'Ethiopie, Roussette labiée, Roussette labiaire. German: Temmincks Epaulettenflughund. Italian: Epomòforo labiàto. Kinande (DRC): Apopo. Malawian: Lichinji, Mleme. Ukrainian: Малий еполетовий крилан [=Malyy epoletovyy krylan].

CONSERVATION STATUS:

Global Justification

Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008l; IUCN, 2009; Taylor, 2016a).

Assessment History

Global

2016: LC ver 3.1 (2001) (Taylor, 2016a). 2008: LC ver 3.1 (2001) [includes *E. minor* (Mickleburgh *et al.*, 2008l; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004d; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

There appear to be no major threats to this species as a whole. Some populations may be threatened by overharvesting for subsistence food (Mickleburgh *et al.*, 2008l; IUCN, 2009; Taylor, 2016a).

CONSERVATION ACTIONS:

Taylor (2016a) supports Mickleburgh *et al.* (2008l) [in IUCN (2009)] who report that this species has been recorded from many protected areas. No direct conservation measures are currently needed for the species as a whole. Additional research is needed into the impact of possible overharvesting of animals on some populations.

GENERAL DISTRIBUTION:

Epomophorus labiatus is largely distributed in Central Africa and East Africa. It appears to range from northern Nigeria and Cameroon, into Chad, southern and central Sudan, Ethiopia and Eritrea, and from here south into eastern Democratic Republic of the Congo, Uganda, Rwanda and Burundi, Kenya and Tanzania (including the islands of Unguja [=Zanzibar] and Mafia [see O'Brien, 2011: 285]), being recorded as far south as Malawi, northern Mozambique and northern Zambia. There is one isolated record from coastal Congo, although the presence of the species in this country, and also in Chad and Nigeria, needs to be confirmed. It has been recorded from lowland sites up to elevations of over 2,000 m asl (2,200 asl at Gondar, Ethiopia) (Mickleburgh *et al.*, 2008l; IUCN, 2009).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 436,697 km^2.

For Ethiopia, Ahmed *et al.* (2023: 1) calculated the current suitable habitat to cover 85,176.1 km^2, and they predict it might decrease with 0.95 % by 2050 and with 2 % by 2070 due to more unfavourable climate conditions.

Senegal records are probably erroneous (see Bergmans, 1988), although Capo-Chichi *et al.* (2004: 161) do refer to these records.

Native: Burundi; Cameroon; Congo (Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Bergmans, 1988; Monadjem *et al.*, 2010d: 552); Djibouti (Pearch *et al.*, 2001: 392); Eritrea (Yalden *et al.*, 1996); Ethiopia (Yalden *et al.*, 1996); Kenya (Aggundey and Schlitter, 1984; Malawi (Ansell, 1986; Bergmans, 1988; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 552); Mozambique (Monadjem *et al.*, 2010d: 552; Monadjem *et al.*, 2010c: 376); Rwanda (Baeten *et al.*, 1984); Saudi Arabia (Gaucher, 1992); Sudan

(Koopman, 1975; Tanzania; Uganda (Kityo and Kerbis, 1996: 59); Yemen (Benda *et al.*, 2011b: 28); Zambia (Ansell, 1973; Bergmans, 1988; Monadjem *et al.*, 2010d: 552).

Presence uncertain: Chad; Congo; Nigeria.

DENTAL FORMULA:
None of the 26 skulls examined by Esquivel *et al.* (2021: Suppl.) had an abnormal number of teeth.

SEXUAL DIMORPHISM:
Dobson (1873: 247) already indicated that Temminck noticed the absence of shoulder-tufts in the female.

MOLECULAR BIOLOGY:
Karyotype
Đulić and Mutere (1973b) recorded the diploid number as 2*n* = 36.

Blood chemistry
Kurpiers *et al.* (2015: 49) reported that in South Sudan bats living in disturbed habitats suffer from electrolyte depletion, anaemia and are also nutritionally deficient when compared with bats from undisturbed habitats. They also indicated that pH and PCO2 levels were higher than found typically in mammal ranges, thus suggesting that these bats experience respiratory acidosis, with elevated acidosis in bats in undisturbed habitats.

cyt *b*
Benda *et al.* (2025: 44) examined the cyt *b* gene in three Kenyan bats and found two of them to be 99.7 % similar to the haplotype of an *Epomophorus gambianus* from the Central African Republic, whereas the third agreed for 99.3 % with the haplotype of an *Epomophorus labiatus* from the RSA. Strangely enough, *E. gambianus* doesn't occur in Kenya. See also *Epomophorus wahlbergi* for a similar observation. Benda *et al.* (2025) stress that more investigation is necessary to understand this issue.

HABITAT:
This species is regularly recorded from woodland (including miombo woodland), savanna, bushland, arid or semi-desert grassland habitats and mosaics of these general habitat types. In East African coastal areas, it has been recorded from mangroves (Mickleburgh *et al.*, 2008l).

Reeder *et al.* (2019: 229) classified this species as being peridomestic (living in and around human habitations).

HABITS:
It has been found resting together in small groups of about a dozen animals (Mickleburgh *et al.*, 2008l).

Happold and Happold (2023: 64) mention that *Epomophorus* cf. can hover briefly and take off from the ground.

DIET:
Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *E. labiatus* this included *Ficus natalensis* Hochst (Natal Fig - Moraceae).

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008l; IUCN, 2009).

Trend
2008: Stable (Mickleburgh *et al.*, 2008l; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Bergmans (1979a), Kingdon (1974), and Kulzer (1958) [in Krutzsch (2000: 110)] indicate that the male reproductive cycle of *E. labiatus* [as *E. anurus*] is apparently in synchrony with the one from the females as there occurs a biseasonal testicular hypertrophy in West Africa.

PARASITES:
Ejotre *et al.* (2015: 28) found that pregnant females were significantly more likely to be infected by hemoparasites than males and non-pregnant females. Reeder *et al.* (2015: 76) furthermore reported that blood parasite levels were not related to stress (as indexed by the neutrophil/lymphocyte ratio).

DIPTERA
Nycteribiidae
Tripselia blainvillii (Leach 1817) single record (Haeselbarth *et al.*, 1966: 113, host referred to as *E. anurus*). Dick *et al.* (2023: 74) mentioned this bat fly as *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817).

ACARI
Myobiidae
Bochkov and Fain (2003) reported the presence of *Binuncus (Binuncus) epomophori* Fain, 1972

Teinocoptidae
Teinocoptes epomophori Rodhain, 1923 was reported by Fain (1967: 367) from an *E. anurus* from Astrida (= Butare), Rwanda and from an *E. labiatus minor* from Bukavu, DRC.

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Entebbe bat virus and Shamonda orthobunyavirus. In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against West Nile virus (WNV), Dengue 2 virus (DENV-2), non-specific Flaviviruses, Babanki virus (BBKV), and Rift Valley fever virus (RVFV).

Coronaviridae
28.6 % (10 out of 35) of the Kenyan *E. labiatus* tested positive for CoV in the study by Tao *et al.* (2017).

Nziza *et al.* (2019: 156) reported the presence of Kenya bat coronavirus/BtKY56/BtKY55 in a rectal swap from a bat from Rwanda. These viruses were assigned to the subgenus *Nobecovirus* by Motayo *et al.* (2020: 4).

Flaviviridae
Dengue virus
Bonilla-Aldana *et al.* (2020: 3) reported this bat as one of the species carrying this virus.

Pegivirus (BPgv)
1 out of 3 bats from Kenya examined by Quan *et al.* (2013: Table S5) were infected by clade k type *Pegivirus*.

Zika virus (ZIKV)
Fagre *et al.* (2021: 1) found ZIKV sfRNA, but not NS5 in one Ugandan *E. labiatus*.

Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen they examined from the Democratic Republic of the Congo did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

UTILISATION:
Bobo and Ntumwel (2010: 232) report that, in the Korup area of Cameroon, "*E. anurus*" is being sold as a medicine on markets, since consuming it would render women fertile. It is hunted for the bushmeat trade (Taylor, 2016a).

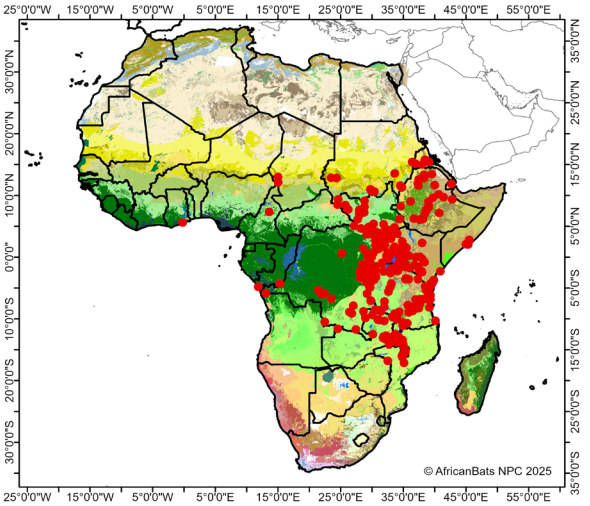

Figure 21. Distribution of *Epomophorus labiatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burundi, Cameroon, Chad, Congo, Congo (Democratic Republic of the), Djibouti, Eritrea, Ethiopia, Ghana, Kenya, Malawi, Mozambique, Rwanda, Somalia, South Africa, South Sudan, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Epomophorus minimus Claessen & De Vree, 1991

1837. *Pteropus labiatus:* Temminck, Mon. Mammal., 2 (11): 83 - 84. Publication date: 1837. - Comments: Partim. One of the type specimens, an adult ♂, which later disappeared (Claessen and De Vree, 1991: 216). - Etymology: From the scientific Latin male adjective *labiātus* meaning "lipped", referring to the expansible lower lip (see Lanza *et al.*, 2015: 36).
1861. *Epomophorus labiatus:* Tomes, Proc. zool. Soc. Lond., 29: 11. - Comments: Partim.
1899. *Ep[omophorus (Epomophorus)] schoensis:* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 44, 53. - Comments: Partim. Not of Rüppell, 1842.
1930. *Epomophorus minor:* Zammarano, Le colonie Italiane, 146. - Comments: Not of Dobson, 1880.
1939. *Epomophorus labiatus minor:* G.M. Allen, Bull. Mus. comp. Zool., 83: 56. - Comments: Partim. Not of Dobson, 1880.
1971. *Epomophorus labiatus labiatus:* Hayman and Hill, Mammals of Africa: Chiroptera, 6 - 7. - Comments: Partim.
1984. *Epomophorus labiatus anurus:* Aggundey and Schlitter, Ann. Carnegie Mus., 53 (5): 124. - Comments: Animals from Katilo. Not of Heuglin, 1864.
*1991. *Epomophorus minimus* Claessen and De Vree, Senckenb. biol., 71: 216. Type locality: Ethiopia: Harar province: Shewa: Bahadu [10 05 N 40 37 E, 600 m]. Holotype: SMF 44238: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971; original number: 16194. Full grown female with well developed nipples (see Claessen and De Vree (1991: 216). Paratype: SMF 44232: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44233: sad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44234: juv ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44235: juv ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44236: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44237: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44239: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44240: ad ♀, skull and alcoholic.

Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44242: sad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 2015. Paratype: SMF 44243: juv ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 5 May 1971. Paratype: SMF 44245: ad ♀, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44246: sad ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44247: ad ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44248: sad ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44250: juv ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. Paratype: SMF 44252: ad ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 - 7 May 1971. Paratype: SMF 44253: juv ♂, skull and alcoholic. Collected by: Dr. Malcolm John Largen; collection date: 3 May 1971. - Etymology: From the Latin superlative masculine adjective *mìnimus* meaning "least, smallest" referring to the relatively small size of the species (see Lanza *et al.*, 2015: 41). (Current Combination).

TAXONOMY:

Included in *E. minor* by Bergmans (1988). Recognized as a full species by Claessen and De Vree (1991); Simmons (2005: 323).

Based on multivariate analyses, Claessen and De Vree (1991) concluded that the type specimen of *Epomophorus minor* fitted within the variation displayed by *E. labiatus* and that this name should be considered a synonym of *E. labiatus*. Consequently, no valid name was available for the smallest form included in the genus *Epomophorus* at that time. For these specimens, they proposed the new name *Epomophorus minimus*. However, Bergmans (1997: 72) provided a further analysis of the problem and rejected this view, reinstating the name *minor*. The situation is currently still not completely resolved with both names being used by various authors. The systematics of the small-sized *Epomophorus* forms, therefore, still remains unclear and needs further investigation.

The most recent literature data do not mention *minimus* (e.g., Simmons and Cirranello, 2023b) or provisionally include it in . minor awaiting further analyses (Almeida *et al.*, 2020: 16). Yet many publications (e.g., Benda *et al.*, 2020: 2583; Hassanin *et al.*, 2020: 1405; Takadate *et al.*, 2020: Suppl.; Aziz *et al.*, 2021: Suppl.; Geldenhuys *et al.*, 2021: Suppl.; Vogeler *et al.*, 2021: 1065; Rainho *et al.*, 2023: 4) still consider it as a valid species. Given that none of these papers provided an indept analysis, we still retain *minimus* as a separate species.

Member of the *gambianus* species group.

COMMON NAMES:

Chinese: 侏颈囊果蝠. Czech: kaloň habešský. English: Least Epauletted Fruit-bat, East African Epauletted Fruit-bat, East African Epauletted Fruit Bat. French: Petit Epomophore, Epomophore nain. German: Winziger Epaulettenflughund. Italian: Epomòforo mìnimo.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008j; IUCN, 2009; Webala, 2016).

Assessment History

Global

2016: LC ver 3.1 (2001) (Webala, 2016). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008j; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004j; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

There appear to be no major threats to this species. It is locally threatened in parts of its range by deforestation of its habitat for timber and firewood (Mickleburgh *et al.*, 2008j; IUCN, 2009; Webala, 2016).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008j) [in IUCN (2009)] report that *E. minimus* it is not known if the species is present in any protected areas. Some individuals have been captured at Lake Bogoria National Reserve, Kenya (Wechuli et al. unpublished data cited in Webala (2016)). Further studies are needed into the distribution, natural history and possible threats to this species (Webala, 2016).

GENERAL DISTRIBUTION:

Epomophorus minimus is an East African species which is present in Uganda, northern Tanzania, Kenya, Ethiopia and Somalia.

Native: Ethiopia (Yalden *et al.*, 1996, Benda *et al.*, 2020: 2583); Kenya (Aggundey and Schlitter, 1984; Somalia (Funaioli and Simonetta, 1966); Tanzania; Uganda (Kityo and Kerbis, 1996: 58).

MOLECULAR BIOLOGY:
cyt *b*
Benda *et al.* (2025: 44) investigated the cyt *b* gene in 9 *E. minimus* specimens from Kenya and found none of them to have unique haplotypes for the species. Six of them had a haplotype that was 99.7 - 99.9 % identical to that of *Epomophorus gambianus* from the Central African Republic (a species not occurring in Kenya); one agreed for 99.0 % with an *Epomophorus wahlbergi* from the RSA; one with an *Epomophorus labiatus* from Djibouti (98.3 %) and the last with *Epomophorus pusillus* from the Central African Republic (99.8 %).

HABITAT:
Recorded from dry and arid savanna habitats.

DIET:
It is possible that this species has a specialised diet to persist in its arid habitat (Mickleburgh *et al.*, 2008j).

POPULATION:
Structure and Density
E. minimus is probably a common species (Mickleburgh *et al.*, 2008j; IUCN, 2009), but patchy distribution may reflect insufficient sampling (Happold, 2013l). It was reported to be the second most abundant species, after *Micropteropus pusillus*, in northern Uganda (Kityo and Kerbis, 1996). Elsewhere it is only known from collection records, with no information on population trends (Webala, 2016).
Trend
2016: Stable (Webala, 2016). 2008: Stable (Mickleburgh *et al.*, 2008j; IUCN, 2009).

VIRUSES:
Drexler *et al.* (2012a: Suppl. Table S1) indicated that three out of six specimens they tested from the Democratic Republic of the Congo were positive for *Rubulavirus*.

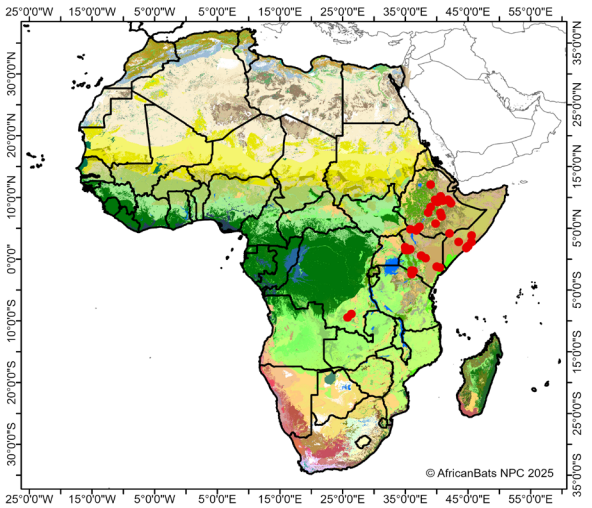

Figure 22. Distribution of *Epomophorus minimus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Ethiopia, Kenya, Somalia, Tanzania, Uganda.

Epomophorus minor Dobson, 1880

*1880. *Epomophorus minor* Dobson, Proc. zool. Soc. Lond., 1879, IV: 715. Publication date: April 1880. Type locality: Tanzania: Zanzibar [ca. 06 10 S 39 12 E]. Holotype: NHMUK 1879.9.12.4: juv ♂, skull and alcoholic. Collected by: Dr. A. Robb. Exchanged from Surgon-General G.E. Dobson see Turni and Kock (2008). Paratype: ZMB 5550: ad ♀, skull and alcoholic. Presented/Donated by: George Edward Dobson. See Turni and Kock (2008: 8). - Comments: Andersen (1912b: 532) furthermore mentions that paratypes were distributed by Dobson to various museums. Considered a valid species by Kock (1969a: 18 - 24), Koopman (1975: 363) and Ansell and Dowsett (1988: 27), but see Claessen and De Vree (1991). - Etymology: From the Latin "*minor*" (= smaller). (Current Combination).
1896. *Epomophorus pusillus:* Pousargues, Ann. Sci. Nat., (8) 3: 255.
? *Epomophorus anurus:* - Comments: Not of Heuglin, 1864.
? *Epomophorus labiatus anurus* - Comments: Not of Heuglin, 1864.
? *Epomophorus labiatus minor:* (Name Combination).
? *Epomophorus labiatus:* (Name Combination).
? *Epomophorus minor minor:* (Name Combination).

TAXONOMY:
Recognized as a full species by Simmons (2005: 323), but considered a synonym of *labiatus* by many other authors (e.g., Benda *et al.*, 2022: 297).

COMMON NAMES:
Czech: kaloň zanzibarský, kaloň menší. English: Minor Epauletted Fruit Bat. German: Zwerg-Epaulettenflughund. Yao (Malawi): Lichinji (applied to all large bats).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Taylor, 2016b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Taylor, 2016b). 2008: LC ver 3.1 (2001) [as part of *E. labiatus*] (Mickleburgh *et al.*, 2008l; IUCN, 2009). 2004: LC ver 3.1 (2001) [as part of *E. labiatus*] (Mickleburgh *et al.*, 2004d; IUCN, 2004). 1996: LR/lc [as part of *E. labiatus*] (Baillie and Groombridge, 1996).

MAJOR THREATS:
There appear to be no major threats to this species as a whole. Some populations may be threatened by overharvesting for subsistence food (Taylor, 2016b).

CONSERVATION ACTIONS:
Taylor (2016b) reports that this species has been recorded from many protected areas. No direct conservation measures are currently needed for the species as a whole. Additional research is needed into the impact of possible overharvesting of animals on some populations.

GENERAL DISTRIBUTION:
Native: Ethiopia, Somalia, Sudan, Kenya, Rwanda, SE Dem. Rep. Congo, Zambia, Tanzania, Zanzibar, Uganda, Malawi (Simmons, 2005: 323).

DENTAL FORMULA:
Esquivel *et al.* (2021: Suppl.) examined 14 skulls and found no aberrant number of teeth.

POPULATION:
Structure and Density
This is a common species (Taylor, 2016b).

Trend
2016: Stable (Taylor, 2016b).

REPRODUCTION AND ONTOGENY:
For Malawi, Happold and Happold (1990b: 564) reported that females are monotocous (having only one pup). The young were born during the late dry season and the wet season.

PARASITES:
Hirst (1923: 980) described a new mite species (*Ancystropus æthiopicus*) from an *E. minor* specimen from Zanzibar.

UTILISATION:
This species is harvested for the bushmeat trade (Taylor, 2016b).

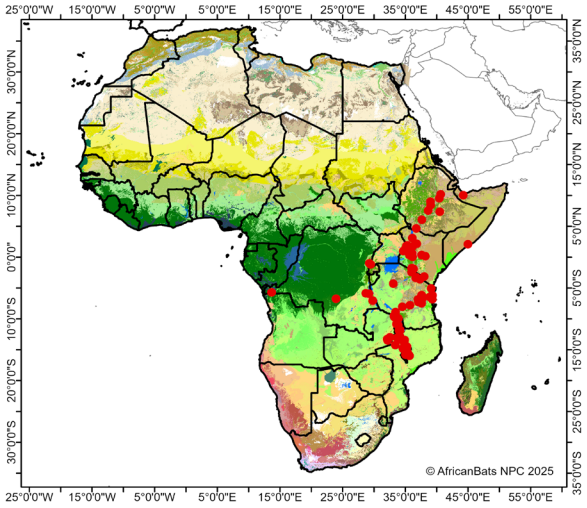

Figure 23. Distribution of *Epomophorus minor*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Mozambique, Somalia, Sudan, Tanzania, Zambia.

Epomophorus pusillus Peters, 1868

1860. *Epomophorus schoënsis:* Tomes, Proc. zool. Soc. Lond., 1860, I: 56. Publication date: February - May 1860. - Comments: Not of Rüppell, 1842.

*1868. *Epomophorus pusillus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 870 (for 1867). Type locality: Nigeria: S Nigeria: Yoruba. Holotype: ZMB 3438: imm ♀, skull and alcoholic. Collected by: A. Mann; collection date: 1862. Presented/Donated by: F. von Krauss. Holotype designated by Bergmans (1989: 96, 99); see Turni and Kock (2008: 9). - Comments: For a discussion on the type locality, see Bergmans (1989). Grubb *et al.* (1998: 70) state that "Peters in effect renamed *Epomophorus schoënsis* Tomes and therefore Tomes's type locality ["Gambia" - fixed by Andersen, 1912b: 559] must stand, even though his syntypes are evidently no longer in existence", but also see Kock *et al.* (2002b: 82) for a discussion on the type locality. Furthermore, Tanshi *et al.* (2022a: 322) indicate that Yoruba is not a locality in Nigeria, and that the type locality should probably be somewhere in southwestern Nigeria, where the Yoruba language is predominantly spoken. - Etymology: From the Latin "*pusillus*" (=very small) (see Owen-Ashley and Wilson, 1998: 4). (Current Combination).

1878. *Epomophorus schoensis:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 14. Publication date: 15 June 1878.

1974. *Micropteropus pussilus:* Ayensu, Ann. Missouri Bot. Gard., 61: 706. (Lapsus).

1978. *Micropterus pusillus:* Arata and Johnson, in: Pattijn, Ebola Virus Haemorrhagic Fever, 135. (Lapsus).

1990. *Micropteropus pusilis:* King, Davies and Lawrie, Vet. Microbiol., 23 (1-4): 168. Publication date: June 1990. (Lapsus).

2007. *Micropteropus prusillus:* Lameed, Biodiversity, 8 (4): 8. (Lapsus).

2024. *Microptreopus pusillus:* de Souza, Gaye, Ndiaye, Morgan, Daouda Sylla, Amadou SY, Diallo and Weaver, Emerg. Inf. Dis., 30 (7): 1490. Publication date: July 2024. (Lapsus).

2025. *Microteropus pusillus:* Ngene, Okwuonu, Ogbonna, Ukwueze and Ejere, Caryologia, 78 (1): 3. Publication date: 1 October 2025. (Lapsus).
? *Epomophorus (Micropteropus) pusillus:* (Name Combination).
? *Micropteropus pusillus:* (Name Combination).
? *Nanonycteris veldkampi:* - Comments: Not of Jentink, 1888.

TAXONOMY:
See Bergmans (1989), Owen-Ashley and Wilson (1998) and Simmons (2005: 327).

COMMON NAMES:
Castilian (Spain): Murciélago Enano. Chinese: 非洲小狐蝠. Czech: kaloň nigerijský. English: Peters' Lesser Epauletted Fruit Bat, Peters' Lesser Fruit-bat, Peters's Dwarf Epauletted Fruit Bat, Dwarf Epauletted Fruit Bat. French: Petit microptère, Roussette naine de Peters. German: Peters' Kleiner Epaulettenflughund, Peter's Zwergepaulettenflughund. Kiluba (DRC): Mulima. Tshokwe (Angola): Tshingunzu.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) [as *Micropteropus pusillus*] in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008q; IUCN, 2009; Bakwo Fils and Kaleme, 2016a).

Assessment History
Global
2016: LC ver 3.1 (2001) as "*Micropteropus pusillus*" (Bakwo Fils and Kaleme, 2016a). 2014: LC ver 3.1 (2001) assessed as "*Micropteropus pusillus*" (Bakwo Fils and Kaleme, 2020). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008q; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004s; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

MAJOR THREATS:
It is locally threatened by habitat loss and degradation. In Equatorial Guinea, local people eat *E. pusillus* (Fa, 2000). This could lead populations to decline (Bakwo Fils and Kaleme, 2016a; Bakwo Fils and Kaleme, 2020).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008q) [in IUCN (2009)], Bakwo Fils and Kaleme (2016a) and Bakwo Fils and Kaleme (2020) who report that in view of the species wide range it seems probable that it is present in many protected areas. In general, no direct conservation measures are currently needed for this species as a whole. Bakwo Fils and Kaleme (2016a) and Bakwo Fils and Kaleme (2020) further recommends that studies are needed in the species home range countries to have indications on population trends and details on its ecology.

GENERAL DISTRIBUTION:
Distributed in West Africa, Central Africa and East Africa. It ranges from Senegal and The Gambia, throughout much of West Africa to Cameroon, from here it is distributed into Equatorial Guinea (Rio Muni), Gabon, Congo, Central African Republic, the Democratic Republic of the Congo, Sudan, Uganda and western Ethiopia and Kenya. It is found as far south as central Angola and Zambia.

Native: Angola (Hayman, 1963; Crawford-Cabral, 1989; Bergmans, 1989; Lopes and Crawford-Cabral, 1992; Monadjem *et al.*, 2010d: 554); Benin (Capo-Chichi *et al.*, 2004: 161); Burkina Faso (Kangoyé *et al.*, 2015a: 605); Cameroon; Central African Republic (Morvan *et al.*, 1999: 1195); Chad; Congo (King and Dallimer, 2010: 66); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 554); Côte d'Ivoire (Heim de Balsac, 1934b: 24); Equatorial Guinea; Ethiopia; Gabon; Gambia; Ghana; Guinea (Fahr and Ebigbo, 2003: 128; Denys *et al.*, 2013: 281; Decher *et al.*, 2016: 261); Guinea-Bissau (Monard, 1939; Bergmans, 1989; Rainho and Ranco, 2001: 28); Kenya; Liberia (Fahr, 2007a: 103); Mali (Meinig, 2000: 104); Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 59); Zambia (Ansell, 1974; Monadjem *et al.*, 2010d: 554).

Presence uncertain: Burundi.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on both the dorsal and ventral sides of the proximal arm and the dorsal side of the distal arm. Furthermore it is moderate on the ventral side of the distal arm and the dorsal side of the plagiopatagium and both the ventral and dorsal sides of the forearm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.6 Pa, aspect ratio 8.7 for a wingspan of 38 cm and a wing area of 164 cm^2 and a body mass of 21 g.

MOLECULAR BIOLOGY:
Karyotype
Haiduk *et al.* (1980; 1981: 226) reported 2*n* = 35, FN = 64, a subtelocentric X and two Y chromosomes for males from Cameroon (XY_1Y_2) (see also Nesi *et al.*, 2011: 552).

Contrary to the above, Tolera *et al.* (2021: 126) reported 2n = 35/36, FN = 48 in bats from Ethiopia. In females, all 36 chromosomes were bi-armed (primarily metacentric and a few sub-metacentric). In males, only 35 chromosomes could be counted, with one unpaired metacentric chromosome, suggesting that the Y chromosome is too small to be detected (or it might have been attached to another chromosome).

Ngene *et al.* (2025) reported 2n = 36 and FN = 79 (p. 6) and FN = 70 (p. 11) for a Nigerian bat.

ROOST:
E. pusillus roosts singly or in pairs in the dense leave cover of shrubs and trees (Kunz, 1996: 44). In Ghana, Ayivor *et al.* (2017: 3) found these bats to roost together with *E. gambianus*, where *pusillus* occupied the lower parts of the trees.

DIET:
Ayensu (1974) reports the following plant species being visited by "*Micropteropus pusillus*" during foraging: *Kigelia africana* (Sausage tree), *Anacardium occidentale* (Cashew tree), *Psidium guajava* (Guava tree), and *Spathodea campanulata* (African Tulip tree).

Seltzer *et al.* (2013: table S2) provided an overview of the plant species found beneath bat feeding roosts. For "*Micropteropus pusillus*" these include *Milicia excelsa* (Welw.) C. C. Berg (African Teak - Moraceae) and *Psidium guajava* L. (apple guava - Myrtaceae).

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by "*Micropteropus pusillus*": *Chlorophora exelsa* Welw., Benth. and Hook. f., *Cola gigantea* A. Chev., 1951, *Ficus capensis* Thunb., 1786, *Ficus vallis-choudae* Delile, 1843, *Psidium guajava* Linnaeus, 1753, *Solanum torvum* Sw., 1788, *Solanum verbascifolium* Kunth, *Vitex doniana* Sweet, 1826.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the African harrier-hawk (*Polyboroides typus* A. Smith, 1829) as diurnal avian predator.

POPULATION:
Structure and Density
This is generally considered to be one of the most common African bats (Mickleburgh *et al.*, 2008q; Bakwo Fils and Kaleme, 2016a). Large numbers are often recorded from fruit trees (Mickleburgh *et al.*, 2008q; IUCN, 2009).

Epomophorus pusillus is seldom gregarious and mostly roosts alone or in two but may be found in groups of up to ten individuals (Bakwo Fils and Kaleme, 2016a). These groups are usually well-spaced throughout the roosting site (Bakwo Fils and Kaleme, 2020).

Trend
2016: Stable (Bakwo Fils and Kaleme, 2016a).
2014: Stable (Bakwo Fils and Kaleme, 2020).
2008: Stable (Mickleburgh *et al.*, 2008q; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Thomas and Marshall (1984) reported that females mated at the age of six months and gave birth at 12 months. Males reached puberty at the age of seven months. They also found that there is a clear relation between the bimodal births and the bimodality of the rainfall.

11 out of 18 females reported by Bergmans (1979a: 177) from Pointe Noire and Loandjili (Congo) were pregnant between 25 November and 13 December.

In Sierra Leone, Weber *et al.* (2019: 19) found two pregnant females on 30 and 31 March and five lactating on 6 and 7 April and 28 May.

MATING:
Haft (2002) [in Nesi *et al.* (2011: 552)] indicates that the male's courting call has a frequency of 2800 Hz.

PARASITES:
Held *et al.* (2016: 119) reported one out of 26 examined Gabonese *E. pusillus* specimens to be infected by the bacterium *Staphylococcus aureus*.

Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Hepatocystis* in 68 out of 72 investigated bats. In the Amurum forest reserve (Nigeria), Atama *et al.* (2019: 1550) found *Hepatocystis* parasites in 42 % of the examined "*Micropteropus pusillus*" bats. Cameron *et al.* (2020: Suppl.) report on GenBank

data for a *Hepatocystis* sp. (Mic_pus_G4_2) from a bat from Guinea.

Tsague *et al.* (2021: 3) found *Hepatocystis* parasites in 19 out of 29 bats from the Centre province in Cameroon.

Hepatocystis parasites were also found in 10 out of 10 bats from Burkina Faso (Thiombiano *et al.*, 2023: 4).

Tsague *et al.* (2024: Suppl.) reported three Cameroonian bats as co-infected by *Trypanosoma* cf. *livingstonei* and *Hepatocystis* sp.

Hirst (1923: 980) indicates that a specimen from Gambia was the host for a mite that was probably referrable to *Ancystropus æthiopicus* Hirst, 1923.

Fain (1967: 367) reported *Teinocoptes epomophori* Rodhain, 1923 (Acari: Teinocoptidae) from a "*Micropteropus pusillus*" specimen from Boma, DRC. He also reported *T. auricularis* Fain, 1959 on this host species from Kabinda, Boma and Beno, DRC.

Bochkov and Fain (2003: 13) mentioned that *Binuncus (Binuncus) epomophori* Fain, 1972 was found on "*Micropteropus pusillus*" specimens from Sudan.

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Lagos bat lyssavirus, Rift Valley fever phlebovirus, Zaire ebolavirus.

Coronaviridae - Coronaviruses
Maganga *et al.* (2014a: 5) tested 533 animals from Congo and found only two testing positive.

Anthony *et al.* (2017b: Suppl.) mention the beta-coronavirus Kenya_CoV_BtKY56.

Joffrin *et al.* (2020: 7) identified the Congolese viruses as Beta-D coronavirus.

For the two Congos, Kumakamba *et al.* (2021: 7) reported 29 out of 416 bats to test positive for coronaviruses.

Viruses found in bats from the DRC and Cameroon were assigned to the subgenus *Nobecovirus* by Motayo *et al.* (2020: 4).

Filoviridae - Filo viruses
Ebolavirus
Muyembe-Tamfum *et al.* (2012: 9) refer to Pourrut *et al.* (2005) who found ZEBOV-specific antibodies.

Two to 10 of the 158 DRC bats examined by Lacroix *et al.* (2021: 7) tested positive for antibodies against Ebola.

Marburg
Towner *et al.* (2007) tested 149 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 19 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found.

Flaviviridae
Raulino *et al.* (2022: 256) found antibodies against Dengue, Usutu, West Nile and Zika viruses.

Nairoviridae
Orthonairovirus
Only two of the 100 specimens from Gabon and Congo tested by Müller *et al.* (2016: 3) were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 152 specimens they examined from the Democratic Republic of the Congo, the Central African Republic, Gabon, Congo, and Ghana tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

Phenuiviridae
Phlebovirus
de Jong *et al.* (2011: 11) and Luis *et al.* (2013: suppl.) report the occurrence of Rift Valley fever virus.

Rhabdoviridae
Lyssavirus - Rabies related viruses
2006 in Nigeria, Dzikwi *et al.* (2010: 269) tested 55 brains by direct fluorescent antibody (DFA) and mouse inoculation test (MTIT) and all tested negative for lyssavirus antigens.

Lagos bat virus (LBV)
Sureau *et al.* (1977) isolated Lagos bat virus in African Central Republic, from where Greenbaum and Carr (2005: 168) also reported monoclonal antibodies. In 2006, 21 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), none tested positive for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Mokola virus (MOKV)
King *et al.* (1990: 168) found monoclonal antibodies for MOKV in bats from the Central

African Republic. They also found antibodies for Duvenhage and Denmark bat virus.

In 2006, 21 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), where none tested positive for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Togaviridae

de Souza *et al.* (2024: 1491) reported 7 out of 88 Senegalese *'Micropteropus pusillus*" specimens tested positive for chikungunya virus (CHIKV).

In their overview table, Maganga *et al.* (2014a: 8) report the following viruses were found on *E. pusillus*: Lagos Bat Virus (LBV), Coronavirus, Zaire Ebola Virus (ZEBOV), Marburg virus (MBGV), Rift Valley Fever virus (RVF).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Mali, Nigeria, Rwanda, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia.

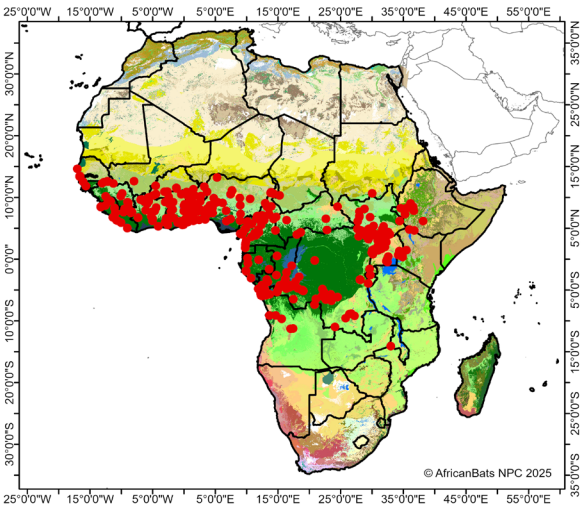

Figure 24. Distribution of *Epomophorus pusillus*.

Epomophorus wahlbergi (Sundevall, 1846)

1846. *Pteropus Haldemani* Hallowell, Proc. Acad. nat. Sci. Philad., 3 (3): 52. Publication date: prior to 15 July 1846. Type locality: Liberia. [Goto Description]. Holotype: ANSP MAM 1229: ad ♀, skull and alcoholic. Collected by: dr. S.M.E. Goheen. Presented/Donated by: Samuel Stehman Haldeman. - Comments: Holotype; ad ♀, SA, in the collection of the Academy of Natural Sciences of Philadelphia, see Andersen (1912b: 524), who further mentions "'W. Africa,' obtained from 'Dr. Goheen, Physician to the American Colonization Society' (from this it might be supposed that the specimen came from Liberia; there can be little doubt, however, that it was obtained elsewhere in W. Africa; no form of *Epomophorus* with the palate-ridges of the *walhbergi* type is known to inhabit the Guinea coast west of the Cameroons)." Allen (1939a: 56) suggests that the specimen might possible have come from Liberia. Considered a valid species by Schutt and Simmons (1998: 27).

*1846. *Pteropus Wahlbergi* Sundevall, Öfvers. kongl. Sv. Vet.-Akad. Förhandl., 3 (4): 118. Type locality: South Africa: KwaZulu-Natal: Port Natal [=Durban], near [29 52 S 31 00 E]. [Goto Description]. Holotype: NRM 602040: ad ♂. Collected by: Johan August Wahlberg; collection date: 27 November 1843; original number: 1040. Paratype: NRM 591042: ad ♀. Collected by: Johan August Wahlberg; collection date: 27 November 1842; original number: 1042. Paratype: RMNH MAM.27257: ad ♀. Collected by: Johan August Wahlberg; collection date: 1839 - 1841. - Comments: Type locality originally: "Prope Port-Natal et in Caffraria interiore occisus" see Acharya (1992: 1). As to the publication date, Andersen (1912b: 526, footnote) mentions "Sundevall's paper was read before the Stockholm Academy on May 13th, 1846, and presumably published in the latter half of May or in June (the 'Öfversigt' appears to have been issued regularly for every month in which the Academy held a meeting). Hallowell's description of *Pt. haldemani* was passed by the Publication Committee on May 26th, 1846, and printed in the May-June issue of the Proceedings of the Philadelphia Academy, which cannot have come out before, in the earliest, in July, since it contains a report of a meeting held on June 30th. The balance of evidence would seem, therefore, to be in favour of the date priority of *Pt. wahlbergi*". Andersen (1912b: 527) also mentions "Type (by selection) in the Riksmuseum, Stockholm, a well-preserved mounted adult male, skull separate (nearly perfect), Tugela River, Natal, 27 Nov. 1843, J. Wahlberg coll., Reg. No. 1040.". - Etymology: Named after Johan August Wahlberg (1810 - 1856), explorer, hunter and outstanding collector of zoological material in Southern Africa. He was killed in 1856 by a wounded elephant near Savuti in northern Botswana (see Gyldenstolpe, 1933; Taylor, 2005, Lanza *et al.*, 2015: 48).

1871. *[Epomophorus macrocephalus] var. unicolor* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 125. Publication date: 14 January 1871 [Goto Description].

1871. *Epomophorus macrocephalus var. unicolor* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 125. Publication date: 14 January 1871. Type locality: Mozambique: Zambesi River: Shupanga [=Chupanga] [18 02 S 35 37 E]. Holotype: NHMUK 1864.1.9.4: sad ♀, skin and skull. Collected by: Dr. Sir John Kirk; collection date: June.

1899. *Ep[omophorus (Epomophorus)] neumanni* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 43, 50. Type locality: Kenya: Mombassa [04 03 S 39 40 E]. [Goto Description]. Lectotype: ZMB 9967: ad ♂, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date: about 1880. Lectotype designated by Andersen (1912b: 525); see Turni and Kock (2008). Paralectotype: ZMB 53873: ♀, skull and alcoholic. Collected by: Michael Rodgers Oldfield Thomas; collection date: 1898. Takaungu, Kenya. Paralectotype: ZMB 53897: ♀, skull and alcoholic. Collected by: Michael Rodgers Oldfield Thomas; collection date: 1898. Takaungu, Kenya. Paralectotype: ZMB 5428: ♀, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date:

ca. 1876. Mombassa. Paralectotype: ZMB 54367: ♂, skull and alcoholic. Collected by: Michael Rodgers Oldfield Thomas; collection date: 1898. Takaungu, Kenya. See Turni and Kock (2008: 9). Paralectotype: ZMB 5597: juv ♂, skull and alcoholic. Collected by: Fischer. Malini, Kenya. Paralectotype: ZMB 9968: juv ♀, skull and alcoholic. Collected by: Prof. Oscar Rudolph Neumann; collection date: January 1898. - Comments: Mombasa is the locality of the lectotype: see Allen (1939a: 57). Acharya (1992: 1) mentions "No type originally designated. Type locality restricted to "Mombassa, British East Africa (=Kenya) by Andersen (1912b: 524)". Matschie mentioned 14 May 1899 in his introduction.

1899. *Ep[omophorus (Epomophorus)] stuhlmanni* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 50. Type locality: Tanzania: Usaramo: Vikindo [06 59 S 39 17 E, 120 m]. [Goto Description]. Lectotype: ZMB 9982/9983: ad ♂, skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann; collection date: 11 January 1894. Lectotype designated by Andersen (1912b: 527); skull damaged [skin: ZMB 9983 + skull: ZMB 9982]. Paralectotype: ZMB 10000: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Zanzibar. Paralectotype: ZMB 10001: ♀, skull and alcoholic. Collected by: Neumann. Zanzibar. Paralectotype: ZMB 10002: ♂, skull and alcoholic. Collected by: Neumann. Zanzibar. Paralectotype: ZMB 2957: ♂, skull and alcoholic. Collected by: Wessel. Zanzibar. Paralectotype: ZMB 67054: ♀, skull only. Collected by: Dr. Franz Ludwig Stuhlmann; collection date: 1894. Dar es Salaam. Paralectotype: ZMB 67055: ♀, skull only. Collected by: Dr. Franz Ludwig Stuhlmann; collection date: 1894. Dar es Salaam. Paralectotype: ZMB 67056: skull only. Collected by: Dr. Franz Ludwig Stuhlmann; collection date: 1894. "Ushindo" [= ?], Tanzania. Paralectotype: ZMB 9252: ♀, skin and skull. Collected by: Fülleborn. Lindi, Tanzania. See Turni and Kock (2008: 9). Paralectotype: ZMB 9978: ♀, skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9979: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9980: ♂, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9981: ♂, skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9984: skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9986: skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9988: skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9989: ♂, skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Vikindo. Paralectotype: ZMB 9990: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Dar es Salaam. Paralectotype: ZMB 9991: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Dar es Salaam. Paralectotype: ZMB 9992: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Dar es Salaam. Paralectotype: ZMB 9993: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Dar es Salaam. Paralectotype: ZMB 9996: ♀, skull and alcoholic. Collected by: Dr. Franz Ludwig Stuhlmann. Zanzibar. Paralectotype: ZMB 9998: ♂, skin and skull. Collected by: Dr. Franz Ludwig Stuhlmann. Dar es Salaam. - Comments: The "type locality" is the locality of the lectotype: see Allen (1939a: 56). Acharya (1992: 1) mentions "No type originally designated. Type locality restricted to Vikindo, Usaramo, German East Africa [=Tanzania] by Andersen (1912b: 527)." In part (see Allen, 1939a: 56). Matschie mentioned 14 May 1899 in his introduction.

1899. *Ep[omophorus (Epomophorus)] zenkeri* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 44, 46. Type locality: Angola: Cabinda: Tschintschoscho [= Chinchoxo] Station [05 05 S 12 02 E]. [Goto Description]. Lectotype: ZMB 9974/9975: ad ♀, skin only. Collected by: dr. Julius Falkenstein; collection date: 1874. Lectotype designated by Andersen (1912b: 524): 8 paralectotypes designated; see Turni and Kock (2008) [skin: ZMB 9974 + skull: ZMB 9975]. Paralectotype: ZMB 3632: ♀, skull and alcoholic. Angola. Ex Mus Lisbon. Paralectotype: ZMB 4801: ♂, skull and alcoholic. Collected by: dr. Julius Falkenstein. Chinchoxo [=Loango Coast]. Paralectotype: ZMB 6129: ♂, skull and alcoholic. Collected by: Büttner. Gabon. Paralectotype: ZMB 9969: ♀, skull and alcoholic. Collected by: von Melchow. Malandje [=Malange], Angola. Paralectotype: ZMB 9970: ♂, skull and alcoholic. Collected by: von Melchow. Malandje [=Malange], Angola. Paralectotype: ZMB 9971: ♀, skull and alcoholic. Collected by: von Melchow. Malandje [=Malange], Angola. Paralectotype: ZMB 9976: ♂, skull and alcoholic. Collected by: dr. Julius Falkenstein. Chinchoxo. Paralectotype: ZMB 9977: ♂, skull and alcoholic. Collected by: dr. Julius Falkenstein. Chinchoxo. See Turni and Kock (2008: 10). - Comments: Allen (1939a: 56) mentioned the lectotype from Chinchoxo, Cabinda, Angola. Acharya (1992: 1) mentions "No type originally designated. Type locality restricted to Chinchoxo, Cabinda, Angola by Andersen (1912b: 524)." Matschie mentioned 14 May 1899 in his introduction.

1990. *Epomophorus walbergi:* King, Davies and Lawrie, Vet. Microbiol., 23 (1-4): 168. Publication date: June 1990. (Lapsus).

2012. *Epomophorus walhbergi:* Monadjem and Reside, Afr. Zool., 47 (2) 321. (Lapsus).

2013. *Epomophorus angolensis:* Van Cakenberghe and Seamark, African Chiroptera Report, 760. - Comments: Not of Gray, 1870 (in part). The specimens not from Angola or Namibia.

2016. *Epomophorus wahlbergyi:* Bahlman, Price-Waldman, Lippe, Breuer and Swartz, J. Anat., 229 (1): 116. Publication date: 1 March 2016. (Lapsus).

2017. *Epomorphorus wahlbergi:* Banyard and Fooks, Microbiol. Aust., 38 (1): 18. Publication date: March 2017. (Lapsus).

2025. *Epomophorus whalberghii:Epomophorus whalberghii:* Conenna, Muñoz-Garcia and Korine, Mammal Rev., xxx (e70005): 3. Publication date: 7 May 2025. (Lapsus).

? *Epomophorus crypturus:* - Comments: Not of Peters, 1852.

? *Epomophorus gambianus:* - Comments: Not of Ogilby, 1836.

? *Epomophorus wahlbergi haldemani:* (Name Combination).

? *Epomophorus wahlbergi wahlbergi:* (Name Combination).

? *Epomophorus wahlbergi:* (Name Combination, Current Combination).

TAXONOMY:



Figure 25. *Epomophorus wahlbergi* from Durban, KwaZulu Natal, South Africa.

Reviewed by Acharya (1992). See Simmons (2005: 323).

COMMON NAMES:
Afrikaans: Wahlberg se vrugtevlermuis, Wahlberg-witkolvrugtevlermuis. Castilian (Spain): Zorra Voladora. Chinese: 韦氏颈囊果蝠. Czech: kaloň Wahlbergův. English: Wahlberg's Epauletted Fruit-bat, Wahlberg's Epauletted Fruit-bat. French: Epomophore frugivore de Wahlberg, Roussette à épaulettes de Wahlberg. German: Wahlbergs Epaulettenflughund. Italian: Epomòforo di Wàhlberg. Malawian: Lichinji, Mleme. Portuguese: Morcego frugivoro de Wahlberg. Tshokwe (Angola): Tshingunzu.

SIMILAR SPECIES:
Taylor and Monadjem (2008: 24) provided data which enabled them to separate *E. wahlbergi* from *E. crypturus*. In the first species, the maxillary width is always larger than in the latter (♂♂: > 14 mm; ♀♀: > 13 mm).

Adams and Snode (2015) analysed the male mating calls of two groups of epauletted bats (*E. wahlbergi* and *E. crypturus*) in the Kruger National Park, and found differences in mean fundamental frequency, mean high frequency, mean low frequency, mean bandwidth, and mean call slope. They hypothesize that these differences may be used to avoid cross-mating between species.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008k; IUCN, 2009; Shoeman, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Shoeman, 2016). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008k; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004f; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Schoeman *et al.*, 2016d). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Mickleburgh *et al.*, 2008k; IUCN, 2009).

However, MacEwan (2016: 3) reports on *E. walhbergi* fatalities as a result of encounters with wind turbine blades. Cistrone *et al.* (2025: 1) found that populations of these bats in South Africa might withstand low to medium levels of turbine-related mortality, these nevertheless pose a significant risk for long-term population declines.

While Shoeman (2016) reports that this species is threatened by loss of habitat because of dune mining in KwaZulu-Natal, South Africa. Over the past 5 years a decline in some populations in KwaZulu-Natal have been observed, with the cause suspected to be loss of coastal forest due to dune mining as well as extensive drought. It is also possible that the Lagos bat virus may be affecting the population as a number of bats caught from Durban and the south coast in South Africa have tested seropositive for the virus (Shoeman, 2016).

McKechnie *et al.* (2021: 687) reported on the death of about 60 *E. wahlbergi* specimens in KwaZulu-Natal (RSA) during a period of extreme high temperatures in early November (late spring in the southern hemisphere), when T_{max} rose to 43 - 45 *C.

CONSERVATION ACTIONS:
Shoeman (2016) supports Mickleburgh *et al.* (2008k) [in IUCN (2009)] who report that it is present in many protected areas and no direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Epomophorus wahlbergi is found in Central Africa, East Africa and southern Africa (it is broadly distributed across southern Africa). It has been recorded from Cameroon (Aellen, 1952), Equatorial Guinea (Rio Muni), Gabon, Congo and

Angola in the west, through southern Democratic Republic of the Congo and Rwanda, being distributed in East Africa from Uganda, Kenya and southern Somalia in the north, through Tanzania (including the islands of Unguja [=Zanzibar], Pemba, and Mafia [see O'Brien, 2011: 285]), Zambia, Malawi and Mozambique into Zimbabwe, eastern and southern South Africa and Swaziland. There is a need to confirm the presence of this species in Cameroon and Equatorial Guinea. It ranges from sea level to around 2,000 m asl (Mickleburgh *et al.*, 2008k; IUCN, 2009).

The Ghanese record (ZMB 4786) was identified as *wahlbergi* by Ossa Gómez (2012: 31), but nevertheless seems odd. Neither Happold (2013m) nor Handbook of the Mammals of the World (2019) mention this species to occur in Ghana. If this really is a *wahlbergi* (as assumed by Ossa Gómez) then something is possibly wrong with the locality. Reichenow who is the collector of this specimen, also collected in Cameroon, which is closer to the general distribution of *wahlbergi*, hence the locality might be incorrectly assigned.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,327,859 km^2. González-Gutiérrez *et al.* (2025: Suppl.) calculated the entire distribution area to be 5,067,655.29 km^2.

In South Africa, its distribution is strongly associated with annual precipitation (Babiker Salata, 2012: 49).

Liberian records are probably erroneous.

Native: Angola (Bergmans, 1988; Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 552); Botswana; Burundi; Congo (Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 552); Eswatini (Monadjem *et al.*, 2010d: 553, Monadjem *et al.*, 2021: 5); Gabon; Kenya; Malawi (Happold *et al.*, 1988; Bergmans, 1988; Happold and Happold, 1997b: 815; Monadjem *et al.*, 2010d: 554); Mozambique (Smithers and Lobão Tello, 1976; Bergmans, 1988; Monadjem *et al.*, 2010d: 554; Monadjem *et al.*, 2010c: 376); Rwanda; Somalia; South Africa (Monadjem *et al.*, 2010d: 553);Tanzania (Stanley and Goodman, 2011: 37); Uganda; Zambia (Ansell, 1978; Bergmans, 1988; Cotterill, 2002b: 6; Monadjem *et al.*, 2010d); Zimbabwe (Monadjem *et al.*, 2010d: 553).

Presence uncertain: Cameroon; Equatorial Guinea, Namibia (Cotterill, 2004a: 260).

DENTAL FORMULA:
At birth, the following dentition is present: $I^2/_2$ $C^1/_1$ $PM^1/_1$ = 16

The permanent dental formula is: $I^2/_2$ $C^1/_1$ $PM^2/_3$ $M^1/_2$ = 28 (Sowler, 1980: 113).

Sowler (1980: 113) also reports that the second deciduous premolars appear between the second and third week, making a total of 20 teeth. All of the permanent teeth are present between week 12 and 14.

Only two of the 155 skulls examined by Esquivel *et al.* (2021: Suppl.) had extra teeth (polyodontia).

DETAILED MORPHOLOGY:
Tongue
Mqokeli and Downs (2012b examined eight *E. wahlbergi* from Pietermaritzburg, South Africa where all studied had an elongated, muscular tongue of 4.4 ± 0.33 cm (mean ± SD) long and 1.1 ± 0.4 cm (mean ± SD) wide. The anterior tip of the tongue of each was narrower compared with the broader posterior part of the tongue. The anterior tip of the tongues was 0.2 ± 0.05 cm thick with a width of 0.7 ± 0.10 cm (mean ± SD). The mid-region of the tongues had a thickness of 0.6 ± 0.05 cm and a width of 1 ± 0.20 cm (mean ± SD). The posterior regions of the tongues were 0.7 ± 0.00 cm thick and 1.5 ± 0.10 cm wide. The dorsal surface of the tongues possessed two types of mechanical papillae, filiform and conical papillae, and two types of gustatory papillae, fungiform and circumvallate papillae, which varied in distribution. Filiform papillae were highly abundant and occurred on the entire surface of the tongue. These papillae were posteriorly directed, with the small filiform papillae situated at the anterior tip of the tongue. Larger filiform papillae were present as a band posterior to these in the anterior to mid-regions of the tongue. Small filiform papillae with fungiform papillae occurred on either side of the giant filiform papillae band. The posterior part of the *E. wahlbergi* tongue (behind the giant filiform papillae) had elongated basket-like filiform papillae. These had large projections and occupied most of the posterior region of the tongue. Fungiform papillae occurred among these filiform papillae. The elongated basket-like filiform papillae were symmetrically arranged with respect to the axis of the tongue. The filiform papillae transformed into conical papillae on the left and right side of the posterior base of the tongue and pointed inwards. Short conical papillae occurred on the midportion of the

posterior region of the tongue. Fungiform papillae were scattered among the filiform papillae, except in areas of giant filiform and conical papillae. At the posterior end of the tongue occurred a triangular arrangement of three circumvallate papillae directed toward the pharynx surrounded by a deep groove.

Brain
Chawana *et al.* (2013: 160) indicate the average brain mass for 2 specimens was reported as 1.81 g.

Vomeronasal complex (VNC)
Smith *et al.* (2024: 6) described this as simple in morphology, triangular or bar-shaped in cross-section and consisting of simple upright bars in the caudal half.

Physiology
Minnaar *et al.* (2014b: 475) studied the evaporative water loss and indicate that they cannot substantiate previous findings of 5 to 10 % of the gas exchanges being done over the wing membrane.

FUNCTIONAL MORPHOLOGY:
Makanya and Mortola (2007: 687) and Kovalyova (2014: 326) indicate that the body skin epidermis for this species thick (61 ± 3 µm, SEM), the stratum corneum alone taking a third of it (21 ± 3 µm). The wing membrane was 27.8 ± 3.1 µm thick, of which the epidermis took 9.8 ± 0.7 (9.1 - 10.5) µm, with a stratum corneum (horny layer) of 4.1 ± 0.3 (3.7 - 4.4) µm. Makanya and Mortola (2007: 687) conclude that the wing web has structural modifications that permit a substantial contribution to the total gas exchange.

Coimbra *et al.* (2016: 191) mention that the eye in this species contains about 200,000 retinal ganglion cells. The minimum angle of resolution was approximately 0.167° (ca. 5-6 mm at 1 m distance).

King *et al.* (2025) investigated the olfactory system of this species.

SEXUAL DIMORPHISM:
Adams and Snode (2013: 54) indicate that males are larger than females and have bulldog-like facial pouches that inflate during mate-calling.

MOLECULAR BIOLOGY:
Karyotype
$2n$ = 36, FN = 68 (Đulić and Mutere, 1973b; Peterson and Nagorsen, 1975; Đulić and Mutere, 1977). Đulić and Mutere (1973b; 1977) reported BA = 34, whereas Peterson and Nagorsen (1975) reported BA = 36 as they included the X (no male studied).

For a bat from Nigeria, Ngene *et al.* (2025: 6) reported $2n$ = 35 and FN = 70, and conclude (p. 11) that this species follows the X0 sex chromosome system, but they show a XXY structure on p. 23.

cyt *b*
Benda *et al.* (2025: 42) investigated the cyt *b* sequence of 18 Kenyan bats and found that in 39 % of them the haplotype agreed with that of *E. wahlbergi* from the RSA, whereas 61 % agreed with the haplotype of *E. labiatus* from Djibouti. The *wahlbergi* haplotype was found in western localities whereas the *labiatus* type was found in the eastern localities. In one locality (Kimana), both haplotypes were found together even in bats collected at the same time.

HABITAT:
Although *E. wahlbergi* was found in bushed *Acacia* steppe, Lönnberg (1912: 27) doesn't regard this species as a steppe mammal, since a forest of tall Acacias and other trees was nearby.

HABITS:
Wickler and Seibt (1976) suggest that male *E. wahlbergi*'s call out to space out other males, but also to attract females. Funakoshi *et al.* (1995: 504) indicate that their communication calls consist of several harmonics covering the 2 - 8 kHz range, with a duration of 200 - 300 msecs, which also contain a slight click at the beginning.

In a study at the University of KwaZulu-Natal, Downs *et al.* (2015: 7) found that in winter bats generally slept for longer periods of time, and more often than in summer, and that no bats were sleeping when the ambient temperature was above 35°C. During the winter season, the percentage of sleeping bats increased between 9 and 12 o'clock as T_a increased. In both seasons, more bats were sleeping with both eyes closed than with only one open. During the first hours after their nightly activity, sleep with both eyes closed was more often observed, but this diminished later on during the day, with one eye open sleep reaching its peak around 10h00.

ROOST:
Day roosts are often located in the dense foliage of riverine or gallery forests, but sometimes caves are used too. Three to six individuals roost in small groups, and roosts are switched every five or six days, sometimes only for a few metres (Kunz, 1996: 44).

Wickler and Seibt (1976) [in McCracken and Wilkinson (2000: 350)] found that *E. wahlbergi* roosts in palm leaves or thatch roofs in mixed sex colonies, containing from three to over 100 animals, where the individuals are spaced at least 2.5 cm apart (except for female-young pairs).

In the Durban area, Taylor *et al.* (1999: 66) reported *E. wahlbergi* to roost along the undersurface midribs of royal palm (*Roystonia elata* (Kunth) O.F. Cook) leaves, and sometimes under eaves of double-storey houses or in recesses under a concrete road bridge.

The bats also regularly change their day roost (see Rollinson *et al.*, 2014: 173), e.g., to reduce the distance from the roost site to their feeding sites. During the winter they changed their roosting sites more often than during the summer (p. 179). These authors also reported that the roost temperatures are generally higher than the ambient temperature, and that roosts in man-made structures had usually a higher temperature than those in natural vegetation (e.g., in *Bougainvillea, Borassus, Trema orientalis*).

DIET:
Voigt *et al.* (2011: 355) found *E. wahlbergi* to be the second most important seed disperser for Syringa fruits (*Melia azedarach*), which is an alien invasive tree species in KwaZulu Natal. Jordaan *et al.* (2011: 961) fed captive specimens with fruits of *Psidium guajava* L. (Myrtaceae) and *Melia azedarach* L. (Meliaceae) during the month of May, and with those of *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae) and *Morus alba* L. (Moraceae) during September. *Solanum mauritianum* Scopoli (Solanaceae) and *Cinnamomum camphora* (L.) J. Presl. (Lauraceae) fruits were also made available to the bats but were not eaten by any of the individuals.

In Congo, Kipalu (2009: 16) reported *E. wahlbergi* visiting/consuming fruits of the Borassus Palm (*Borassus aethiopum*), African Peach (*Nauclea diderichii*), and Mango (*Mangifera indica*).

In Kenya, Krishnamoorthy *et al.* (2022: 8) captured an adult female over water near a Mango grove, of which they suspected it also visited flowering Baobab trees (Adansonia digitata).

Seltzer *et al.* (2013: table S2) provided an overview of the plant species found beneath bat feeding roosts. For *E. wahlbergi* these include *Rauvolfia caffra* Sond. (Quinine Tree - Apocynaceae), *Ficus natalensis* Hochst (Natal Fig - Moraceae) and *Syzygium cordatum* Hochst. (Water-berry Tree - Myrtaceae).

In KwaZulu-Natal, Raji and Downs (2022: Suppl.) registered 8958 visits of *E. wahlbergi* on *Ficus burkei* (Miq.) Miq., 1867 [=*Ficus thonningii* Blume, 1839], *Ficus lutea* Vahl, 1805, *Ficus natalansis* Hochst., 1845, *Ficus sur* Forssk. 1775 and *Ficus sycomorus* Linnaeus, 1753. Raji and Downs (2023: 1) reported that the germination of *Ficus* seeds was positively influenced by the bat's mastication and the gut passage. In that study (p. 3), they found that *Ficus sur* fruits were eaten more than fruits of four other *Ficus* species (58.2 ± 5.7 g), but the bats ate daily over 50 % of their body mass in fig fruits. The authors also found that ingested fruits of Ficus lutea germinated after 12 days, whereas entire control fruits germinated after 13 days and depulped control fruits after 28 days.

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Epomophorus wahlbergi*: *Ficus natalensis* Hochst., 1845, *Ficus sur* Forssk. 1775, *Melia azedarach* Blanco, 1837, *Morus alba* Linnaeus, 1753, *Psidium guajava* Linnaeus, 1753.

Govender *et al.* (2016: 315) found that *E. wahlbergi* preferred ripe figs over green ones.

Wickler and Seibt (1976) [in Bonaccorso *et al.* (2014: 50)] reported *E. wahlbergi* feeding on leaves of *Balanites wilsonianea* (Balanitaceae) in East Africa. Bonaccorso *et al.* (2014: 50) indicated this might also be the case in the Kruger National Park. Based on data from captive feeding experiments Bonaccorso *et al.* (2014: 50) extrapolated that the Skukuza bat colony (133 animals in 2007) would have dispersed 3.2 million fig seeds per night.

Downs *et al.* (2011b: 148) indicate that *E. wahlbergi*'s body mass was significantly higher in winter than in summer, which is possibly not attributable to an increase in body fat, but rather to excessive eating as result in increased metabolic costs.

Rollinson *et al.* (2013: 340) found that in the urban environment of Pietermaritzburg, South Africa, the bats had a greater home range in winter than in spring, which was linked with the reduction of fruiting plant species. They also found (p. 343) that male home ranges were smaller than those of females (0.46 km^2 versus 0.78 km^2). Their mean foraging distance was 1.45 ± 0.2 km in winter and 0.88 ± 0.08 km in spring.

Namah *et al.* (2019: 2) expected *E. wahlbergi* to be the pollinator of sausage trees (*Kigelia africana* (Lam.) Benth.) in the Kruger Park (RSA), but could not find any proof of this. Nor could they confirm pollination by any other species of bat. However, a further study by Newman *et al.* (2021) using camera traps, did confirm that these bats were indeed pollinating these trees.

Coleman and Downs (2012: 431) investigated the effect of sugar type and concentration on *E. wahlbergi* and suggest that these bats do not appear to have a selective pressure on the sugar composition of the fruit they eat. Mqokeli and Downs (2014: 161) performed some tests with equicaloric solutions (15 % glucose or 15 % sucrose with 0, 2.58, 5.68, 7.23 g soy protein/kg H_2O). Volumetric intake of the respective glucose and sucrose solutions varied among individual bats, with total volumetric intake being highest for solutions with no protein. The authors concluded that this suggests *E. wahlbergi* has low protein dietary requirements, which may be a response to the low-protein fruit available in the wild. They do point out that the bats may supplement their diet by actively preying on insects, but this needs to be investigated.

Blood plasma glucose concentrations – *Epomophorus wahlbergi*'s blood plasma glucose concentration was lower (5.24 ± 0.38 mmol/l) at 18:00 before feeding and increased during/after feeding (8.19 ± 1.24 mmol/l) but bats appeared to regulate it within limits (Mqokeli and Downs, 2012a: 348). Glucose intake of *E. wahlbergi* is generally high irrespective of sugar concentration (Coleman and Downs, 2012; Downs *et al.*, 2011a). Mqokeli and Downs (2012a: 349) found that blood plasma glucose concentration differed significantly with time. The greatest individual variation in blood plasma glucose concentrations were recorded at 24:00 possibly because of varying feeding and digestion rates (Mqokeli and Downs, 2012a: 350). Mqokeli and Downs (2012a: 349) found that blood plasma glucose concentrations were generally higher than the upper limit of the normal mammalian blood plasma glucose range. Mqokeli and Downs (2012a) showed diet variations in blood plasma glucose concentrations with an increase in concentrations during or directly after feeding. Mqokeli and Downs (2012a: 349) found that the body masses differed significantly at the respective blood sampling times. The lowest mean body mass (± S.E) was at 18:00 (99.69 ± 5.55 g) while the highest mean body mass was at 24:00 (105.05 ± 5.75 g). There was a significant difference in body mass between the 12:00 and 18:00 sampling times, and between the 24:00 and 18:00 sampling times. At 24:00 all bats had fed on the fruit provided and at 06:00 little fruit remained. The increase in body mass at 24:00 was about 6 %.

Germination experiments performed with four *E. wahlbergi* specimens captured on Mount Kilimanjaro (Tanzania), and fed with fig fruit parts of *Ficus sur* trees resulted in an overal germination percentage of 49.3 % after 13 days (Helbig-Bonitz *et al.* (2013: 123). In their study, Vogeler and Tschapka (2021: 1067) considered *E. wahlbergi* to be a generalist species, which is less affected by human transformations of landscapes in the Mount Kilimanjaro area.

Predators:

Broadley (in Schätti, 1984: 340) reports that these bats were eaten by Gaboon vipers (*Bitis gabonica* (A. M. C. Duméril, Bibron and A. H. A. Duméril, 1854)) kept in captivity.

Mikula *et al.* (2016: Supplemental data) mention the following diurnal avian predators: Dickinson's kestrel (*Falco dickinsoni* Sclater, 1864), Wahlberg's eagle (*Hieraaetus wahlbergi* (Sundevall, 1851)), Crowned eagle (*Stephanoaetus coronatus* (Linnaeus, 1766)); Trumpeter hornbill (*Bycanistes bucinator* (Temminck, 1824)).

Population:

Structure and Density

Common (Mickleburgh *et al.*, 2008k; IUCN, 2009; Shoeman, 2016). Shoeman (2016) reporting that population numbers increasing.

Trend

2016: Stable (Shoeman, 2016). 2008: Stable (Mickleburgh *et al.*, 2008k; IUCN, 2009).

Lifespan:

Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 10.1 years.

Activity and behaviour:

During their research in the Mount Kilimanjaro region, Vogeler and Tschapka (2021: 1067) captured eight times as many females than males, suggesting this might have been the result of proximity of maternity colonies to water and foraging areas and/or the increased activity of the females as they have higher energy requirements for reproduction. The females would therefore be more restricted to smaller areas, as compared to males, which might forage over larger distances and as such would be encountered in lower densities.

REPRODUCTION AND ONTOGENY:
Close to the equator, this species has two birth periods in February-March and in October-December (Bergmans, 1979a; O'Shea and Vaughan, 1980), or an extended period from October to January (Wickler and Seibt, 1976; Bernard and Cumming, 1997). Further south in Malawi and Zambia this species has been described as 'aseasonally polyoestrus' with births from September to March (Happold and Happold, 1990b). In southern Africa, this species has been described as 'seasonally polyoestrus' (Taylor, 2005). Although Taylor (1998) reported that in the KwaZulu-Natal province of South Africa 'breeding occurs throughout the year with peaks in July and in the summer'. However, this statement was based on an unpublished dataset by C. Sapsford, and further details were not presented (Taylor, 2005) in [Skinner and Chimimba, 2005]). In Zimbabwe, gravid females have been recorded in June and December (Smithers and Wilson, 1979), suggesting an extended breeding season. By contrast, in Kruger National Park, South Africa, parturition has been recorded in November-December (Pienaar *et al.*, 1980). In Swaziland, subadults were present throughout the year with two peaks (January-May and August-October), while lactating females were only present between December and May (Monadjem and Reside, 2012: 322).

Lönnberg (1912: 47) mentioned that two of the three females captured on 20 March 1911 at the upper Luazomela River, Kenya were carrying young of approximately 6 cm. Stanley and Goodman (2011: 37) reported a pregnant female collected in the South Pare Mountains, Tanzania, on 20 July 1993.

One female, taken by Bergmans (1979a: 174) in Congo on 21-22 November was lactating, while three others, taken between 28 November and 13 December, were pregnant.

Pakenham (1984: 25) mentioned he collected juveniles and sucking young in November on Zanzibar.

Szekely *et al.* (2015: Suppl.) report a gestation period of 165 days, and two litters per year.

MATING:
This species has a polygynandrous mating system (Webber *et al.*, 2017: Suppl.).

Wickler and Seibt (1976) [in Krutzsch (2000: 111)] indicate that male mating patterns also include courtship vocalizations (calling territories). Males also establish nocturnal display sites where females visit the males for mating (see McCracken and Wilkinson, 2000: 349). At Skukuza (Kruger National Park), Adams and Snode (2015: 4) found the following values for the male mating calls: mean fundamental frequency: 7.88 ± 0.11 kHz (first harmonic) followed by a second harmonic: 15.71 ± 0.23 kHz.

Adams and Snode (2013: 54) investigated the male-male competition for females during the mating season and found (p. 58) that the most dominant individuals were calling nearest to a ripe fig tree, and therefore more likely to be noticed by a foraging female. None of the males they observed were calling from nonfruiting sycamore fig trees. Adams (2015: 2) mentioned that males maintained a minimum distance of 25 m from one another and that they were never calling from the same tree.

Chaverri *et al.* (2018: 1942) point out the role of the retractile white shoulder tufts, which are erected during courtship by wing-flapping males. They also suggest that these movements may help spread pheromones.

PARASITES:
BACTERIA
One out of five bats tested by Dietrich *et al.* (2016b: 3) in Pafuri (RSA) tested positive for *Bartonella* bacteria, and one out of two bats from Rocktail Bay (RSA) tested positive for *Rickettsia*, as did one out of 80 tested from Umbilo (RSA).

gram-negative
Helmick *et al.* (2004: 88) reported a novel *Pasteurella*-like organism found in lung tissue of two captive Wahlberg's epauleted fruit bats, which were recently shipped, and died soon after release from a 30-day quarantine period.

HAEMOSPORIDA
Garnham (1948, 1950) [in Miltgen *et al.* (1977: 595)] described some liver schizonts and gametocytes, which he assigned to the genus *Hepatocystis*.

ACARI
Teinocoptidae
Fain (1967: 367) reported *Teinocoptes epomophori* Rodhain, 1923 from an *E. wahlbergi haldemani* specimen from Boma, DRC, and *Teinocoptes auricularis* from an *E. wahlbergi* from Zanzibar.

Trombiculidae
Schoutedenichia (Schoutedenichia) cordiformis Vercammen-Grandjean, 1958 was reported by Stekolnikov (2018a: 101), who also reported (p.

153) *Microtrombicula homopholis* (Lawrence, 1949).

CESTODA
Hymenolepididae
Jenzen and Howell (1983: 135) referred to Mahon (1954) , who described *Vampirolepsis aelleni* from a bat from the DRC.

DIPTERA
Nycteribiidae
Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Epomophorus wahlbergi*: *Dipseliopoda biannulata* (Oldroyd, 1953) and *Eucampsipoda africana* Theodor, 1955.

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 to 1999, two individuals from Mpumalanga Province, South Africa for antibody to SARS-CoV in sera, none were found to be positive.

Four out of 63 (6.3 %) Kenyan bats tested by Tao *et al.* (2017: Suppl.) were positive for CoV.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Lagos bat virus (LBV)
Isolated from South Africa (Crick *et al.*, 1982: 211; King *et al.*, 1990: 169; Meredith and Standing, 1981; Swanepoel, 2004; Markotter *et al.*, 2006b; Hayman *et al.*, 2011a: 88; Nadin-Davis *et al.*, 2011: 238; Coertse *et al.*, 2011: 251; Willoughby *et al.*, 2017: Suppl.). Coertse *et al.* (2021: 3) indicate that all the LVB detections in this bat came from the KwaZulu province in the RSA.

Mokola virus (MOKV)
King *et al.* (1990: 168) found monoclonal antibodies for MOKV in bats from South Africa. They also reported antibodies for Duvenhage and Denmark bat virus.

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 4 specimens they examined from the Democratic Republic of the Congo tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

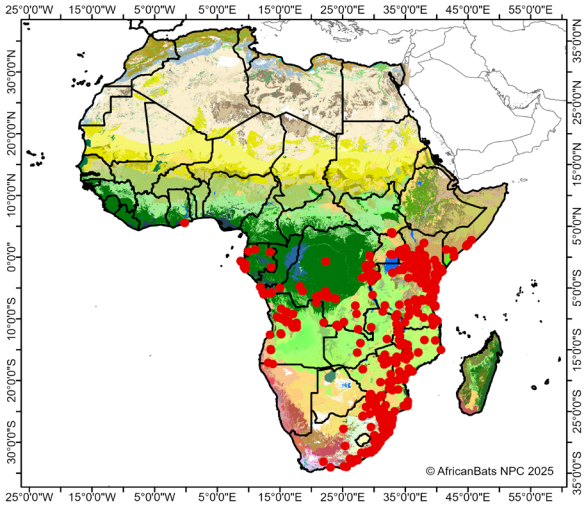

Figure 26. Distribution of *Epomophorus wahlbergi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Burundi, Cameroon, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Kenya, Malawi, Mozambique, Namibia, Rwanda, Somalia, South Africa, South Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Genus ***Epomops*** J. E. Gray, 1866

*1871. *Epomops* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 126. Publication date: 14 January 1871 [Goto Description]. - Comments: Type species: *Epomophorus franqueti* Tomes, 1860. - Etymology: Probably an abbreviation of *Epomophorus* and the Greek "*οψ*", meaning aspect, referring to its resemblance to that genus (see Palmer, 1904: 268).
2007. *Epomop:* Lameed, Biodiversity, 8 (4): 8. (Lapsus).
2014. *Hepomops:* Nina, Acta Med. Port., 27 (5): 627. Publication date: Sep-Oct 2014. (Lapsus).
2016. *Epomos:* Pancer, Gut and Litwińska, Post. Mikrobiol., 55 (2): 207. (Lapsus).
2019. *Epomopos:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

TAXONOMY:
Reviewed by Bergmans (1989). See Simmons (2005: 323).

Andersen (1912b: 487), Grubb *et al.* (1998: 69) mention "Gray, 1866, Proc. Zool. Soc., Lond.: 65" as first publication in which the name *Epomops* was used.

The results of the phylogenetic analyses by Almeida *et al.* (2016: 82) showed that the genus *Epomops* is not monophyletic as a DNA fragment of *E. dobsonii* shows a close relationship with

Epomophorus wahlbergi, which seems to support the similarities or transitional traits of *dobsonii* with *Epomophorus* reported by Bergmans (1989: 118).

Included in the Epomophorinii tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Hassanin *et al.* (2020: 5) include it in the Epomophorina subtribe of the Epomophorini tribe.

Based on the analyses of mitochondrial and nuclear data, Hassanin *et al.* (2016: 525) suggest that the genus *Epomops* contains only one species, which can be divided into two subspecies: *E. franqueti franqueti* in Central Africa and *E. f. buettikoferi* in West Africa.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Epomops*: ***buettikoferi*** (Matschie, 1899); ***franqueti*** (Tomes, 1860).

COMMON NAMES:
Czech: Grayovi kaloni. English: Clamorous Fruit-bats, Noisy Fruit-bats, Singing Fruit-bats, Epauletted bats, Epaulet bats, African Epauletted bats. French: Epomophores de l'ouest. German: Epaulettenflughunde.

MOLECULAR BIOLOGY:
Genetics
The Cyt*b* analyses performed by Hassanin *et al.* (2016: 525) revealed that bats from West Africa, identified as either *E. franqueti* or *E. buettikoferi*, share very similar or identical haplotypes, which are divergent from those sequenced for all individuals of *E. franqueti* collected in Central Africa.

PARASITES:
HAEMOSPORIDA
Perkins and Schaer (2016: Suppl.) mention the presence of *Hepatocystis epomophori* Rodhain, 1926 in *Epomops* sp. bats. Nine out of 10 (90 %) South Sudanese bats examined by Schaer *et al.* (2017: 2) were infected by *Hepatosystis* sp.

VIRUSES:
Raulino *et al.* (2022: 256) reported antibodies against Chikungunya virus , Dengue virus and Zika virus from bats, which might be either *Epomops franqueti* or *Epomops buettikoferi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Ghana, Niger.

Epomops buettikoferi (Matschie, 1899)

*1899. *Ep[omophorus (Epomophorus)] büttikoferi* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 43, 45. Type locality: Liberia: Junk river: Schieffelinsville [06 11 N 10 30 W]. [Goto Description]. Holotype: RMNH MAM.19640: ♂. Collected by: F.X. Stampfli; collection date: 3 August 1884. The RMNH catalog menti!ons two numbers: 19640.a (skull) and 19640.b (wet specimen). - Comments: Matschie dated his introduction to 14 May 1899. - Etymology: In honour of J. Büttikofer, who collected animals in Liberia.
1972. *Epomophorus (Epomops) franqueti buettikoferi:* Püscher, Z. Säugetierk., 37 (3): 155. (Name Combination).
1996. *Epomophorus buettiforteri:* Kuhl, Obligate and opportunistic interactions, 52. (Lapsus).
2000. *Epomops buetticoferi:* Konstantinov, Pema, Labzin and Farafonova, Plecotus et al., 3: 145. (Lapsus).
2007. *Epomops buetikoferi:* Rainho, Sousa, Monteiro, Schwarz da Silva and Palmeirim, Morcegos e aves das florestas de Cantanhez e Cacine, 17. (Lapsus).
2013. *Epomops buettifoferi:* Seltzer, Ndangalasi and Cordeiro, Biotropica, 45 (4): table S2. Publication date: 22 February 2013. (Lapsus).
2016. *E[pomops] f[ranqueti] buettikoferi:* Hassanin, Nesi, Marin, Kadjo, Pourrut, Leroy, Gembu, Musaba Akawa, Ngoagouni, Nakouné, Ruedi, Tshikung, Pongembo Shongo and Bonillo, C. R. Biologies, 339 (11-12): 525. Publication date: 14 October 2016. (Name Combination).
2019. *Epomopos buettikoferi:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).
2023. *E[opomops] buetticoffi:* Peeters, Champagne, Ndong Bass, Goumou, Ndimbo Kumugo, Lacroix, Esteban, Meta Djomsi, Karim Soumah, Mbala Kingebeni, Mba Djonzo, Lempu, Thaurignac, Mpoudi Ngole, Kouanfack, Mukadi Bamuleka, Likofata, Muyembe Tamfum, De Nys, Capelle, Toure, Delaporte,..., Viruses, 15 (9) (1927): 6. Publication date: 15 September 2023. (Lapsus).
? *Epomops buettikoferi:* (Current Combination).

TAXONOMY:
See Bergmans (1989) and Simmons (2005: 323).

COMMON NAMES:
Czech: kaloň Büttikoferův. English: Buettikofer's Clamorous Fruit-bat, Buettikofer's Epauletted Bat, Buettikofer's Epauletted Fruit Bat, Büttikofer's Fruit Bat. Ewe (Ghana): Aguto. French: Epomophore de Büttikofer, Epomophore de Buettikofer, Roussette de Büttikofer, Roussette de Buettikofer. German: Büttikofers Epaulettenflughund.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008as; IUCN, 2009; Monadjem, 2016a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2016a). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008as; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bg; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996). 1994: VU (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
It is possible that there are no major threats to this species. Populations might be threatened by deforestation in parts of the species range, however, the extent to which it depends on forest cover is unclear (Mickleburgh *et al.*, 2008as; IUCN, 2009; Monadjem, 2016a).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008as) [in IUCN (2009)] suggest that further studies are needed into the dependence of this species on forested areas.

Current conservation efforts
This species has been recorded from a number of protected areas in West Africa (Mickleburgh *et al.*, 1992), and in fact appears to thrive outside of these protected areas (Monadjem, 2016a).

Conservation needs/priorities
Monadjem (2016a) recommends studies are needed on the species' population sizes, distribution, and extent of occurrence throughout its range. Monitoring of population sizes and locations over time are also important to establish whether these are stable or experiencing trends of decline.

The threats to these bats are poorly understood. Studies are needed on the species' natural history and habitat requirements and the relationship between habitat and population sizes. Mickleburgh *et al.* (2008as) [in IUCN (2009)] suggested studies are needed into the dependence of this species on forested areas, and its tolerance of deforestation and habitat degradation (Monadjem, 2016a).

GENERAL DISTRIBUTION:
Epomops buettikoferi is a lowland West African species which ranges from Senegal and Guinea-Bissau in the west, to central Nigeria in the east. Bergmans (1975: 147) indicates it is restricted to the West African "moist forest" block.

Native: Cameroon (Bakwo, 2009: 12); Côte d'Ivoire (Henry *et al.*, 2004: 24); Ghana (Decher and Fahr, 2007: 10 - 11); Guinea (Denys *et al.*, 2013: 281; Decher *et al.*, 2016: 259); Guinea-Bissau (Rainho and Ranco, 2001: 26); Liberia (Monadjem and Fahr, 2007: 50); Nigeria; Senegal; Sierra Leone.

DENTAL FORMULA:
One of the eight skulls examined by Esquivel *et al.* (2021: Suppl.) had less than the normal number of teeth (oligodontia).

MOLECULAR BIOLOGY:
Karyotype
Denys *et al.* (2013: 281) determined the karyotype of four specimens from the Guinean Mount Nimba area and found 2*n* = 36 in females (34 autosomes and two X gonosomes), and 2n = 35 in males (X0 gonosomes); NFa = 68. X = submetacentric or medium-sized.

ROOST:
E. buettikoferi roosts alone or in small groups, near its feeding area (Kunz, 1996: 52).

DIET:
Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *E. buettikoferi* this included *Milicia excelsa* (Welw.) C. C. Berg (African Teak - Moraceae).

POPULATION:
Structure and Density
It appears to remain common in many areas, with the exception of Nigeria (Mickleburgh *et al.*, 2008as; IUCN, 2009). West of Ghana, this species is typically one of the most abundant (in terms of captures) pteropodids in primary and secondary forest, and forest edge habitats (Monadjem, 2016a).

Mickleburgh *et al.* (2008as) in IUCN (2009) suggest that populations may be declining in areas of ongoing deforestation.

Trend
2016: Decreasing (Monadjem, 2016a). 2008: Decreasing (Mickleburgh *et al.*, 2008as; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 93) mentions that males attain puberty at the age of eleven months.

Weber *et al.* (2019: 19) reported one pregnant female on 30 March and six lactating (24, 30, 31 March, 1, 7 April) in Sierre Leone.

MATING:
The male mating pattern in *E. buettikoferi* includes courtship vocalizations (calling territories) (see Krutzsch (2000: 111).

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Hepatocystis* in seven out of 25 investigated bats.

VIRUSES:
Coronaviridae
One of three Ghaianan bats tested by Suu-Ire *et al.* (2022: 6) contained RNA of Kenya bat coronavirus/BtKY56/BtKY55. RNA of an almost identical virus was recovered from a bat from Côte d'Ivoire.

Filoviridae
Ebolavirus
Bonilla-Aldana *et al.* (2020) reported this bat as one of the species carrying this virus.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Lagos bat virus
Hayman *et al.* (2008a) detected antibodies in Ghana.

Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen they examined from Ghana did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

UTILISATION:
This species is hunted for bushmeat (Monadjem, 2016a).

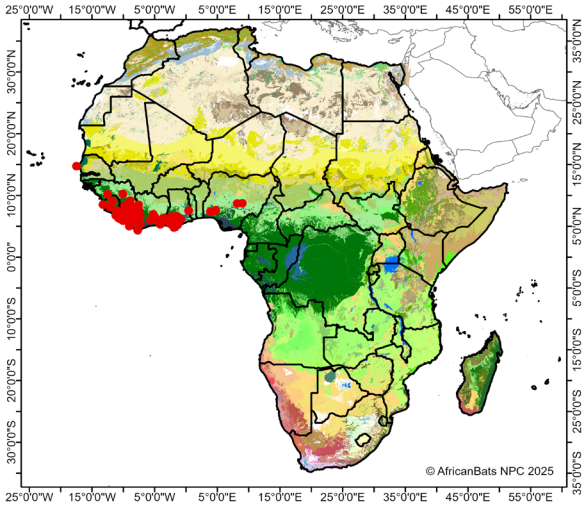

Figure 27. Distribution of *Epomops buettikoferi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Côte d'Ivoire, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone.

Epomops franqueti (Tomes, 1860)

*1860. *Epomophorus franqueti* Tomes, Proc. zool. Soc. Lond., 1860, I: 54, pl 75. Publication date: February - May 1860. Type locality: Gabon: "Gabon". [Goto Description]. Holotype: MNHN ZM-MO-1852-257: ad ♂, mounted skin and skull. Collected by: dr. Franquet. Skull has number A6767; see Rode (1941: 233), who uses number 164. Previously mentioned as A.107-776-C.52-1852-257.

1861. *Epomophorus comptus* H. Allen, Proc. Acad. nat. Sci. Philad., 13 (11): 158. Publication date: prior to 28 December 1961. Type locality: "Africa": West Africa. [Goto Description]. Holotype: ANSP MAM 1240/3325: ♀, skin and skull. Collected by: Paul Belloni Du Chaillu. - Comments: Andersen (1912b: 497) and Allen (1939a: 57) mentioned "=Gaboon" as type locality. Andersen (1912b: 498) mentions "as having been collected by Du Chaillu the specimen is no doubt from Gaboon." Type in Phildalphia Museum, unmounted skin, skull extracted, ♀.

1910. *Epomops franqueti strepitans* K. Andersen, Ann. Mag. nat. Hist., ser 8, 5 (25): 106. Publication date: 1 January 1910. Type locality: Nigeria: 150 mi up the Niger: Asaba [06 11 N 06 43 E]. Holotype: NHMUK 1895.5.3.7: ad ♂, skin and skull. Presented/Donated by: Dr. W.H. Cross. See Andersen (1912b: 497).

2016. *Epomos franqueti:* Pancer, Gut and Litwińska, Post. Mikrobiol., 55 (2): 207. (Lapsus).

2017. *Epomops frangueti:* Dammann, Semin. Cell Dev. Biol., 70: 160. Publication date: 8 July 2017. (Lapsus).

2019. *Epomopos franqueti:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

2019. *Epomops frangeti:* Kaswera Kyamakya, Nebesse Mololo and Gambalemoke Mbalitini, IJEAB, 4 (2): 330. Publication date: March-April 2019. (Lapsus).

2020. *Epomophorus franquenti:* Motayo, Oluwasemowo and Akinduti, PeerJ, 8 (e10434): 4. Publication date: 26 November 2020. (Lapsus).

? *Epomophorus (Epomops) franqueti:* (Name Combination).

? *Epomops franqueti franqueti / strepitans:* (Name Combination).

? *Epomops franqueti franqueti:* (Name Combination).

? *Epomops franqueti:* (Current Combination).

TAXONOMY:
See Bergmans (1989) and Simmons (2005: 324).

COMMON NAMES:
Czech: kaloň Franquetův, kaloň plavý. English: Franquet's Clamorous Fruit-bat, Franquet's Fruit Bat, Franquet's Epauletted Fruit Bat, Singing Fruit Bat. Ewe (Ghana): Aguto. French: Epomophore de Franquet, Chien volant à épaulettes du Congo, Roussette de Franquet. German: Franquets Epaulettenflughund, Franquet's Epaulettenflugfuchs.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008by; IUCN, 2009; Kityo and Nalikka, 2016; Kityo and Nalikka, 2020).

Assessment History
Global
2016: LC ver 3.1 (2001) (Kityo and Nalikka, 2016). 2014: LC ver 3.1 (2001) (Kityo and Nalikka, 2020). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008by; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ci; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Malhi *et al.* (2013) estimated deforestation rates for Africa to be at 0.29 million ha yr−1 between 2000 – 2010 which figure is much lower than any where else in the tropics of the world. Notwithstanding the foregoing, since the core habitat of the species is forest, reduction in its extent poses an increasing risk of habitat loss (Kityo and Nalikka, 2016).

There is currently an increasing perception that bats are playing a major role in the spread of zoonoses, rightly or wrongly, this puts bats into direct line for persecution and extermination (Kityo and Nalikka, 2016).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008by) [in IUCN (2009)], Kityo and Nalikka (2016) and Kityo and Nalikka (2020) who report that *E. franqueti* is present in many protected areas. No direct conservation measures are currently needed for this adaptable species as a whole.

GENERAL DISTRIBUTION:
Epomops franqueti is a widespread species, which is present in much of West Africa and Central Africa, with some records from East Africa. It ranges from Côte d'Ivoire and Ghana in the west, to Cameroon, and then through Central Africa to southern Sudan, Rwanda and Uganda in the east. It has been recorded as far south as northern Angola, southern Democratic Republic of the Congo and northeastern Zambia.

The record (MNHN ZM-MO-1984-1165) from Madagascar is a possible misidentification/or incorrect locality information and needs verification.

Native: Angola (Bergmans, 1989; Monadjem *et al.*, 2010d: 554); Benin (Capo-Chichi *et al.*, 2004: 161); Cameroon; Central African Republic (Morvan *et al.*, 1999: 1195); Congo (King and Dallimer, 2010: 65; Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 554); Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Guinea (Ziegler *et al.*, 2002: 75); Nigeria; Rwanda; Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 59); Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 554).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 7 specimens: Fa: 93.51 ± 5.246 mm, mass: 114.7 ± 35.86 g, wing loading: 19.7 ± 3.81 N/m^2, aspect ratio: 5.4 ± 0.43.

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on the dorsal side of the proximal and distal arm and the forearm, whereas it is moderate on the ventral side of these wing parts.

DENTAL FORMULA:
18 of the 46 skulls examined by Esquivel *et al.* (2021: Suppl.) had less than the normal number of teeth (oligodontia).

DETAILED MORPHOLOGY:
Brain
Chawana *et al.* (2013: 160) report an average brain mass of 2.42 g (n = 2).

Other
A wild-caught Nigerian bat was found to suffer from oxalate nephrosis, possibly due to a dietary aetiology, resulting from the seasonal availability of high ascorbic acid or oxalate containing fruits (Aina *et al.*, 2020: 56).

Dobson (1881: 686) provides a detailed description of the pharynx, larynx, and hyoid bones. Meckel's cartilages (a.k.a. Meckelian cartilages) are discussed by Friant (1964).

FUNCTIONAL MORPHOLOGY:
Coimbra *et al.* (2016: 191) found that the eye of *E. franqueti* has a bright yellow tapetum lucidum, which covers almost the entire extension of its dorsal hemisphere. There are about 200,000 retinal ganglion cells. The minimum angle of resolution was approximately 0.167° (ca. 5-6 mm at 1 m distance).

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 19.4 Pa, aspect ratio 6.5 for a wingspan of 60 cm and a wing area of 552 cm^2 and a body mass of 109 g.

MOLECULAR BIOLOGY:
Karyotype
In Kenya, Peterson and Nagorsen (1975) recorded 2*n* = 36. Haiduk *et al.* (1980) reported 2*n* = 36, FN = 68, BA = 34, a subtelocentric X chromosome and a subtelocentric Y chromosome for specimens from Cameroon. Haiduk *et al.* (1981: 224) mention 2*n* = 36, FN = 66. Primus *et al.* (2006) reported a male without Y chromosome (2*n* = 35) from Gabon.

Blood chemistry
Dammann (2017: 160) refers to Ifuta *et al.* (1988: 379), who found that levels of T_4 (plasma concentrations of thyroxine) were about 10 times lower in this bat than in other mammals. These low values might be stress related as several hours elapsed between the capture of the bats and taking blood samples. However, these low values were not found for T_3 (Plasma concentrations of triiodothyronine). Dammann (2017) suggests that the low levels of T_4 might be related to the longevity in bats.

Ekeolu and Adebiyi (2018: 391) investigated blood parameters in 17 *E. franqueti* specimens from Nigeria and found no significant sex-related differences, except for erythrocyte osmotic fragility, which was significantly higher in female than in male bats at 0.1 % NaCl.

HABITAT:
This species is associated with lowland tropical moist forest, where it has been recorded in both primary and secondary habitat. Populations are also present in the mosaic habitats of tropical moist forest with woodland and grassland (Bergmans, 1989). It is an adaptable species that can be found in disturbed areas, seemingly being only absent from heavily degraded or urban areas.

In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported that this species was only found in disturbed habitats in the Afromontane forest biome, and not in undisturbed habitats.

HABITS:
Bradbury (1977) [in McCracken and Wilkinson (2000: 351)] found that females and juvenile animals were feeding near the territory of a calling male, which would suggest that additional resources could be available in that area.

ROOST:
The species roosts alone or in small groups, often close to water, in the dense leave cover of shrubs or trees (Brosset, 1966c; Jones, 1972; Kunz, 1996: 44).

DIET:
In Congo, Kipalu (2009: 16) reported *E. franqueti* visiting/consuming fruits of *Chlorophora excelsa* (African Teak) and *Ficus mucuso*.

Gembu Tungaluna (2012: 95 - 97) reported the following fruits being eaten in the Kisangani area (DRC) in the various seasons: First heavy rain season (September - November): *Persea americana* Mill., 1786 (Avocado) (24%), *Carica papaya* L. (Papaya) (16%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, Otaheite Apple, Great Hog Plum) (14%), *Annonidium mannii* (Oliv.) Engl. & Diels (Junglesop) (11%), *Musanga cecropioides* R. Br. & Tedlie (African Corkwood Tree, Umbrella Tree) (8%), *Ficus leprieuri* Miq., 1867 (8%), *Myrianthus arboreus* P. Beauvois, 1805 (Giant Yellow Mulberry, Bush Pineapple, Corkwoord) (5%), *Elaeis guineensis* Jacq. (African Oil Palm, Macaw-fat) (3%), *Ficus wildemanniana* Warb. (3%), *Musa* sp. (3%).

First mild rain season (December - February): *Musanga cecropioides* (40%), *Elaeis guineensis* (20%), *Myrianthus arboreus* (13%), *Carica papaya* (13%), *Ficus wildemanniana* (7%), *Ficus vallis-choudae* Delile (7%).

Second heavy rain season (March - May): *Carica papaya* (23%), *Dacryoides edulis* H.J. Lam (Safou, African Pear, Bush Pear, Nsafu, Bush Butter Tree, Butterfruit) (15%), *Musanga cecropioides* (15%), *Myrianthus arboreus* (8%), *Elaeis guineensis* (8%), *Oncoba welwitschii* Oliv. (8%), *Ficus* sp3 (8%), *Musa* sp. (8%), *Ficus leprieuri* (7%).

"Dry" season (June - August): *Ficus wildemanniana* (100%).

From Nigeria, Aina *et al.* (2020: 57) reported the retrieval of fruits of Heart-leaved Fig (*Ficus polita* Vahl, 1805 - Moracea) and Sponge Gourd (*Luffa cylindrica* M. Roem. - Cucurbitaceae) from bats captured for their anatomical study.

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Epomops franqueti*: *Carica papaya* Linnaeus, *Diospyros mespiliformis* Hochst. ex A. DC., *Mangifera indica* Linnaeus, *Musa* sp., *Solanum torvum* Sw., 1788.

PREDATORS:
Charles-Dominique (1974: 144) reported on a potto *Perodicticus potto* (Statius Müller, 1766) eating a juvenile *E. franqueti*.

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008by; IUCN, 2009). Kityo and Nalikka (2016) reports that it is a fairly abundant species in the right habitat (Kityo and Nalikka, 2020).

Trend
2016: Stable (Kityo and Nalikka, 2016). 2014: Stable (Kityo and Nalikka, 2020). 2008: Stable (Mickleburgh *et al.*, 2008by; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
For a selection of sounds, check https://search.macaulaylibrary.org.

REPRODUCTION AND ONTOGENY:
From southern Sudan, Bates (1905: 72) reports on two females (probably of this species) carrying a half-grown young on 31 August and 1 September.

A male with probably active testes was caught on 2-3 November in Pointe Noire (Congo) by Bergmans (1979a: 171), and a lactating female with an embryo was captured in Brazzaville on 23 December. Furthermore, females with developed nipples were collected in March, May, November and December.

MATING:
Brosset (1966c) and Bradbury (1977) [in McCracken and Wilkinson (2000: 349)] indicate that males establish nocturnal display sites where females visit males for mating.

PARASITES:
BACTERIA
Gram-negative bacterium
Nowak *et al.* (2017: 6) tested three bats from the Republic of Congo of which two tested positive for *Escherichia. coli*. Mbehang Nguema *et al.* (2020: 7) reported the presence of *E. coli*, *Enterobacter cloacae* and *Klebsiella pneumoniae* in feacal samples collected near Makokou in Gabon.

HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 52 *E. franqueti* specimens from East Africa and found 35 of them infected with *Hepatocystis* sp. Perkins and Schaer (2016: Suppl.) refer to the presence of *Hepatocystis brosetti* Miltgen *et al.*, 1977 in Gabon, from where it was described by Miltgen *et al.* (1977: 589). Landau *et al.* (2012: 142) also mention it as type host for *Hepatocystis epomophori* (Rodhain, 1926). Boundenga *et al.* (2018: 10581) reported 21 out of 160 (13.12 %) bats from the Franceville (Gabon) area to be infected by *Hepatocystis* sp. Surprisingly, Rosskopf *et al.* (2018: 31) were unable to find any *Hepatocystis* parasites in the 21 Gabonese bats they examined and they suggest that this might be linked with the fact their bats were collected during the dry season.

DIPTERA
Nycteribiidae
Basila tenuispina Theodor 1957 from Stanleyville, Congo (Democratic Republic of the) (Haeselbarth *et al.*, 1966: 111).

ACARI
Teinocoptidae
Teinocoptes epomophori Rodhain, 1923 was reported from an *E. franqueti* specimen from Stanleyville (= Kisangani), DRC by Fain (1967: 367).

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Marburg marburgvirus, Rift Valley fever phlebovirus, Shamonda orthobunyavirus, Zaire ebolavirus.

Circoviridae
Bat associated cyclovirus 8 and Chimpanzee associated cyclovirus 1 - These two viruses were reported by Vidovszky *et al.* (2023: Suppl.) from bats from the DRC.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 to 1999 five individuals from Bandundu Province, DRC for antibody to SARS-CoV in sera, none were found to be positive (0/5).

Anthony *et al.* (2017b: Suppl.) mention the beta-coronavirus Eidolon_bat_CoV.

Joffrin *et al.* (2020: 7) identified the Congolese viruses as Beta-D coronavirus.

For the two Congos, Kumakamba *et al.* (2021: 7) reported 23 out of 146 bats to test positive for coronaviruses.

The viruses found in bats from the DRC and Cameroon were assigned to the subgenus *Nobecovirus* by Motayo *et al.* (2020: 4).

One of 18 Ghaianan bats tested by Suu-Ire *et al.* (2022: 6) contained RNA of Kenya bat coronavirus/BtKY56/BtKY55.

Filoviridae - Filo viruses
Ebolavirus
Pourrut *et al.* (2007) found homogeneous ZEBOV [Zaire Ebolavirus] infection in the wild populations of *E. franqueti* in Gabon and the Democratic Republic of the Congo. Lacroix *et al.* (2021: 7) found antibodies against Ebola in 0 to 8 DRC bats (out of a total of 179 examined). Eight out of 117 bats had immunoglobulin G (IgG) specific for Ebola in Gabon during a test performed by Leroy *et al.* (2005: 575). 10 out of 27 bats were found to be positive for EBOV antibodies in the Greater Accra region, Ghana (Hayman *et al.*, 2012d: 1208).

Bausch and Schwarz (2014: 1) and Pigott *et al.* (2014: 9) indicate that *E. franqueti* is one of the leading candidates for introducing Ebola in Guinea (together with *Hypsignathus monstrosus* and *Myonycteris torquata*). However, no proof has been provided that this was indeed the case.

Marburgvirus
Towner *et al.* (2007) tested 296 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 47 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found.

Flaviviridae
Flavivirus
Maganga *et al.* (2014a: 5) tested 128 bats from Congo, of which 2 tested positive. Shchelkanov *et al.* (2020a: 18) reported on bats from the DRC, infected by Bat Flavivirus RC, which probably refer to the previous.

Nairoviridae
Nairovirus
Of the 99 specimens from Gabon and Congo tested by Müller *et al.* (2016: 3), 7 were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Phenuiviridae
Phlebovirus
Fagre and Kading (2019: 4) report that Rift Valley fever virus (RVFV) was either isolated from this bat or that molecular evidence was found (see also de Jong *et al.* (2011: 11) and Luis *et al.* (2013: suppl.)).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 100 specimens they examined from Gabon, Congo, Ghana and the Central African Republic tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

In their overview table, Maganga *et al.* (2014a: 8) report that the following viruses were already found on *E. franqueti*: Zaire Ebola virus (ZEBOV), Reston Ebola virus, Marburg virus (MBGV), Flavivirus.

Togaviridae
de Souza *et al.* (2024: 1491) reported that three Senegalese bats tested positive for chikungunya virus (CHIKV).

UTILISATION:
This species is hunted for the bushmeat trade (Kityo and Nalikka, 2016).

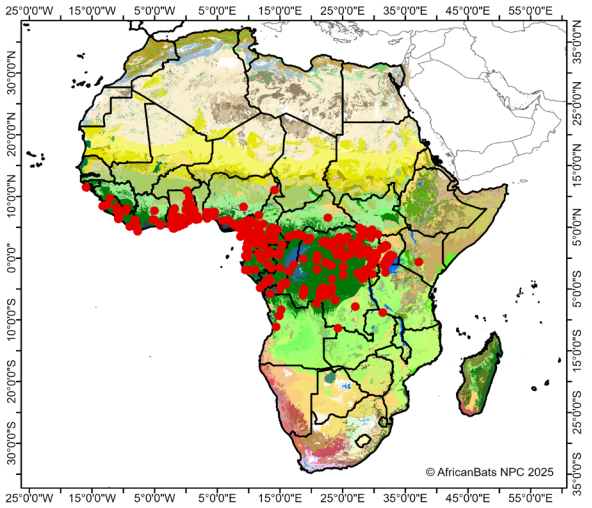

Figure 28. Distribution of *Epomops franqueti*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea-Bissau, Kenya, Liberia, Nigeria, Rwanda, Sierra Leone, South Sudan, Tanzania, Togo, Uganda, Zambia.

Genus ***Hypsignathus*** H. Allen, 1862

*1861. *Hypsignathus* H. Allen, Proc. Acad. nat. Sci. Philad., 13 (11): 156. Publication date: prior to 28 December 1861 [Goto Description]. - Comments: Type species: *Hypsignathus monstrosus* H. Allen, 1861. - Etymology: From the Greek "*υψι*", meaning on high or aloft and "*γνάθος*", meaning jaw, possibly referring to the 'deeply arched mouth' (see Palmer, 1904: 343). (Current Combination).

1862. *Sphyrocephalus* A. Murray, Proc. zool. Soc. Lond., 1862, I: 8. Publication date: June 1862 [Goto Description]. - Comments: Type species: *Sphyrocephalus labrosus* Murray,1862 (=*Hypsignathus monstrosus* H. Allen, 1861). Preoccupied by *Sphyrocephala* Westwood, 1848, a dipteran and *Sphyrocephalus* Schmarda, 1859, a turbellarian (see Palmer, 1904: 642; Langevin and Barclay, 1990: 1). Andersen (1912b: 501 - footnote) also mentions "Murray probably originally intended to name this genus *Zygænocephalus* in allusion to the Hammer-headed Sharks *Zygæna*, and had that name printed on the plate, but for some reason or other changed it in the text to *Sphyrocephalus*.". - Etymology: From the Greek "*σφύρα*", meaning hammer and "*κεφαλή*", meaning head (see Palmer, 1904: 642; Murray, 1862: 8).

1862. *Zygænocephalus* A. Murray, Proc. zool. Soc. Lond., 1862, I: pl 1. Publication date: June 1862. - Comments: Type species: *Zygænocephalus labrosus* Murray,1862 (=*Hypsignathus monstrosus* H. Allen, 1861). This name was attached to the plate illustrating Murray's description of *Sphyrocephalus* and serves as a replacement for *Sphyrocephalus* Murray, 1862: see Langevin and Barclay (1990: 1). - Etymology: From the Greek "*ξύγαινα*", a hammer-headed shark and "*κεφαλή*", meaning head (see Palmer, 1904: 717).

? *Epomophorus (Hypsignathus):* (Name Combination).

? *Hypsygnathus:* (Lapsus).

TAXONOMY:

Revised by Bergmans (1989). See Simmons (2005: 324).

Included in the Epomophorinii tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Included in the Epomophorini tribe and Epomophorina subtribe by Hassanin *et al.* (2020: 5).

Currently (Simmons and Cirranello, 2023b) recognized species of *Hypsignathus*: ***monstrosus*** H. Allen, 1861.

COMMON NAMES:

Afrikaans: Hamerkopvrugtevlermuis. Czech: kladivohlaví kaloni. English: Hammer-headed bats. French: Hypsignates. German: Hammerkopf-Flughunde.

Hypsignathus monstrosus H. Allen, 1862

*1861. *H[ypsignathus] monstrosus* H. Allen, Proc. Acad. nat. Sci. Philad., 13 (11): 157. Publication date: prior to 28 December 1861. Type locality: "Africa": Western Africa: possibly Gabon (see Andersen, 1912b: 506). [Goto Description]. Holotype: ANSP MAM 969/2771: ad ♂, skin and skull. Collected by: Paul Belloni Du Chaillu. - Comments: Type specimen collected by Mr. Du Chaillu (Murray, 1862: 8); Allen (1861: 158) mentions the name as Duchaillu. Andersen (1912b: 508) mentions the type specimen as being an adult ♂, SS, in the collection of the Philadelphia museum. Publication date: Volume 13 issue 11 covers the meetings of June-July 1861, but was probably only printed in 1862, as Murray (1862: 8) indicates that he received a copy of this publication on 19 February 1862. But we also found a reference to issue 23 of volume 13 (for the meeting of 26 November 1861) having been published on 31 December 1861, which might indicate that issue 11 might have been published in 1861. (Current Combination).

1862. *Sphyrocephalus labrosus* A. Murray, Proc. zool. Soc. Lond., 1862, I: 8. Publication date: June 1862. Type locality: Nigeria: Eastern region: Old Calabar river [ca. 04 56 N 08 22 E]. [Goto Description]. Holotype: NHMUK 1862.1.23.1[b]: ad ♂, skull and alcoholic. Collected by: Reverend William C. Thomson. Presented/Donated by: Mr. A. Murray Esq. - Comments: The publication contains 14 January 1862 as date, but see Duncan (1937) for the actual publication date.

1862. *Zygaenocephalus labrosus:* A. Murray, Proc. zool. Soc. Lond., 1862, I: pl 1. Publication date: June 1862. (Name Combination).

1876. *Epomophorus macrocephalus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 474. Type locality: Gabon: Dongila. - Comments: Not of Ogilby (see Andersen, 1912b: 507).

1879. *Epomophorus monstrosus:* Dobson, Proc. zool. Soc. Lond., 1878, IV: 879. Publication date: April 1879. (Name Combination).

1896. *Epomophorus (Hypsignathus) monstrosus:* Pousargues, Ann. Sci. Nat., (8) 3: 250. (Name Combination).

1899. *Hypsignathus haldemani* Matschie, Sber. Ges. naturf. Freunde Berlin, 29. - Comments: Not *Pteropus haldemani* Halowell, 1846: See Langevin and Barclay (1990: 1).

1968. *Epomophorus monstruosus:* Andral, Brès, Sérié, Casals and Panthier, Bull. Wld. Hlth. Org., 38 (6): 860. (Lapsus).

1975. *Hypsignathus montrosus:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 362. (Lapsus).

1978. *Hypsignathus monstrousus:* Germain, Elsevier / North-Holland Biomedical Press - Amsterdam, 133. (Lapsus).

2017. *Hypsignathus monstrous:* Ohemeng, Lawson, Ayivor, Leach, Waldman and Ntiamoa-Baidu, Anthrozoös, 30 (2): 184. Publication date: 16 May 2017. - Comments: Weiß (2013: 66) already mentioned this combination in her PhD thesis. (Lapsus).

2019. *Hypsignathus monstruosus:* Kaswera Kyamakya, Nebesse Mololo and Gambalemoke Mbalitini, IJEAB, 4 (2): 330. Publication date: March-April 2019. (Lapsus).

2021. *Hypsignathus monostrous:* Ohimain, Curr. Opin. Pharmacol., 60: 69. Publication date: 3 August 2021. (Lapsus).
? *Epomophorus (Hypsignathus) monstrosus:* (Name Combination).
? *Hypsignathus monstrosus:* (Current Combination).
? *Hypsygnathus monstrosus:* (Lapsus).

TAXONOMY:
See Langevin and Barclay (1990), Bergmans (1989) and Simmons (2005: 324).

COMMON NAMES:
Castilian (Spain): Cabeza Martillo. Chinese: 锤头果蝠. Czech: kaloň kladivohlavý, kaloň štítohlavý. English: Hammer-headed bat, Hammer-headed Fruit Bat. French: Hypsignathe monstrueux, Chien volant à tête en marteau, chauve-souris à tête de marteau. German: Hammerkopf, Hammerkopf-Flughund. Kinande (DRC): Mulina. Tanoboase (Ghana): ahwenekron. Tshokwe (Angola): Tshingunzu. Vai (Liberia): Tuña.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008az; IUCN, 2009; Tanshi, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Tanshi, 2016). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008az; IUCN, 2009). 2004: LC ver 3.1 (2001) (IUCN, 2004; Mickleburgh *et al.*, 2004bw). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is locally threatened by habitat destruction, particularly the loss of riverine forests. In parts of its range it is hunted for subsistence food (Mickleburgh *et al.*, 2008az; IUCN, 2009; Tanshi, 2016). It is persecuted for its noise during leks and is hunted for food across its range (Tanshi, 2016). The extent to which this constitutes a threat is unknown and requires investigation.

Duke (1934: 74) provided some suggestions on how to shoot this bat as this seemed to be the only way to get rid of its terrible noise.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008az) [in IUCN (2009)] report that there appear to be no direct conservation measures in place. It has been recorded from Tai National Park (Côte d'Ivoire). Okomu National Park (Nigeria) and Afi Mountain Wildlife Sanctuary (Nigeria), Atewa Forest Reserve (Ghana) and several others across its range (Tanshi, 2016).

Mickleburgh *et al.* (2008az) [in IUCN (2009)] recommend that further studies are needed into the distribution of this species.

GENERAL DISTRIBUTION:
Hypsignathus monstrosus is widespread in West and Central Africa. It ranges from Guinea-Bissau in the west, to northwestern Angola in the south, and as far east as western Ethiopia and western Kenya (near Lake Victoria). It has been recorded to at least 1,800 m asl.

Three specimens are mentioned from Ethiopia (one without specific locality - MNHN ZM-MO-1983-1149) and one each from Dogy River Bridge (BRTC 58448) and Bora River Bridge (BRTC 58449). The latter two are in iDigBio as *H. monstrosus* (with TCWC as museum acronym), but on an older listing V. Van Cakenberghe found them mentioned as females, which might leave space for misidentification. The Paris Museum specimen, however, is a male. The map in Happold (2013r) shows a spot on the same location, so the identification might be correct, but these do need confirmation.

Native: Angola (Crawford-Cabral, 1989; Bergmans, 1989; Monadjem *et al.*, 2010d: 554); Benin; Burkina Faso (Kangoyé *et al.*, 2015a: 605); Cameroon; Central African Republic (Hayman *et al.*, 1966; Morvan *et al.*, 1999: 1195; Monadjem *et al.*, 2010d: 554); Congo (King and Dallimer, 2010: 65; Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 554); Côte d'Ivoire (Heim de Balsac, 1934b: 24); Equatorial Guinea; Ethiopia (Lavrenchenko *et al.*, 2004b: 131); Gabon; Ghana (Decher and Fahr, 2007: 11); Guinea (Denys *et al.*, 2013: 281); Guinea-Bissau (Rainho and Ranco, 2001: 21); Kenya; Liberia (Monadjem and Fahr, 2007: 50); Nigeria (Happold, 1987; Capo-Chichi *et al.*, 2004: 161); Sierra Leone (Grubb *et al.*, 1998); Sudan; Togo; Uganda (Kityo and Kerbis, 1996: 59).

Presence uncertain: Gambia, Sáo Tomé [its presence could not be confirmed by Rainho *et al.* (2022: 603].

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
The peculiar head of the males of this species, made Johnston (1906: 689) describe it as: "In these bats [Epomophori] the head is unusually large and long; but it is so monstrous and hideous in the biggest of the sub-family - the hammer-headed bat, *Hypsignathus* - as to provoke the appropriate specific term of *monstrosus*. This animal is the creation of a nightmare imagination. It might be recommended to the designers of an instructive pantomime or Wagnerian opera." Duke (1934: 72) compares its head with the gargoyles of the Nôtre Dame, and described it as half hippo, half horse.

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data: Fa: 115.7 mm, mass: 211 g, wing loading: 21.2 N/m^2, aspect ratio: 5.8.

DENTAL FORMULA:
None of the 13 skulls examined by Esquivel *et al.* (2021: Suppl.) had an aberrant number of teeth.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Eisenberg and Wilson (1978: 744) indicate that the cranial volume of *H. monstrosus* is slightly smaller than was expected from a regression line they calculated for all frugivorous bats. The lower score could be linked with the partially carnivorous diet of these bats as found by Van Deusen (1968).

Davies *et al.* (2013a: 4) provide an illustration of the bony labyrinth of *H. monstrosus*'s inner ear.

DETAILED MORPHOLOGY:
Brain
The average brain mass for two *H. monstrosus* specimens was found to be 3.81 g by Chawana *et al.* (2013: 160), whereas Tambusso and Fariña (2015: Suppl.) mention a mass of 3.4 g for an average body mass of 340 g.

FUNCTIONAL MORPHOLOGY:
The study of Coimbra *et al.* (2016: 191) found that the eye of *H. monstrosus* possesses a bright yellow tapetum lucidum, which covers almost the entire extension of its dorsal hemisphere. Its retinal area is about 200 mm^2 and contains about 3000,000 retinal ganglion cells. The minimum angle of resolution was approximately 0.122° (ca. 40 mm at 10 m distance).

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 36.3 Pa, aspect ratio 6.7 and tip shape index of 1.76 for a wingspan of 88 cm and a wing area of 1150 cm^2 and a body mass of 427 g.

Kawashima *et al.* (2017: 48) examined the postcranial skeleton of six *H. monstrosus* specimens and found that five had 15 thoracic vertebrae and one had 14; all had seven cervical, three lumbar and four sacral vertebrae.

Carter (2020: 301) [referring to Langevin and Barclay (1990)] indicated that the larynx of *H. monstrosus* males is half the length of the vertebrate column and has enlarged cricoid, thyroid and arytenoids, which is associated with the production of loud calls to attract females. The size of the larynx in males also counts for 20 % of the body cavity (Altringham, 2011: 130).

SEXUAL DIMORPHISM:
Besides the obvious morphological sexual dimorphism with males having an enlarged rostrum, larynx, and lips that are used to produce loud honking calls to attract females, Muñoz-Romo *et al.* (2021: 158) also point out that odour might be important as adult, heavy males spread a musty smell, which is absent in females. Males can also weight up to twice the weight of females (Mittelbach, 2021: 24).

MOLECULAR BIOLOGY:
Karyotype
Peterson and Nagorsen (1975) and Haiduk *et al.* (1980; 1981: 225) reported 2*n* = 36, FN = 68, BA = 34, a subtelocentric X chromosome and a subtelocentric Y chromosome for specimens from Kenya and Cameroon, respectively. 2*n* = 36 was also reported by Primus *et al.* (2006).

HABITAT:
Using LiDAR data, Russo *et al.* (2025c: 1, 3) found that in Southern Cameroon *Hypsignathus monstrosus* preferred areas of intermediairy canopy height (13.9 - 32.0 m) near canopy gaps of at least 500 m^2. The area where they did their study consisted mainly of *terra firma* forest, *Raphia* palm-dominated swamps, and grass-covered inselbergs. Most of the bats they followed made long flights (up to 17.7 km) shortly after sunset and before sunrise. The flights were limited to three or less destinations.

HABITS:
Schloesing *et al.* (2023: 1) mention that the probability of a bat returning to a specific feeding area within the next 48 hours depends on the time it spent at that area. The longer its stayed, the higher the probability.

ROOST:
During the day, *H. monstrosus* roosts in trees, in most cases as singles of either sex, but also in mixed sex groups of up to 17 individuals. Males typically roost at the periphery of larger groups (see Bradbury, 1977).

DIET:
Duke (1934: 72) indicates that *H. monstrosus* starts to feed soon after dark, and that it eats fruits of various kinds, especially guavas and certain kinds of wild figs. Gautier-Hion and Michaloud (1989: 1829) reported that 88 % of 133 oral swabs and fecal samples analysed from May to October in Makokou (Gabon) contained figs. They reported (p. 1831) that females forage at about 1 to 4 km from their roosts, whereas males travel up to 10 km, and also that figs only form 38 % of the females diet against 58 % in males.

Van Deusen (1968) [in Courts (1998: 190)] observed this bat attacking live chickens and scavenging the carcasses of small birds.

Seltzer *et al.* (2013: table S2) provided an overview of the plant species found beneath bat feeding roosts. For *H. monstrosus* this included *Milicia excelsa* (Welw.) C. C. Berg (African Teak - Moraceae).

From the Kisangani area (DRC), Gembu Tungaluna (2012: 99 - 100) reported the following fruits being eaten during the various seasons: First heavy rain season (September - November): *Persea americana* Mill., 1786 (Avocado) (21%), *Annonidium mannii* (Oliv.) Engl. & Diels (Junglesop) (18%), *Carica papaya* L. (Papaya) (14%), *Dacryoides edulis* H.J. Lam (Safou, African Pear, Bush Pear, Nsafu, Bush Butter Tree, Butterfruit) (14%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, Otaheite Apple, Great Hog Plum) (11%), *Uapaca guineensis* Müll. Arg., 1864 (Sugar Plum, Red Cedar, False Mahogany, Rikio) (7%), *Myrianthus arboreus* P. Beauvois, 1805 (Giant Yellow Mulberry, Bush Pineapple, Corkwoord) (4%), *Elaeis guineensis* Jacq. (African Oil Palm, Macaw-fat) (4%), *Ficus wildemanniana* Warb. (4%), *Ficus leprieuri* Miq., 1867 (3%).

First mild dry season (December - February): *Myrianthus arboreus* (50%), *Musanga cecropioides* R. Br. & Tedlie (African Corkwood Tree, Umbrella Tree) (50%).

Second heavy rain season (March - May): *Musanga cecropioides* (75%), *Ficus leprieuri* (25%).

No data for the "Dry" season (June - August).

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Hypsignathus monstrosus*: *Adenia cissampeloides* (Planch. ex Hook.) Harms, 1897, *Anthocleista nobilis* G. Don, *Chlorophora excelsa* Welw., Benth. and Hook. f., *Ficus capensis* Thunb., 1786, *Ficus leprieuri* Miq., 1867, *Ficus lyrata* Werb., 1894, *Ficus ovata* Vahl, 1805, *Ficus polita* Vahl, 1805, *Ficus scott-eliotti* Mildbr. and Burret, 1911, *Ficus thonningii* Blume, 1839, *Ficus vallis-choudae* Delile, 1843, *Mangifera indica* Linnaeus, *Psidium guajava* Linnaeus, 1753.

PREDATORS:
Neil (2017: 131) reported on a hammer-headed fruit bat being captured by a Long-tailed hawk, *Urotriorchis macrourus* (Hartlaub, 1855) in Gabon. The hawk left its wounded prey on the ground, after which the bat was able to escape.

POPULATION:
Structure and Density
It is a locally common species. Roosts can contain as many as 25 bats, but the average roost size is fewer than five animals (Mickleburgh *et al.*, 2008az; IUCN, 2009; Tanshi, 2016).

Trend
2016: Unknown (Tanshi, 2016). 2008: Unknown (Mickleburgh *et al.*, 2008az; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Bradbury (1977) observed females hover in front of selected males before copulation.

Carpenter (1986: 90) and McGuire and Guglielmo (2009: 1291) reported that the respiratory quotient for this species indicates that fat provided 77 - 92 % of the fuel during flight, and a decline in respiratory quotient during long flights may prove that fat is indeed the only fuel source following initial carbohydrate use. Carpenter (1986: 93) also indicates that at airspeeds of 5.5 m/s the heart beats at a frequency of 620 beats per minute, whereas the respiration rate is 293 breadths per minute.

The courtship calls, which likely have a territorial function, consist of a simple syllable type in series (Bradbury, 1977 in Smotherman *et al.*, 2016: 538).

For a selection of sounds, check https://search.macaulaylibrary.org.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 120, 121) indicate that females attain sexual maturity at 5 to 6

months of age, whereas males need 18 months. Kurta and Kunz (1987: 82) report that, at birth, the young weights about 16.2 % of the mother's body mass (38.0 g versus 234.0 g).

MATING:
The mating system of this species is polygynandry (Webber *et al.*, 2017: Suppl.).

Bradbury (1977) reported that *H. monstrosus* exhibit lek behaviour at their mating sites: Males form large choruses during the night that are visited by females, and they respond to the presence of females by increasing the repetition rate of their calls and by moving their wings. He also found that females favour larger males with bulbous muzzles and enormous hypertrophied larynxes, which are acting as resonating chambers. Male sites are spaced about 10 m apart, and individual males use the same site every night.

In Congo, Schloesing *et al.* (2023: 6) found that males roosting close to lek sites (< 10 km) were more likely to visit the lek and spend more time there.

Olson *et al.* (2019: 2) indicate that the lek behaviour might be restricted to the Central African populations, as in West Africa the reproductive strategy seems to be harem-based.

In Abidjan (Côte d'Ivoire), Niamien *et al.* (2015b: 230) found that *H. monstrosus* males preferred relatively low (5 - 10 m) *Terminalia catappa* L. trees (Indian almond - Combretaceae) for their leks. The individual trees were about 5 m apart. The males were present from August to October (small dry season to start of small wet season), and from February to May (end of large dry season to start of large wet season). In the other months no males were observed.

Bradbury (1977) [in Fasel *et al.* (2016: 2)] reported on uneven copulation rates, whereby harem males mate at a higher frequency than other males.

PARASITES:
BACTERIA
Gram-negative bacterium
Nowak *et al.* (2017: 6) tested two bats from the Republic of Congo, both of which were positive for *E. coli*.

HAEMOSPORIDA
Ayala *et al.* (1981: 21) examined blood smears from 142 *H. monstrosus* specimens from Gabon and found 139 of them to be infected by hemosporidian parasites of the genus *Hepatocystis*. They also indicate that the bats probably became infected before the age of six months and that the infection rate varied according to sex, age and female reproductive status. Schaer *et al.* (2013a: 17416) report the same parasites in five out of 10 investigated bats. Perkins and Schaer (2016: Suppl.) mention *Hepatocystis carpenteri*, described by Miltgen *et al.* (1980), from Gabon and *H. epomophori* and *H.* sp. from various countries.

Hepatocystis sp. Infections were also reported by Boundenga *et al.* (2018: 10581) from bats from Gabon (1 out of 21 examined: 4.8%).

Hepatocystis gametocytes were reported from this bat for the first time in the DRC by Rodhain (1913), although he referred the bats erroneously to *Epomops franqueti franqueti* (see Miltgen *et al.*, 1977: 595).

Hepatocystis parasites were also found in the single *Hypsignathus* sp. from South Sudan examined by Schaer *et al.* (2017: 2). GenBank data for a *Hepatocystis* sp. (Hyp_mon_L2_1) from Liberia were also reported by Arnuphapprasert *et al.* (2020: Suppl.).

ACARI
Fain (1967: 364) reported *H. monstrosus* from Epulu, DRC as new host for *Teincoptes auricularis* Fain, 1959 (Acari: Teinocoptidae). The parasites were found around the nipples of the host.

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Lagos bat lyssavirus, Marburg marburgvirus, Mokola lyssavirus, Nipah henipavirus, Reston ebolavirus, Zaire ebolavirus.

Raulino *et al.* (2022: 256) reported the presence of antibodies against Chikungunya virus, Dengue virus, O'nyong nyong virus, Usutu virus, West Nile virus and Zika virus.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, 11 individuals from Bandundu Province, DRC for antibody to SARS-CoV in sera, one was found to be positive (9.1 %).

Filoviridae - Filo viruses
Ebolavirus
Pourrut *et al.* (2007) found homogeneous ZEBOV [Zaire Ebolavirus] infection in the wild populations of *H. monstrosus* in Gabon and the Democratic Republic of the Congo. Hayman *et al.* (2010) tested the blood of 3 adult females from Ghana

for Ebola virus using indirect fluorescent tests for antibodies against EBOV subtype Zaire, none tested positive. However, Hayman *et al.* (2012d: 1208) found 7 out of 16 bats to be positive for EBOV antibodies in Ghana's Greater Accra region. Four out of 17 bats had immunoglobulin G (IgG) specific for Ebola in Gabon during a test performed by Leroy *et al.* (2005: 575).

Bausch and Schwarz (2014: 1) and Pigott *et al.* (2014: 8) indicate that *H. monstrosus* is one of the leading candidates for introducing Ebola in Guinea (together with *Epomops franqueti* and *Myonycteris torquata*). However, no proof has been provided that this was indeed the case.

Marburgvirus
Towner *et al.* (2007) tested 56 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 12 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found. Hayman *et al.* (2010) tested the blood of 3 adult females from Ghana for Marburg virus using indirect fluorescent tests for antibodies against MARV subtype Leiden, none tested positive.

Peterson *et al.* (2007: 1547) indicate that the geographic distribution of *H. monstrosus* covers the entire range of the Ebola virus, but not that of the Marburg virus.

Nairoviridae
Orthonairovirus
Only one of the 101 specimens from Gabon and Congo tested by Müller *et al.* (2016: 3) was positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae
Henipavirus
Krüger *et al.* (2013: 13889) demonstrated that the surface glycoproteins F and G of an African henipavirus (M74) induce syncytium formation in a kidney cell line derived from *H. monstrosus*.

Hayman *et al.* (2008b) detected antibodies Nipah virus in one bat collected in Ghana in 2007.

Drexler *et al.* (2012a: Suppl. Table S1) reported that 2 out of 4 specimens they examined from Gabon, Congo, Ghana and the Central African republic tested positive for *Henipavirus* and *Rubulavirus*.

In their overview table, Maganga *et al.* (2014a: 8) reported that the following viruses were already found on *H. monstrosus*: Zaire Ebola virus (ZEBOV), Reston Ebola virus, Marburg virus (MBGV), Coronavirus (SARS-CoV), Nipah virus (NPHV).

Bennett *et al.* (2018: 65) studied viruses in the blood of *H. monstrosus* from the Republic of Congo and found that four out of five viruses are phylogenetically and genomically allied with viruses of arthropods: a nodavirus ("hypsignathus nodavirus", provisionally genus *Hypnovirus*, family Nodaviridae), a dicistrovirus ("hypsignathus dicistrovirus", genus *Cripavirus*, family Dicistroviridae), and two distinct variants of the recently recognized tombus-like viruses ("Hypsignathus monstrosus tombus-like virus 1 and 2", family Tombusviridae). The fifth virus was a novel hepatitis B-like virus ("Hypsignathus monstrosus hepatitis B virus (HMHBV)", family Hepadnaviridae), which is of mammalian origin. They also suggest that the viruses from arthropod origin might have been accidentally ingested, as the insects they are associated with, are themselves parasites of fruits eaten by the bats. (In a Corrigendum to their paper, the authors indicate that the characterization of their putative HBV sequences should be considered inconclusive as contamination of reagents might have occurred.)

UTILISATION:
Bobo and Ntumwel (2010: 232) report that in the Korup area of Cameroon the whole animal is used for medicinal purposes, as it would render women fertile when consumed.

The species is hunted for food, and being Africa's largest bat, it is targeted, although because it forms small groups or individuals, it is not the most hunted fruit bat species (Mildenstein *et al.*, 2016).

ANTHROPOPHILOUS:
Jeffreys (1944: 73) [referring to Goddard (1925)] mentions "From Sierra Leone comes an account of the gruesome habits of the large fruit bat. 'One of the most uncanny superstitions is that of the 'Boman' in which anthropologists will recognise the vampire of European superstition. This creature is said to suck the blood of sleeping children until they die: it can turn into a stone or snake at will. The 'Boman' is in reality the hammer-headed bat (*Hypsignathus monstrosus*), the largest fruit bat found in Africa; its dull and monotonous cry at the time when fruit is ripening has struck terror into many a village, whose inhabitants will sally forth from their houses and beat tins to drive it away, cursing its father and mother and all its ancestors the while.'"

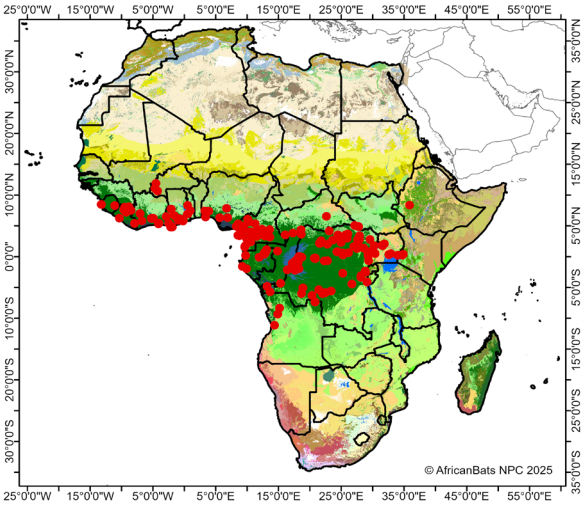

Figure 29. Distribution of *Hypsignathus monstrosus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Burkina Faso, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Sierra Leone, South Sudan, The Gambia, Togo, Uganda.

Genus ***Nanonycteris*** Matschie, 1899

*1899. *[Epomophorus (]Nanonycteris[)]* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 35, 58 [Goto Description]. - Comments: Described as a subgenus of *Epomophorus* Bennett, 1836. Type species: *Epomophorus veldkampii* Jentink, 1888. Matschie dated his introduction on 14 May 1899. - Etymology: From the Greek "*νάνος*", meaning dwarf and "*νυκτερις*", meaning bat (see Palmer, 1904: 448).
1943. *Nannonycteris:* Pohle, Sber. Ges. naturf. Freunde Berlin, 78 (for 1942). (Lapsus).
2007. *Nnonycteris:* Lameed, Biodiversity, 8 (4): 8. (Lapsus).
2019. *Nanonycteri:* Mbu'u, Mbacham, Gontao, Kamdem, Nlôga, Groschup, Wade, Fischer and Balkema-Buschmann, Vector-Borne Zoon. Dis., xxx: "6". Publication date: 13 April 2019. (Lapsus).
? *Epomophorus:* - Comments: Not of Gray, 1836.
? *Nanonycteris:* (Name Combination, Current Combination).

TAXONOMY:
Revised by Bergmans (1989). See Simmons (2005: 328).

Included in the Epomophorinii tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Hassanin *et al.* (2020: 5) include it in the Epomophorina subtribe of the Epomophorini tribe.

Currently (Simmons and Cirranello, 2024a) recognized species of *Nanonycteris*: ***veldkampii*** (Jentink, 1888).

COMMON NAMES:
Czech: Veldkampovi kaloni. English: Dwarf Fruit-bats, Little Flying Cow. French: Roussettes naines. German: Zwergflughunde.

Nanonycteris veldkampii (Jentink, 1888)

*1888. *Epomophorus veldkampii* Jentink, Notes Leyden Mus., 10: 51 (for 1887). Publication date: April 1888. Type locality: Liberia: Fisherman Lake: Buluma [06 43 N 11 14 W]. [Goto Description]. Holotype: RMNH MAM.20400: ad ♀, skull and alcoholic. Collected by: Johann Büttikofer and C.F. Sala; collection date: 19 April 1881. - Etymology: Jentink (1887b: 52) states: "I call this new species *veldkampii*, as Büttikofer wishes to connect the name of one of his Liberian friends with this new acquisition. Mr. Veldkamp, at present Consul for the Netherlands in Liberia, has helped our travellers as much as he could, has promoted their investigations in every way and finally assisted to Sala's funeral.".
2000. *Nanonycteris weldkampi:* Konstantinov, Pema, Labzin and Farafonova, Plecotus et al., 3: 145. (Lapsus).
2015. *N[anonycteris] Weldkampi:* Sylla, Pourrut, Diatta, Diop, Ndiaye and Gonzalez, Afr. J. Microbio. Res., 9 (22): 1464. Publication date: 3 June 2015. (Lapsus).
2018. *Nanonycteris veldkompi:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Lapsus).
? *Epomophorus (Nanonycteris) veldkampii:* (Name Combination).
? *Nanonycteris veldkampii:* (Name Combination, Current Combination).

TAXONOMY:
See Bergmans (1989) and Simmons (2005: 328).

COMMON NAMES:
Czech: kaloň Veldkampův. English: Veldkamp's Dwarf Fruit-bat, Veldkamp's Bat, Little Flying

Cow, Flying Calf. French: Roussette naine de Veldkamp, Chauve-souris de Veldkamp, Nanonyctère, Petite vache-volante. German: Veldkamps Zwergflughund.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008be; IUCN, 2009; Monadjem *et al.*, 2017ao).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ao). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008be; IUCN, 2009). 2004: LC ver 3.1 (2001) [as *Nononycteris veldkampi*] (Mickleburgh *et al.*, 2004cb; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
In general, there appear to be no current major threats to this species as a whole. The species is dependent on certain food trees where they visit flowers, and habitat degradation might be a problem in parts of the range (Mickleburgh *et al.*, 2008be; IUCN, 2009; Monadjem *et al.*, 2017ao).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008be) [in IUCN (2009)] and Monadjem *et al.* (2017ao) report that, in view of the species wide range, it seems probable that it is present in a number of protected areas. There is a need to determine if there have been any local declines in this species resulting from the loss of food trees.

GENERAL DISTRIBUTION:
Nanonycteris veldkampii is widely distributed in West Africa and western parts of Central Africa. It ranges from Guinea and Sierra Leone in the west, through each country in West Africa to Cameroon, with a single record from the southern region of Central African Republic. It is generally a lowland species, but has been recorded up to 1,200 m asl.

Native: Benin (Capo-Chichi *et al.*, 2004: 161); Burkina Faso (Kangoyé *et al.*, 2012: 6023; 2015a: 605); Cameroon; Central African Republic; Côte d'Ivoire (Heim de Balsac, 1934b: 24); Ghana (Decher and Fahr, 2007: 12); Guinea (Denys *et al.*, 2013: 281); Liberia (Monadjem and Fahr, 2007: 50); Nigeria; Sierra Leone; Togo.

DENTAL FORMULA:
None of the six skulls examined by Esquivel *et al.* (2021: Suppl.) had an anomalous number of teeth.

HABITAT:
Monadjem *et al.* (2016y: 364) indicate that this species occurs in forested habitats between 500 and 1200 m in the Mount Nimba area of Liberia and Guinea.

ROOST:
N. veldkampii roosts singly or in small groups of well-spaced individuals (Kunz, 1996: 44).

MIGRATION:
Thomas (1983) [in Kangoyé *et al.* (2015a: 605)] reported that this species migrates during the wet season from the forest zone to the northern Sudanian zone. From Ghana, this was confirmed by Decher *et al.* (2021: 268).

DIET:
Ayensu (1974) reports feeding visits to *Parkia clappertonia* (Dawadawa), *Ceiba pentandra* (Silk-Cotton tree or Kapok tree), *Psidium guajava* (Guava tree), and *Carica papaya* (Papaya or pawpaw).

Fahr (2011a: 114) shows a picture of *N. veldkampii* feeding on *Cola cordifolia*.

Seltzer *et al.* (2013: table S2) provide an overview of the plant species found beneath bat feeding roosts. For *N. veldkampii* this included *Psidium guajava* L. (apple guava - Myrtaceae).

POPULATION:
Structure and Density
This species can be abundant, although this partly depends on migration patterns (Mickleburgh *et al.*, 2008be; IUCN, 2009; Monadjem *et al.*, 2017ao).

Trend
2016: Unknown (Monadjem *et al.*, 2017ao). 2008: Unknown (Mickleburgh *et al.*, 2008be; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Weber *et al.* (2019: 20) reported on five pregnant (25, 30, 31 March, 2 April) and 11 lactating (25, 27, 30, 31 March, 1, 3, 7, 8 April) in Sierra Leone.

PARASITES:
HAEMOSPORIDA
Witsenburg *et al.* (2012: Suppl. Table 1) and Arnuphapprasert *et al.* (2020: Suppl.) report on GenBank data for *Hepatocystis*, retrieved from *N. veldkampii* from Liberia and Côte d'Ivoire. These parasites were also reported by Schaer *et al.* (2013a: "2") from six out of 8 investigated bats.

ACARI
Bochkov and Fain (2003) reported the following Myobid parasites: *Binuncus (Binuncus) epomophori* Fain, 1972 and *Binuncus (Binuncus) myonycteris* Uchikawa, 1986 (although the host for the latter was identified as *Myonycteris torquata*).

VIRUSES:
Coronaviridae - Coronaviruses
The single Guinean specimen tested by Lacroix *et al.* (2020: 7) was positive for CoV.

Filoviridae - Filoviruses
Ebolavirus
One out of four specimens tested by Hayman *et al.* (2012d: 1208) in the Greater Accra region, Ghana, was positive for EBOV antibodies.

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) reported that none of the 23 specimens they examined from Ghana tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

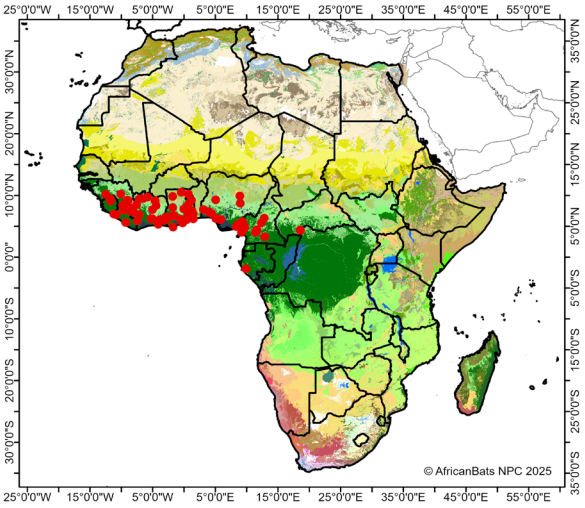

Figure 30. Distribution of *Nanonycteris veldkampii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Togo.

TRIBE Myonycterini Lawrence and Novick, 1963

*1963. *Myonycterini* Lawrence and Novick, Breviora, 184: 9. Publication date: 18 April 1963.
2025. *Myoncterini:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: Suppl. Publication date: 18 July 2025. (Lapsus).

TAXONOMY:
Includes the genera ***Megaloglossus*** Pagenstecher, 1885 and ***Myonycteris*** Matschie, 1899.

Genus ***Megaloglossus*** Pagenstecher, 1885

*1885. *Megaloglossus* Pagenstecher, Zool. Anz., 8 (193): 245. Publication date: 27 April 1885 [Goto Description]. - Comments: Type species: *Megaloglossus woermanni* Pagenstecher, 1885. - Etymology: From the Greek "*μέγας*" or "*μέγαλο*", meaning great or large and "*γλοσσα*", meaning tongue (see Palmer, 1904: 405). (Current Combination).
1891. *Trygenycteris* Lydekker, in: Flower and Lydekker, Mammals Living and Extinct, 655. - Comments: Type species: *Megaloglossus woermanni* Pagenstecher, 1885. Proposed to replace *Megaloglossus*, thought to be preoccupied by *Megaglossa* Rondani, 1865 (Diptera): see Allen (1939a: 63). - Etymology: From the Greek "*τρύγη*", meaning ripe fruit and "*νυκτερίς*", meaning bat (see Palmer, 1904: 696).

TAXONOMY:
Reviewed by Hill (1983).

Based on the female reproductive morphology, Hood (1989: 219) concluded that *Megaloglossus* does not belong ot the clade of macroglossine bats.

Bergmans (1997: 69) suggests that *Megaloglossus* should be included in the tribe Myonycterini Lawrence & Novick, 1963 (together

with the genera *Myonycteris* and *Lissonycteris*), within the subfamily Epomophorinae, and not within the Macroglossinae.

Included in the Myonycterini tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Hassanin *et al.* (2020: 5) include it in the Myonycterina subtribe of the Epomophorini tribe.

Currently (Simmons and Cirranello, 2023b) recognized species of *Megaloglossus*: ***azagnyi*** Nesi, Kadjo and Hassanin, 2012; ***woermanni*** Pagenstecher, 1885.

COMMON NAMES:
Czech: dlouhojazyční kaloni. English: African Long-tongued Fruit-bats, African Nectar Fruit-bats. French: Mégaloglosses. German: Afrikanische Langzungen-Flughunde.

VIRUSES:
Filoviridae - Filo viruses
Ebolavirus
Although the distribution area of the *Megaloglossus* species largely overlaps with the area where Ebola outbreaks occurred, no seropositive individuals were found yet (Olivero *et al.*, 2019: 1).

Megaloglossus azagnyi Nesi, Kadjo and Hassanin, 2012

1997. *Macroglossus woermanni:* Barnett and Prangley, Mammal Rev., 27 (3): 139. Publication date: September 1997. - Comments: This is probably a lapsus as all other references to "i woermanni" are linked with *Megaloglossus*". As Barnett and Prangley (1997) dels with mammals from Guinea, we consider this name as a synonym of *Megaloglosus azagnyi*. (Lapsus).

*2012. *Megaloglossus azagnyi* Nesi, Kadjo and Hassanin, in: Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylogenet. Evol., 66(1): 134. Type locality: Côte d'Ivoire: Lagunes region, Azagny National Park [0613007N 0501532W, 125m]. Holotype: MNHN ZM-2011-993: ad ♀, alcoholic (skull missing). Collection date: 5 December 2009; original number: G09095. Presented/Donated by: [No Name]. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2011-1000: ad ♂. Locality: Côte d'Ivoire; Azagny, near; Gboyo. Paratype: MNHN ZM-2011-1001: sad ♀. Locality: Côte d'Ivoire; Azagny, near; Gboyo. Paratype: MNHN ZM-2011-1002: ad ♀. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2011-994: ad ♀. Locality: Côte d'Ivoire; Lamto Reserve. Paratype: MNHN ZM-2011-995: ad ♀. Locality: Côte d'Ivoire; Lamto Reserve. Paratype: MNHN ZM-2011-996: ad ♀. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2011-997: sad ♀. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2011-998: ad ♂. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2011-999: ad ♀. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-2014-598: sad ♀, skull and alcoholic. Original number: G09052. This number wasn't explicitly mentioned in the original description, but included in the online catalog of the MNHN. It most probably is the specimen mentioned by its collection number as this is the only "missing" paratype from Lamto. Paratype: MNHN ZM-G09052: sad ♀. Locality: Côte d'Ivoire; Lamto Reserve. Paratype: MNHN ZM-G09070: ad ♂. Locality: Côte d'Ivoire; Lagunes region; Azagny National Park; 0613007N 0501532W. Paratype: MNHN ZM-G09133: ad ♀. Locality: Côte d'Ivoire; Azagny, near; Gboyo. Paratype: MNHN ZM-GAN005. Locality: Liberia; Mt. Nimba. Paratype: MNHN ZM-GAN028. (Current Combination).

TAXONOMY:
Nesi *et al.* (2012) examined cytochrome *b* sequences and found West African *Megaloglossus* to be significantly different from Central African specimens.

COMMON NAMES:
German: Westlicher Woermanns Langzungen-Flughund.

SIMILAR SPECIES:
Decher and Weber (2021: 467) indicate that *M. azagnyi* is in general slightly smaller than . woermanni, which caused earlier authors to consider this difference as a clinal variation.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Decher and Weber (2021: 467) suggest that the separation from *M. woermanni* occurred somewhere in the Middle Pleistocene, either along the Dahomey Gap or along the mountain area of Camerun.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Monadjem, 2016b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2016b).

MAJOR THREATS:
It may be locally threatened by habitat loss and degradation, often resulting from conversion of

land to agricultural use or the harvesting of timber and firewood (Monadjem, 2016b).

CONSERVATION ACTIONS:
Monadjem (2016b) reports that this species has been recorded within several protected areas and also survives outside of such areas.

GENERAL DISTRIBUTION:
This species occurs in Côte d'Ivoire, Liberia, and probably Guinea and Sierra Leone to Ghana and Togo.

In their study, Nesi *et al.* (2012) did not include specimens from the area between the Dahomey Gap and the Niger delta, but Herkt *et al.* (2017: Appendix S9) found their maps predicted moderately high habitat suitability for *M. azagnyi* in this area whereas suitability for *M. woermanni* was estimated to be very low. Therefore, they assigned the specimens from this area to *M. azagnyi*.

Native (mostly reported as *M. woermanni*): Benin; Côte d'Ivoire (Heim de Balsac, 1934b: 24); Ghana (Decher and Fahr, 2007: 12); Liberia (Monadjem *et al.*, 2016y: 364); Nigeria (West of the Niger Delta); Sierra Leone; Togo.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_2$, $C^1/_1$, $PM^3/_3$, $M^2/_3$ = 34.

SEXUAL DIMORPHISM:
Males possess a yellowish ruff with a presently unknown function (Decher and Weber, 2021: 468).

HABITAT:
In the Mount Nimba area, Happold (2013dh: 364) report this species to occur in old growth or secondary forest at relatively low altitudes (450 - 690 m) on both the Liberian and Guinean sides.

Decher and Weber (2021: 469) mention a home range of 99.8 - 102.9 ha for males in southern Benin, whereas females have a home range of 139.0 - 146.8 ha (based on radio tracked animals which were followed for 5 to 9 days). The feeding area covered 12.3 and 74.2 ha respectively.

DIET:
In Côte d'Ivoire, Pettersson (2005) reported "*M. woermanni*" to feed on nectar and pollen of and *Parkia bicolor* (African locust-bean - Fabaceae), *Maranthes aubrevillei* and *M. glabra* (Chrysobalanaceae). Furthermore, *Anthocleista nobilis* (Cabbage tree, Cabbage palm - Gentianaceae) was the only tree flowering throughout the year and is probably a keystone species in this area for *M. woermanni* during periods of low food availability.

Decher and Weber (2021: 469) mentions *Anthocleista nobilis* as year-round food source in southern Côte d'Ivoire

POPULATION:
Structure and Density
The species is locally abundant (Monadjem, 2016b).

Trend
2016: Unknown (Monadjem, 2016b).

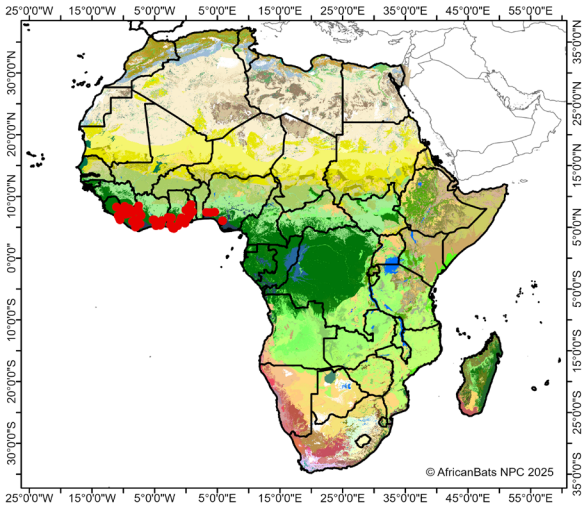

Figure 31. Distribution of *Megaloglossus azagnyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Togo.

Megaloglossus woermanni Pagenstecher, 1885

*1885. *Megaloglossus woermanni* Pagenstecher, Zool. Anz., 8 (193): 245. Publication date: 27 April 1885. Type locality: Gabon: Ssibange farm [00 25 N 09 28 E]. [Goto Description]. Holotype: ZMB 54589: ad ♀, mounted skin and skull. Collected by: H. Soyaux; collection date: 21 January 1885; original number: 9489. Bergmans (1997: 60, 63) mentions old number "9489", but this is a writing error in the file card; see Turni and Kock (2008). - Etymology: In honour of Mr. Adolf Woermann (see Pagenstecher, 1885c: 128). (Current Combination).

1966. *Megaloglossus woermanni prigoginei* Hayman, in: Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 26. Type locality: Congo (Democratic Republic of the): Kiliza [03 42 S 28 10 E, 1 370 m]. Holotype: RMCA 32577: ad ♂, skin and skull. Collected by: Dr. Alexandre Prigogine; collection date: 25 May 1964; original number: 1248. See Bergmans (1997: 60). Paratype: RMCA 20429: ♂. Collected by: Dr. Alexandre Prigogine; original number: 494. Paratype: RMCA 21586: Collected by: Schepens; original number:

6. Paratype: RMCA 32394: juv ♀. Collected by: Dr. Alexandre Prigogine; original number: 1226. Paratype: RMCA 32578: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1249. Paratype: RMCA 32579: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1250. Paratype: RMCA 32580: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1251. Paratype: RMCA 32581: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1252. Paratype: RMCA 32582: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1253. Paratype: RMCA 32583: ♀. Collected by: Dr. Alexandre Prigogine; original number: 1254.

1993. *prigoginii:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 154. (Lapsus).

2003. *Megaloglossus woermani:* Giannini and Simmons, Cladistics, 19 (6): 508. (Lapsus).

? *Megaloglossus woermanni woermanni:* (Name Combination).

Taxonomy:

See Bergmans and Van Bree (1972), Bergmans (1997) and Simmons (2005: 326 - 327).

Common Names:

Castilian (Spain): Murciélago de Lengua Larga. Czech: kaloň dlouhojazyčný. English: Woermann's Long-tongued Fruit-bat, Woermann's Bat, Woermann's Fruit bat, Nectar Bat, African Long-tongued Bat. French: Macroglosse de Woermann, Mégaloglosse de Woermann. German: Woermann's Langzungen-Flughund, Afrikanischer Langzungen-Flughund.

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008p; IUCN, 2009; Bakwo Fils *et al.*, 2016; Bakwo Fils *et al.*, 2020).

Assessment History

Global

2016: LC ver 3.1 (2001) (Bakwo Fils *et al.*, 2016). 2014: LC ver 3.1 (2001) (Bakwo Fils *et al.*, 2020). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008p; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004w; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

Major threats:

It is locally threatened by habitat loss and degradation, often resulting from conversion of land to agricultural use or the harvesting of timber and firewood (Mickleburgh *et al.*, 2008p; IUCN, 2009; Bakwo Fils *et al.*, 2016; Bakwo Fils *et al.*, 2020).

Conservation actions:

Mickleburgh *et al.* (2008p) [in IUCN (2009)], Bakwo Fils *et al.* (2016) and Bakwo Fils *et al.* (2020) who report that there appear to be no direct conservation measures in place, however, in view of the species wide range it seems possible that it is present within some protected areas. Further studies are needed into the distribution and natural history of this species.

General distribution:

Megaloglossus woermanni was formerly considered to occur throughout much of West and Central Africa. However, Nesi *et al.* (2012) assigned the West African specimens to a separate species, restricting the distribution area to Cameroon and from here south and east into Equatorial Guinea, Congo, Central African Republic, Democratic Republic of the Congo, Angola and western Uganda.

In their study, Nesi *et al.* (2012) did not include specimens from the area between the Dahomey Gap and the Niger delta, but Herkt *et al.* (2017: Appendix S9) found their maps predicted moderately high habitat suitability for *M. azagnyi* in this area whereas suitability for *M. woermanni* was estimated to be very low. Therefore, they assigned the specimens from this area to *M. azagnyi*.

González-Gutiérrez *et al.* (2025: Suppl.) calculated that the entire distribution area for this species covers 2,805,063 km^2.

Native: Angola (Crawford-Cabral, 1989; Bergmans, 1997; Monadjem *et al.*, 2010d: 554); Cameroon; Central African Republic (Morvan *et al.*, 1999: 1195); Congo (King and Dallimer, 2010: 65); Congo (The Democratic Republic of the) (Schouteden, 1944; Dowsett *et al.*, 1991: 259; Bergmans, 1997; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 554); Equatorial Guinea (Fahr and Ebigbo, 2003: 128); Gabon; Nigeria (East of the Niger delta); Uganda (Kityo and Kerbis, 1996: 58).

Presence uncertain: Bioko.

Dental Formula:

Two of the eight skulls examined by Esquivel *et al.* (2021: Suppl.) had an aberrant number of teeth (either oligodontia or polyodontia). Van Cakenberghe *et al.* (2000: 301) reported eight out of 43 skulls having one to three additional teeth.

DETAILED MORPHOLOGY:
Brain
Chawana *et al.* (2013: 160) indicate that the average brain mass is 0.60 g (n = 2). Bhagwandin *et al.* (2020: 3027) found that the bat's brain contained 124,496 white matter interstitial cells (WMICs) for a brain mass of 0.62 g.

Reproductive
Hood (1989: 215) described the uterus as distinctly V-shaped, with extremely long horns and a short common body, which is about a quarter of the total length of the uterus and slightly rounded in shape. The cervical canals are short and narrow, and the cervicovaginal junction is abrupt, with cervical histological characteristics ending at the external os of each cervical canal.

FUNCTIONAL MORPHOLOGY:
Coimbra *et al.* (2016: 191) mention that the retinal area covers about 40 - 50 mm^2. The eye contains about 90,000 retinal ganglion cells. The minimum angle of resolution was about 0.227° (ca. 8 mm at 1 m distance).

Kulzer and Storf (1980: 409) investigated the thermoregulatory response by measuring body temperature and rate of oxygen consumption. At high ambient temperatures, the bats increase their oxygen consumption and at low ambient temperatures, they enter a lethargic sleep.

MOLECULAR BIOLOGY:
Karyotype
Haiduk *et al.* (1980, 1981: 228) reported 2*n* = 34, FN = 62, BA = 30, a metacentric X chromosome and a metacentric Y chromosome for specimens from Cameroon. The same karyotype was reported by Primus *et al.* (2006) for specimens from Gabon.

Genetics
Hollar and Springer (1997), Juste B. *et al.* (1999), Teeling *et al.* (2000), Colgan and da Costa (2002) and Cantrell *et al.* (2008).

HABITAT:
Juste B. and Perez del Val (1995: 144) found *M. woermanni* to occur to 1,800 m altitude on Bioko Island, where it occurred more frequently in cultivated areas than in lowland rainforests.

HABITS:
Weber *et al.* (2009) found that spatial use was characterized by small home ranges and high site-fidelity, mean home range sizes (minimum convex polygon) were larger in females (139.0 and 146.8 ha) than in males (99.8 and 102.9 ha) in Lama Forest Reserve, southern Benin.

Kulzer and Storf (1980) [in Lovegrove (2011: 152)] indicate that *M. woermanni* uses daily torpor.

DIET:
Pettersson *et al.* (2004: 162) indicate that *M. woermanni* is the only nectar specialist in Africa, whereas there are 14 such specialists in Asia, Australia and Polynesia.

Weber *et al.* (2009) frequently observed *M. woermanni* visiting flowers of cultivated bananas.

In Cameroon, Grünmeier (1993: 35) reported the following pollen from the gut and faeces: *Anthocleista* sp. (Gentianaceae), *Mucuna flagellipes* Hook.f. (Fabaceae), *Kigelia africana* (Lam.) Benth. (Bignoniaceae), *Celtis* sp. (Cannabaceae), *Citrus* sp.(Rutaceae), Bombacaceae indet.

In Uganda, Ssali and Sheil (2019: 1) found *M. woermanni* to be the second most common flower visitor of African wild bananas or “false bananas" (*Ensete ventricosum* (Welw.) Cheesman (Musaceae)), after the African dormouse (*Graphiurus murinus*). As this plant produces flowers (and fruits) year-round, it probably will act as a food resource in periods of the year when other types of food are not available.

POPULATION:
Structure and Density
It is a locally abundant species (Mickleburgh *et al.*, 2008p; IUCN, 2009; Bakwo Fils *et al.*, 2016; Bakwo Fils *et al.*, 2020).

Trend
2016: Stable (Bakwo Fils *et al.*, 2016). 2014: Stable (Bakwo Fils *et al.*, 2020). 2008: Stable (Mickleburgh *et al.*, 2008p; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Czekala and Benirschke (1974: 220) mention an adult female, collected in January 1973 by M. Eisentraut, containing two foetuses of different size, probably due to implantation occurring at two different times (p. 229).

Two females collected in Dimonika (Congo) on 10 March were pregnant with a large embryo (Bergmans, 1979a: 181).

PARASITES:
BACTERIA
Gram-negative Enterobacteriae
Mbehang Nguema *et al.* (2020: 7) reported the presence of *E. coli* and *Klebsiella pneumoniae* in feacal samples collected near Makokou in Gabon.

ACARI
Myobiidae
Fain (1973: 303) described *Binuncus (Binuncus) megaloglossus* from a *M. woermanni* from Boende, DRC.

VIRUSES:
Coronaviridae - Coronaviruses
For the two Congos, Kumakamba *et al.* (2021: 7) reported 10 out of 118 bats to test positive for coronaviruses. Montecino-Latorre *et al.* (2022: 9) mention these viruses to be Eidolon bat coronavirus/Kenya/KY24/2006.

Filoviridae - Filo viruses
Marburgvirus
Towner *et al.* (2007) tested 37 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 20 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found.

Flaviviridae
Pegivirus (BPgV)
Quan *et al.* (2013: Table S5) reported 1 out of 3 examined specimens from the Democratic Republic of the Congo to be infected by clade H type *Pegivirus*.

Paramyxoviridae
Orthorubulavirus
Drexler *et al.* (2012a: Suppl. Table S1) reported that one of the 34 specimens they examined from Gabon, Congo, the Democratic Republic of the Congo, the Central African Republic, and Ghana tested positive for a *Rubulavirus* that was found to be closely related to human mumps virus.

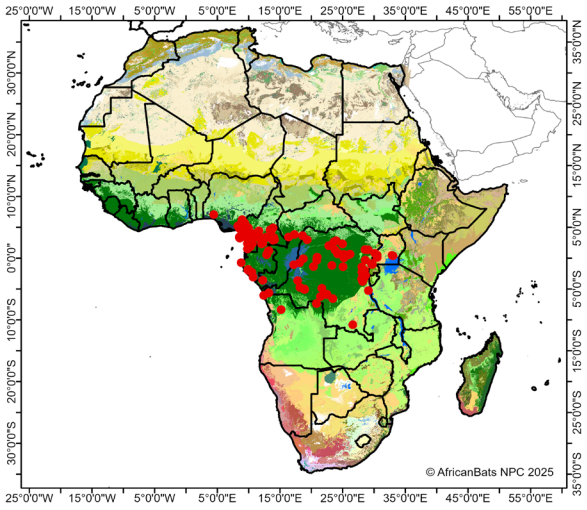

Figure 32. Distribution of *Megaloglossus woermanni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Gabon, Nigeria, Uganda.

Genus ***Myonycteris*** Matschie, 1899

*1899. *[Xantharpyia (]Myonycteris[)]* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 61, 63 [Goto Description]. - Comments: Type species: *Cynonycteris torquata* Dobson, 1878. Originally described as subgenus of *Xantharpyia*. Matschie dated his introduction on 14 May 1899. - Etymology: Derived from the Greek "*mys*" (= mouse) and "*nycteris*" (= bat) meaning mouse-like bat.
1899. *Myonycteris* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, p 63.
1934. *Mynonycteris:* Taylor, Monogr. Bur. Sci. Manila, 30: 172. - Etymology: From the Greek "*μύξ*" or "*μυόξ*", meaning mouse and "*νυκτεριο*", meaning bat (see Palmer, 1904: 440). (Lapsus).
1964. *Lyssonycteris:* Brosset, Mammalia, 28 (3): 450 (footnote). (Lapsus).
2012. *Lissonycteris:* Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylogenet. Evol., 66 (1): 126.
2015. *Cyonycteris:* Lanza, Funaioli and Riccucci, The bats of Somalia and neighbouring areas, 60. - Etymology: From the Greek adjective "*λισός*" (lissós), meaning "smooth" and the feminine Greek substantive "*νυκτερίς*" (nykterís) [genitive "*νυκτερίδος*" (nikterídos)] meaning "bat", or combined "smooth bat", referring to the smooth fur of the species (see Lanza *et al.*, 2015: 59). (Lapsus).
2019. *Myonicteris:* Nziza, Goldstein, Cranfield, Webala, Nsengimana, Nyatanyi, Mudakikwa, Tremeau-Bravard, Byarugaba, Tumushime, Mwikarago, Gafarasi, Mazet and Gilardi, EcoHealth, 17: 155. Publication date: 6 Decembe 2019. (Lapsus).
2021. *Myonycters:* Ohimain, Curr. Opin. Pharmacol., 60: 69. Publication date: 3 August 2021. (Lapsus).
? *Myonycteris sp.*
? *Myonycteris sp. TLG-2017*

TAXONOMY:
Revised by Bergmans (1976; 1997).

Lawrence and Novick (1963) separated *Lissonycteris* from *Rousettus* because of ethological differences concerning the use of the

limbs, and the absence of echolocation in *Lissonycteris*. Juste B. *et al.* (1997) presented allozyme evidence corroborating earlier chromosome studies (Haiduk *et al.* (1980, 1981), DNA-hybridisation results (Kirsch *et al.*, 1995) and cladistic analysis (Springer *et al.*, 1995) that support the recognition of *Lissonycteris* as a distinct genus. Bergmans (1994: 79; 1997: 136), Lavrenchenko *et al.* (2004b: 136), and Simmons (2005: 325) also consider *Lissonycteris* to be a valid genus.

Included in the Myonycterini tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Included in the Myonycterina subtribe of the Epomophorini tribe by Hassanin *et al.* (2020: 5).

Currently (Simmons and Cirranello, 2023b) recognized subgenera and species of *Myonycteris*:
Myonycteris Matschie, 1899: ***angolensis*** (Bocage, 1898); ***leptodon*** K. Andersen, 1908; ***relicta*** Bergmans, 1980; ***torquata*** (Dobson, 1878).
Phygetis K. Andersen, 1912: ***brachycephala*** (Bocage, 1889).

COMMON NAMES:
Czech: límcoví kaloni, měkkosrstí kaloni. English: Collared Fruit-bats, Little Collared Fruit-bats, Dwarf Epauletted Bat, Lesser Epauletted Bat, Smooth-haired Fruit-bats, Soft-furred Fruit-bats. French: Lissonyctères, Myonyctères, Roussettes à collier. German: Halskrausen-Flughunde, Samtfell-Flughunde.

PARASITES:
Szentiványi *et al.* (2019a: Suppl.) indicated that a non-specified Ugandan *Myonycteris* was parasitized by a *Dipseliopoda* bat fly (Nycteribiidae), which was infected by Kanyawara virus (KYAV).

VIRUSES:
Goldberg *et al.* (2017: 3, 4) described a new virus from Uganda (Kanyawara virus (KYAV), genus *Ledantevirus, Rhabdoviridae*, Mononegavirales) from a new nycteribiid bat fly (genus *Dipseliopoda* Theodor, 1955, which in turn was captured on a (probably) new species of bat belonging to the genus *Myonycteris*. The bat was originally identified as *M. angolensis*, but an analysis of its mitochondrial DNA showed it to belong to an outgroup.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Equatorial Guinea, Guinea.

Subgenus *Myonycteris (Myonycteris)* Matschie, 1899

*1899. *[Xantharpyia (]Myonycteris[)]* Matschie, Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde, 61, 63 [Goto Description]. - Comments: Type species: *Cynonycteris torquata* Dobson, 1878. Originally described as subgenus of *Xantharpyia*. Matschie dated his introduction on 14 May 1899. - Etymology: Derived from the Greek "*mys*" (= mouse) and "*nycteris*" (= bat) meaning mouse-like bat.

*1912. *Rousettus (Lissonycteris)* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, xiv, 23. Publication date: 23 March 1912. - Comments: Described as a subgenus of *Rousettus* Gray, 1821. Type species: *Cynonycteris angolensis* Bocage, 1898. - Etymology: From the Greek adjective "*λισός*" (lissós), meaning "smooth" and the feminine Greek substantive "*νυκτερίς*" (nykterís) [genitive "*νυκτερίδος*" (nikterídos)] meaning "bat", or combined "smooth bat", referring to the smooth fur of the species (see Lanza *et al.*, 2015: 59).

? *Lissonycteris:* (Current Combination).

? *Myonycteris (Myonycteris):* (Current Combination).

Myonycteris (Myonycteris) angolensis (Bocage, 1898)

*1898. *Cynonycteris Angolensis* Bocage, J. Sci. mat. phys. nat., ser 2, 5 (19): 133, 138, text-fig. Publication date: June 1898. Type locality: Angola: Quibula, Cahata, north of Quanza River: Pungo Andongo [09 40 S 15 35 E, 1 200 m]. [Goto Description]. Syntype: MLZA T113 [a]: ad ♀, mounted skin (skull missing). Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Destroyed by fire in 1978; see Bergmans (1997: 37). Syntype: MLZA T113 [b]: juv, mounted skin (skull not removed). Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Destroyed by fire in 1978; see Bergmans (1997: 37). Syntype: NHMUK 1897.8.6.1: juv ♀, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Presented/Donated by: Lisbon Museum. See Andersen (1912b: 54), Bergmans (1997: 37). - Comments: From the feminine scientific Latin adjective *angolènsis,* meaning "Angolan" referring to the country where the type specimen was collected (see Lanza *et al.*, 2015: 60). - Etymology: Referring to the country where the type specimen was collected.

1920. *Rousettus (Lissonycteris) crypticola* Cabrera, Bol. r. Soc. espan. Hist. nat. , 20 (3 - 4): 106. Type locality: Equatorial Guinea: Bioko: Malabo, Basilé: San Fernando, cave of [03 44 N 08 49 E, 1 100 m]. Holotype: MNCN 53 / 20-II-25-5: ad ♀, complete skeleton. Collected by: D. Manuel M. de la Escalera; collection date: 26 July 1919; original number: 2.057. See Cabrera (1920: 107); Ibáñez and Fernández (1989: 7); Bergmans (1997: 35). Publication date: March - April 1920. Paratype: MNCN 54: juv ♂, skin only. Collected by: D. Manuel M. de la Escalera; collection date: 26 July 1919. See Ibáñez and Fernández (1989: 7); Bergmans (1997: 35).
1964. *Lyssonycteris angolensis:* Brosset, Mammalia, 28 (3): 450 (footnote). (Lapsus).
2013. *Myonycteris angolensis:* Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylogenet. Evol., 66 (1): 135. Publication date: 10 October 2012. (Name Combination).
2019. *Myonicteris angolensis:* Nziza, Goldstein, Cranfield, Webala, Nsengimana, Nyatanyi, Mudakikwa, Tremeau-Bravard, Byarugaba, Tumushime, Mwikarago, Gafarasi, Mazet and Gilardi, EcoHealth, 17: 155. Publication date: 6 December 2019. (Lapsus).
? *Lissonycteris angolensis:* (Name Combination).
? *Rousettus (Lissonycteris) angolensis:* (Name Combination).
? *Rousettus angolensis angolensis:* (Name Combination).
? *Rousettus angolensis:*

Taxonomy:



Figure 33. *Myonycteris angolensis*, Zanzibar Island.

Peterson *et al.* (1995: 48), Schaer *et al.* (2013a), and Kerbis Peterhans *et al.* (2013: 189) include *angolensis* in the genus *Myonycteris*. Simmons (2005: 325) recognizes *goliath*, *petraea*, *ruwenzorii* and *smithii* as subspecies of *angolensis*, indicating that more than one species may be present in this complex.

Known subspecies of *M. angolensis*: ***angolensis*** (Bocage, 1898); ***goliath*** Bergmans, 1997; ***petraea*** Bergmans, 1997; ***smithii*** (Thomas, 1908).

Common Names:

Afrikaans: Bocage se vrugtevlermuis, Bocage-vrugtevlermuis. Castilian (Spain): Ruseta de Angola. Chinese: 安哥拉领果蝠. Czech: kaloň měkkosrstý. English: Angolan Soft-furred Fruit-bat, Angolan Long-haired Fruit-bat, Angolan Rousette, Angolan Fruit Bat, Bocage's Fruit-bat, Long-haired Rousette, Canon Smith's Rousette. French: Lissonyctère d'Angola, Roussette d'Angola, Roussette de Bocage, Roussette à longs poils. German: Angolanischer Samtfell-Flughund, Angola-Weichfellflughund. Italian: Lissonittèride angolàna, Lissonictèride angolàna. Kiluba (DRC): Mulima. Kinande (DRC): Mulima. Malawian: Lichinji, Mleme. Portuguese: Morcego Frugivoro de Bocage.

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) [as *Lissonycteris angolensis*] in view of its wide distribution, presumed large population, its occurrence in a number of protected areas, its tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008o; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) [assessed including *L. goliath*, *L. petraea*, *L. ruwenzorii*, *L. smithii* as synonyms] (Mickleburgh *et al.*, 2008o; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004z; IUCN, 2004). 2003: LR/lc [assessed as *Rousettus angolensis*] (IUCN, 2003). 1996: LR/lc [assessed as *Rousettus angolensis*] (Baillie and Groombridge, 1996).

Regional

None known.

Major threats:

There appear to be no major threats to this species as a whole (Mickleburgh *et al.*, 2008o; IUCN, 2009).

Conservation actions:

Mickleburgh *et al.* (2008o) [in IUCN (2009)] report that this species is present in a number of protected areas.

General distribution:

Myonycteris angolensis is widely distributed at elevations ranging from sea level to 4,000 m asl, in West Africa, Central Africa and East Africa, with some distinct populations present within

southern Africa. It ranges from Senegal and The Gambia in the west, through most of West Africa to Cameroon; from here it ranges southwards into Congo, eastern Democratic Republic of the Congo and Angola, and eastwards into Central African Republic, southern Sudan, eastern and southern Democratic Republic of the Congo and Rwanda and Burundi. In East Africa it is distributed from Ethiopia in the north through Uganda, Kenya and Tanzania. In southern Africa has been recorded from northwestern Angola, central and southern Cameroon, Central African Republic, central Congo, Equatorial Guinea (Bioko, Mbini), Gabon, eastern Nigeria, and northwestern and southwestern Democratic Republic of the Congo.

Native: Angola (Crawford-Cabral, 1989; Bergmans, 1997; Monadjem *et al.*, 2010d: 554); Burkina Faso (Kangoyé *et al.*, 2015a: 605); Burundi; Cameroon; Central African Republic; Congo (Bates *et al.*, 2013: 333); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 554); Côte d'Ivoire; Equatorial Guinea; Ethiopia; Gambia; Ghana; Guinea (Denys *et al.*, 2013: 281); Guinea-Bissau (Veiga-Ferreira, 1948; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 35); Kenya; Liberia; Mozambique; Nigeria; Rwanda; Senegal; Sierra Leone; Sudan; Tanzania (Stanley and Goodman, 2011: 40); Togo; Uganda; Zambia (Ansell, 1967; Ansell, 1974; Monadjem *et al.*, 2010d: 554); Zimbabwe.

Presence uncertain: Benin; Gabon.

General description of external morphology:

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 8 specimens: Fa: 77.70 ± 1.634 mm, mass: 78.1 ± 7.31 g, wing loading: 17.7 ± 1.52 N/m^2, aspect ratio: 15.9 ± 0.46.

An albino specimen - of "*Lissonycteris angolensis*?" - was reported from a cave in Uganda by Neal (1971) and Lucati and López-Baucells (2016: Suppl.).

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on the dorsal side of the proximal and distal arm and forearm and on the ventral side of the proximal arm. Additionally, it is moderate on the ventral side of the distal arm and forearm, on the dorsal side of the propatagium and both the dorsal and ventral sides of the plagiopatagium.

Dental formula:

Two of the nine skulls examined by Esquivel *et al.* (2021: Suppl.) had either more or less teeth than normal.

Detailed morphology:

Hairs

Chernova (2002) studied the structure of the cuticle of guard hairs of several Pteropodid bats and found that the structure of these hairs in *angolensis* was nonring-forming as in *Epomophorus wahlbergi* as oposed to ring-forming as in *Myonycteris angolensis* [as *Rousettus*].

Functional morphology:

Mainoya and Howell (1979: 164) found no glandular cells in the neck skin patch of male "*Rousettus angolensis*", and concluded that this patch serves as a visual cue during social encounters.

Amador *et al.* (2019: Suppl.) [referring to Monadjem *et al.* (2011)] mention a wing loading value of 17.7 Pa, aspect ratio 5.9 for a wingspan of 50 cm and a wing area of 430 cm^2 and a body mass of 78 g.

Molecular Biology:

Karyotype

Haiduk *et al.* (1980, 1981: 223) reported 2*n* = 36, FN = 66, BA = 32, and a subtelocentric X chromosome. Denys *et al.* (2013: 281) also reported 2*n* = 36 and Fna = 66, but with two medium-sized submetacentric X chromosomes.

Habitat:

Vogeler and Tschapka (2021: 1067) indicate that *M. angolensis* occurs very localised in the rain forest zone, more specifically in rocky habitats, and as such, might be more affected by human activities.

In their study on the influence of African cocoa farms, Ferreira *et al.* (2023: 1) found that this species was primarily present in low shade farms.

Habits:

Food is brought to the mouth with their hindfeet, not with their thumbs nor second fingers (Happold and Happold, 2023: 70).

Roost:

Weber and Fahr (2006: 4) indicate that [as *Lissonycteris angolensis*] largely or exclusively depends on the availability of caves as day roosts.

POPULATION:
Structure and Density
This species can be common in some localities (Mickleburgh *et al.*, 2008o; IUCN, 2009).

Trend
2008: Decreasing (Mickleburgh *et al.*, 2008o; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Stanley and Goodman (2011: 38) reported pregnant females collected in the West and East Usambara Mountains (Tanzania) on 1 July 1991, and between 25 July and 5 August 1992. They also found six pregnant females in the South Pare Mountains between 18 and 23 July 1993, and on 25 August 1994.

In Sierra Leone, Weber *et al.* (2019: 20) captured two lactating females on 25 March.

PARASITES:
BACTERIA
Bartonellae
McKee *et al.* (2021: Suppl.) reported a *Bartonella* sp. from Nigerian "*Lissonycteris angolensis*".

HAEMOSPORIDIA
Adam (1973: 3) reported *Plasmodium voltaicum* Van Der Kaay, 1964 (Haemosporida) from the Republic of Congo. He also mentioned that this parasite can be detected in the blood of the bats six to eight days after infection and then persists chronically for an persistent period. Schaer *et al.* (2013a: 17416) recorded the same parasite in three out of three investigated bats, and Perkins and Schaer (2016: Suppl.) mention it furthermore from Ghana and Guinea. Arnuphapprasert *et al.* (2020: Suppl.) reported on GenBank data from a *Plasmodium* sp. (M_ang_G1_1) from Guinea.

Adam (1973: 4) also reported on a [as *Lissonycteris angolensis*] specimen that was transported from the Republic of Congo to Paris and that was infected by *Hepatocystis perronae*.

ACARI
Teinocoptidae
Fain (1967: 363) described *Teinocoptes ituriensis* from "*Rousettus (Lissonycteris) angolensis*" from Saliboko, Lake Albert, Ituri, Congo.

Trombiculidae
Trombigastia (Trombigastia) rousetti was described by Vercammen-Grandjean and Fain (1958: 16) from "*Rousettus (Lissonycteris) angolensis*" from Nyakibanda, Rwanda (Stekolnikov, 2018a: 120). They also described (p. 18) *Trombigastia (Trombigastia) hirsuta* from bats from Katana, N of Bukavu, DRC (Stekolnikov, 2018a: 118). Fain (1959b: 346) mentions *Nycteridocoptes macrophallus* Fain, 1958 from "*R. angolensis*" from Mulungu, DRC. Stekolnikov (2018a: 130, 152) also reported *Chiroptella adami* Taufflieb, 1972 on "*Lissonycteris angolensis smithii*" from Senegal, and *Microtrombicula hexasternalis* Vercammen-Grandjean, 1965 on bats from Bukavu, DRC.

DIPTERA
Nycteribiidae
Eucampsipoda africanum Theodor 1955, widely distributed over the Ethiopian region and recorded from localities in Senegal to the Sudan and southwards mirroring the hosts distribution (Haeselbarth *et al.*, 1966: 115). *Dipseliopoda biannulate* (Oldroyd 1953) distributed over the tropical parts of Africa and recorded from localities in Nigeria, Cameroon, the Congo and the Sudan and Kenya (Haeselbarth *et al.*, 1966: 116). *Cyclopodia greeffi* Karsch 1884 found in a belt across central Africa, between lat. 10° south and north, while in West Africa it occurs further north up to lat. 20° (Haeselbarth *et al.*, 1966: 117).

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) [as "*Lyssonycteris angolensis*"] tested between 1986 to 1999, for antibody to SARS-CoV in sera in 16 individuals from Oriental Province, DRC, one was tested positive (1/16, 6.3 %) and two individuals from Bandundu Province, DRC, none tested positive (0/2) (1/18, 5.6 %).

None of the nine Kenyan specimens tested by Tao *et al.* (2017: Suppl.) were positive for CoV, whereas three out of 42 (7.1 %) of the Guinean specimens tested by Lacroix *et al.* (2020: 7) were positive.

Nziza *et al.* (2019: 157) found a new Coronavirus in a rectal swap of a "*Rousettus angolensis*" from the Nyungwe National Park, Rwanda.

Meyer *et al.* (2024: 4) reported that "*Lissonycteris angolensis*" specimens from Ghana were infected by CoV 2b viruses.

Flaviviridae
Raulino *et al.* (2022: 256) found antibodies against Dengue virus in "*Lissonycteris angolensis*".

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 3 specimens they examined from the Democratic Republic of the Congo tested

positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

Polyomaviridae
Polyomavirus
Conrardy *et al.* (2014: 259) tested 11 specimens from the Kakamega cave (Kenya) and found one of them to test positive for this virus. This was also the case for the single specimen from Kisumu.

Togaviridae
In their study on Senegalese fruit bats, de Souza *et al.* (2024: 1491) found one *"Lissonycteris angolensis*" testing positive for chikungunya virus (CHIKV).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

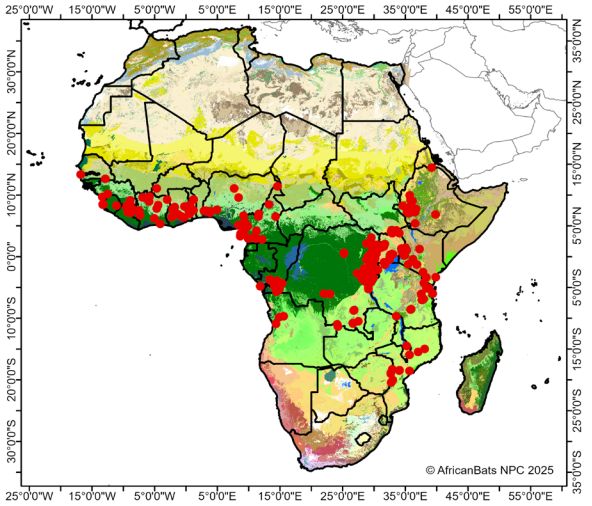

Figure 34. Distribution of *Myonycteris (Myonycteris) angolensis*.

Myonycteris (Myonycteris) angolensis angolensis (Bocage, 1898)

*1898. *Cynonycteris Angolensis* Bocage, J. Sci. mat. phys. nat., ser 2, 5 (19): 133, 138, text-fig. Publication date: June 1898. Type locality: Angola: Quibula, Cahata, north of Quanza River: Pungo Andongo [09 40 S 15 35 E, 1 200 m]. [Goto Description]. Syntype: MLZA T113 [a]: ad ♀, mounted skin (skull missing). Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Destroyed by fire in 1978; see Bergmans (1997: 37). Syntype: MLZA T113 [b]: juv, mounted skin (skull not removed). Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Destroyed by fire in 1978; see Bergmans (1997: 37). Syntype: NHMUK 1897.8.6.1: juv ♀, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta; collection date: 1891. Presented/Donated by: Lisbon Museum. See Andersen (1912b: 54), Bergmans (1997: 37). - Comments: From the feminine scientific Latin adjective *angolènsis,* meaning "Angolan" referring to the country where the type specimen was collected (see Lanza *et al.*, 2015: 60). - Etymology: Referring to the country where the type specimen was collected.
2015. *Myonycteris angolensis angolensis:* ACR. (Name Combination).
? *Lissonycteris angolensis angolensis:* (Name Combination).

GENERAL DISTRIBUTION:
Recorded from northwestern Angola, central and southern Cameroon, Central African Republic, central Congo, Equatorial Guinea [Bioko, Mbini], Gabon, eastern Nigeria, and northwestern and southwestern Democratic Republic of the Congo.

PARASITES:
Trombiculidae
Zajkowska *et al.* (2018: 118) mentioned *Microtrombicula hexasternalis* Vercammen-Grandjean, 1965 from a Congolese (DRC) "*Lissonycteris angolensis angolensis*".

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Cameroon, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Kenya, Tanzania, Uganda.

Myonycteris (Myonycteris) angolensis goliath (Bergmans, 1997)

*1997. *Lissonycteris angolensis goliath* Bergmans, Beaufortia, 47 (2): 46. Publication date: 20 June 1997. Type locality: Zimbabwe: Inyanga: Gleneagles (Estate) [18 17 S 32 54 E]. [Goto Description]. Holotype: NHMZ 59831: ad ♀, skin and skull. Collected by: Michael P. Stuart Irving *et al.*; collection date: 19 March 1970; original number: T1854. 8 paratypes; see Bergmans (1997: 46). Paratype: NHMZ 59826: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: NHMZ 59827: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: NHMZ 59828: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: NHMZ 59829: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: NHMZ 59832: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: NHMZ 59833: Collected by: Michael P. Stuart Irwin; collection date: 19 March 1970. Paratype: ZMA MAM.24710: ad ♀, skin and skull. Collected by: S. Irwin; collection date: 19 March 1970; original number: T1853. Paratype: ZMA MAM.24719: ad ♀, skin and skull. Collected by: S. Irwin; collection date: 19 March 1970; original number: T1853. Locality: Gleneagles (18 15 - 18 30 S, 32 45 - 33 0 E, 6000ft), see Bergmans (2011: 841).

The ZMA catalog mentions two numbers: 24719.a (skull + loose bones) and 24719.b (study skin). - Etymology: Referring to the biblical giant with the same name.

2001. *Lissonycteris goliath:* Cotterill, Durban Mus. Novit., 26: 53. (Name Combination, Current Combination).
2015. *Myonycteris angolensis goliath:* ACR. (Name Combination).

TAXONOMY:
Bergmans (1997) showed that craniological characters also distinguish *Lissonycteris* from *Rousettus*, and assigned the specimens from Zimbabwe to a new subspecies (*L. a. goliath*). Liberally applying the evolutionary species concept, which holds that any diagnosable or allopatric population is a valid species, Cotterill (2001e) elevated *goliath* to full species rank. Bergmans (2011: 841) still considers it a subspecies, at most.

COMMON NAMES:
English: Harrison's fruit bat. French: Lissonyctère goliath. German: Harrisons Samtfell-Flughund.

CONSERVATION STATUS:
Global Justification

Assessment History
Global
VU A3c+4c ver 3.1 (2001) (IUCN, 2004; Mickleburgh *et al.*, 2004ar); LC ver 3.1 (2001) included as a synonym of *L. angolensis* (Mickleburgh *et al.*, 2008o; IUCN, 2009).

MAJOR THREATS:
May be threatened by loss of habitat resulting from logging operations, and disturbance of cave roosting sites. It is possible that some populations of this species are threatened by over harvesting for subsistence food (Mickleburgh *et al.*, 2008o; IUCN, 2009).

CONSERVATION ACTIONS:
There is a need to protect the habitat (Mickleburgh *et al.*, 2008o; IUCN, 2009).

GENERAL DISTRIBUTION:
Lissonycteris goliath is known from four localities in south-east Africa (the border area of Mozambique and Zambia) between sea level and 1,800 m asl.

Native: Mozambique (Monadjem *et al.*, 2010d: 554; Monadjem *et al.*, 2010c: 376); Zambia; Zimbabwe (Monadjem *et al.*, 2010d: 554).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Malawi, Mozambique, Tanzania, Zambia, Zimbabwe.

Myonycteris (Myonycteris) angolensis petraea (Bergmans, 1997)

*1997. *Lissonycteris angolensis petraea* Bergmans, Beaufortia, 47 (2): 44. Publication date: 20 June 1997. Type locality: Ethiopia: Ilubabor province: 10 km from Agaro: Jimma, road to [07 50 N 36 38 E]. [Goto Description]. Holotype: MNHN ZM-MO-1972-482a: ad ♂, skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4017. 10 paratypes; see Bergmans (1997). Paratype: MNHN ZM-MO-1972-482b: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4018. Paratype: MNHN ZM-MO-1972-482c: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4019. Paratype: MNHN ZM-MO-1972-482d: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4024. Paratype: MNHN ZM-MO-1972-482e: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4027. Paratype: MNHN ZM-MO-1972-482f: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4032. Paratype: MNHN ZM-MO-1972-482g: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4044. Paratype: MNHN ZM-MO-1972-482h: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4045. Paratype: MNHN ZM-MO-1972-482i: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4046. Paratype: MNHN ZM-MO-1972-482j: skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10 - 13 June 1968; original number: 4051. Paratype: ZMA MAM.25180: ad ♂, skull and alcoholic. Collected by: Jean Pierre Dorst *et al.*; collection date: 10-13 June 1968. Locality: 10 km from Agaro (07 50 N 36 38 E), at the road to Jimma (07 39 N 36 47 E), Ethiopia, 1650 m (see: Bergmans, 2011: 842).
2001. *Lissonycteris petraea:* Cotterill, Durban Mus. Novit., 26: 53. (Name Combination).
2015. *Myonycteris angolensis petraea:* ACR. (Name Combination).

TAXONOMY:
Simmons (2005: 325) states that the status of *petraea* remains unclear but recognized it as a subspecies of *angolensis*.

COMMON NAMES:
English: Petra fruit bat. French: Lissonyctère d'Ethiopie. German: Äthiopischer Samtfell-Flughund.

CONSERVATION STATUS:
Assessment History
Global
VU A4c ver 3.1 (2001) (IUCN, 2004; Mickleburgh *et al.*, 2004ab); LC ver 3.1 (2001) included as a synonym of *L. angolensis* (Mickleburgh *et al.*, 2008o; IUCN, 2009).

CONSERVATION ACTIONS:
There is a need to protect the habitat (Mickleburgh *et al.*, 2008o; IUCN, 2009).

GENERAL DISTRIBUTION:
Found only in Ethiopia, where it has been recorded from six localities between 1,190 and 2,600 m asl.

Native: Ethiopia.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

Myonycteris (Myonycteris) angolensis ruwenzorii (Eisentraut, 1965)

*1965. *Rousettus angolensis ruwenzorii* Eisentraut, Bonn. zool. Beitr., 16 (1/2): 3, fig 1. Type locality: Uganda: Ruwenzori East. [Goto Description]. Holotype: NHMUK 1906.12.4.1: ♂. - Etymology: Referring to the country where the type specimen was collected.
2015. *Myonycteris angolensis ruwenzorii:* ACR. (Name Combination, Current Combination).
? *Lissonycteris angolensis ruwenzorii:* (Name Combination).

COMMON NAMES:
English: Ruwenzori Long-haired rousette. French: Lissonyctère du Ruwenzori, Roussette à long poils du Ruwenzori. German: Ruwenzori-Langhaarflughund.

GENERAL DISTRIBUTION:
M. a. ruwenzorii has been recorded from Ethiopia, Kenya, Mozambique, Rwanda, southern Sudan, Tanzania, Uganda, northeastern and southeastern Democratic Republic of the Congo, Zambia and Zimbabwe.

PARASITES:
DIPTERA
Nycteribiidae
Bennett *et al.* (2020b: 3) studied viruses present in nycteribiid bat flies infesting Ugandan "*Lissonycteris angolensis ruwenzorii*", which according to their GenBank numbers belonged to the genus *Dipseliopoda* Theodor, 1955.

VIRUSES:
Reoviridae
Orthoreovirus
Bennett and Goldberg (2020: 2) reported the first African bat Pteropine orthoreovirus (PRV), which they provisionally named Kasama virus (PRV16K).

Rhabdoviridae
Ledantevirus
Demos *et al.* (2019c: 9) found Kanyawara ledantevirus (KYAV) genome fragments in the saliva of bat-fly infected bats, which might point to an occasional infection of the bats as the virus is generally insect associated.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burkina Faso, Burundi, Congo (Democratic Republic of the), Ethiopia, Kenya, Rwanda, South Sudan, Tanzania, Uganda.

Myonycteris (Myonycteris) angolensis smithii (Thomas, 1908)

*1908. *Rousettus smithii* Thomas, Ann. Mag. nat. Hist., ser 8, 2 (10): 375. Publication date: 1 October 1908. Type locality: Sierra Leone: Freetown [08 30 N 13 15 W]. [Goto Description]. Holotype: NHMUK 1908.9.11.1: sad ♀. Collected by: Canon F.C. Smith. Presented/Donated by: Canon F.C. Smith. - Comments: Grubb *et al.* (1998: 67) mention that the type locality is almost certainly Freetown, according to Rosevear (1965: 84).
1974. *Lissonycteris angolensis smithi:* Bergmans, Bellier and Vissault, Rev. Zool. afr., 88 (1): 38. (Name Combination).
2012. *Myonycteris angolensis smithii:* Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylogenet. Evol., suppl 3. (Name Combination).
? *Lissonycteris angolensis smithii:* (Name Combination).
? *Lissonycteris smithii:* (Name Combination).
? *Rousettus angolensis smithi:* (Name Combination).
? *Rousettus smithi:* (Name Combination, Alternate Spelling).

TAXONOMY:
Mentioned as *smithii* by Allen (1939a: 63), Meester *et al.* (1986: 30), Koopman (1993a), Bergmans (1997: 33), Grubb *et al.* (1998: 67), Kock *et al.* (2002b: 79), but as *smithi* by Peterson *et al.* (1995: 48), who also consider it a valid species in the genus *Myonycteris*. Kock *et al.* (2002b: 79) include it as subspecies in *angolensis*, due to clinal differentiation (as does Bergmans, 1997: 33). Simmons (2005: 325)

follows Kock *et al.* (2002b), who support Bergmans (1997), in treating *smithii* as a subspecies of *angolensis*.

COMMON NAMES:
English: Smith's fruit bat. French: Lissonyctère de Simth. German: Smiths Samtfell-Flughund.

CONSERVATION STATUS:
Assessment History
Global
LC ver 3.1 (2001) (IUCN, 2004; Mickleburgh *et al.*, 2004u); LC ver 3.1 (2001) included as a synonym of *L. angolensis* (Mickleburgh *et al.*, 2008o; IUCN, 2009).

GENERAL DISTRIBUTION:
Distributed in the lowlands of western Africa, where its distribution follows the savanna and forest zone, it is found up to 1,400 m asl on Mount Nimba.

Native: Bioko; Burkina Faso; Ghana; Guinea (Decher *et al.*, 2016: 262); Guinea Bissau; Côte d'Ivoire; Liberia; Nigeria; Sierra Leone; Senegal; Togo.

HABITAT:
Monadjem *et al.* (2016y: 364) indicate that the (sub)species is restricted to montane forests in West Africa.

MIGRATION:
Based on different capture numbers during the dry and wet seasons in Ghana, Decher *et al.* (2021: 268) indicate that this might suggest some sort of migration and/or sexual segregation as was already reported by Wolton *et al.* (1982) as Mount Nimba.

PARASITES:
ACARI
Trombiculidae
Ševčík *et al.* (2020: 9) reported the presence of *Chiroptella adami* Taufflieb, 1972.

DIPTERA
Nycteribiidae
Decher *et al.* (2021: 268) collected one *M. a. smithii* which was parasitized by a *Dipseliopoda biannulata* (Oldroyd, 1953).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burkina Faso, Cameroon, Congo, Côte d'Ivoire, Equatorial Guinea, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone, The Gambia, Togo.

Myonycteris (Myonycteris) leptodon K. Andersen, 1908

*1908.	*Myonycteris leptodon* K. Andersen, Ann. Mag. nat. Hist., ser 8, 2 (11): 450. Publication date: 1 November 1908. Type locality: Sierra Leone: "Sierra Leone". [Goto Description]. Holotype: NHMUK 1891.2.13.1: ad ♂. Collected by: J. Hickman Esq. Collection date: prior to 1891.
1971.	*M[yonycteris (Myonycteris)] t[orquata] leptodon:* Hayman and Hill, in: Meester and Setzer, The mammals of Africa. Order Chiroptera. (Name Combination).
1971.	*Myonycteris torquata leptodon:* Jones, J. Mamm., 52 (1): 129. Publication date: February 1971. (Name Combination).
?	*Myonycteris (Myonycteris) leptodon:* (Name Combination).
?	*Myonycteris (Myonycteris) torquata leptodon:* (Name Combination).

TAXONOMY:
Based on the study of cytochrome *b* sequences, Nesi *et al.* (2012) concluded that West African *Myonycteris torquata* (Dobson, 1878) differed considerably from those from Central African.

COMMON NAMES:
German: Sierra-Leone Halskrausen-Flughund

ETYMOLOGY OF COMMON NAME:
From the Greek λεπτός meaning slender or narrow and όδους meaning tooth.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Monadjem, 2016c; 2020a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2016c).
2014: LC ver 3.1 (2001) (Monadjem, 2020a).

MAJOR THREATS:
It may be locally threatened by habitat loss and degradation, often resulting from conversion of land to agricultural use or the harvesting of timber and firewood (Monadjem, 2016c; 2020a).

CONSERVATION ACTIONS:
This species has been recorded within a number of protected areas and also survives outside of such areas (Monadjem, 2016c; 2020a).

GENERAL DISTRIBUTION:
Nesi *et al.* (2012) indicated that the *M. torquata* specimens from West Africa were considerably different from those from the remaining part of the continent, but they did not include specimens from the area between the Dahomey Gap and the Niger delta. Herkt *et al.* (2017: Appendix S9) were not able to determine a preferential habitat type in that area for either *M. torquata* or *M. leptodon*. They were, however, able to determine that the Dahomey Gap was a pronounced break in the habitat suitability predictions of both species. Therefore, they considered the specimens on the western side of the Gap to belong to *leptodon* and on the eastern side to *torquata*.

Native: Native: Côte d'Ivoire (Heim de Balsac, 1934b: 24); Ghana (Decher and Fahr, 2007: 12); Guinea (Simmons, 2005: 328; Denys *et al.*, 2013: 281; Decher *et al.*, 2016: 263); Liberia (Monadjem and Fahr, 2007: 50); Sierra Leone (Simmons, 2005: 328); Togo.

HABITAT:
In the Mount Nimba area, Monadjem *et al.* (2016y: 364) recorded this species from a wide range of forested habitats on both Liberian and Guinean sides, between 450 m and 1,350 m.

POPULATION:
Structure and Density
It is a locally abundant species that may constitute the most commonly captured fruit bat at certain localities such as at Tai National Park in Ivory Coast, and sites in Liberia (Monadjem and Fahr, 2007).

Trend
2016: Unknown (Monadjem, 2016c). 2014: Unknown (Monadjem, 2020a).

REPRODUCTION AND ONTOGENY:
Weber *et al.* (2019: 20) captured one lactating female on 7 April in Sierra Leone.

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2013a: "2") report the presence of hemosporidian parasites of the genus *Hepatocystis* in 11 out of 63 investigated bats. Arnuphapprasert *et al.* (2020: Suppl.) reported on the GenBank data for these parasites on bats from Liberia and Côte d'Ivoire.

ACARI
Myobiidae
Bochkov and Fain (2003: 13) mentioned *Binuncus (Binuncus) myonycteris* Uchikawa, 1986 from "*Myonycteris torquata*"..

VIRUSES:
Filoviridae - Filo viruses
Ebolavirus
Nesi *et al.* (2012: 126) suggest that the high nucleotide distance between Ebola virus Côte d'Ivoire and Ebola virus Zaire can be correlated with the Plio/Pleistocene divergence between their putative reservoir host species, i.e., *Myonycteris leptodon* and *Myonycteris torquata*, respectively.

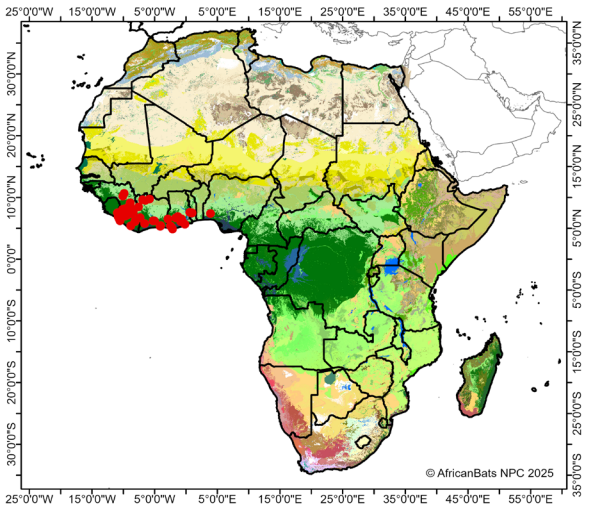

Figure 35. Distribution of *Myonycteris (Myonycteris) leptodon*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Togo.

Myonycteris (Myonycteris) relicta Bergmans, 1980

*1980. *Myonycteris relicta* Bergmans, Zool. Meded. RMNH, Leiden, 55 (14): 171, 173, figs 1 - 10. Publication date: 4 March 1980. Type locality: Kenya: Coast province: Kwale district: Shimba Hills, Lukore area: Mukanda River [ca. 04 13 S 39 25 E]. [Goto Description]. Holotype: RMNH MAM.27909: ad ♂. Collected by: Robert N. Kyongo; collection date: 30 July 1978; original number: RK 594. See Bergmans (1997: 56).
The RMNH catalog mentions two numbers: 27909.a (skull + loose bones) and 27909.b (skin). Paratype: ZMB 54936: ad ♂, skull and alcoholic. Collection date: January 1900. See Turni and Kock (2008). Paratype: ZMB 54937: ad ♀, skull and alcoholic. Collection date: January 1900. See Turni and Kock (2008). (Current Combination).
? *Myonycteris (Myonycteris) relicta:* (Name Combination).

TAXONOMY:
Bronner *et al.* (2003) state that *Myonycteris relicta* was described by Bergmans (1980) based on the re-identification of a specimen from the Nguru Mountains, and two specimens from the Usambara Mountains, in Tanzania. Peterson *et al.* (1995: 48) regarded *M. relicta* as a species of *Rousettus*, in contrast to Koopman (1982), Corbet and Hill (1980), Koopman (1993a: 143), Bergmans (1997) and Simmons (2005: 328) who retained this taxon in *Myonycteris*.

COMMON NAMES:
Chinese: 孤领果蝠. Czech: kaloň východoafrický. English: East African Collared Fruit-bat, Relict Collared Fruit-bat, East African Little Collared Fruit Bat, Bergmans's Small Fruit Bat, Bergmans's Collared Fruit Bat. French: Myonyctère d'Afrique orientale, Chauve-souris frugivore à collier d'Afrique orientale, Roussette du Kenya. German: Reliktärer Halskrausen-Flughund.

ETYMOLOGY OF COMMON NAME:
First described by Wim Bergmans after examining and reclassifying specimens previously ascribed to *Rousettus* (*Lissonycteris*) *angolensis* and following his discovery of the type specimen from the Mukonda River in Kenya (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Although lowland forests in Zimbabwe, Mozambique, Kenya and Tanzania are declining due to logging, fuelwood extraction and conversion to agriculture, it is impossible to provide evidence that the decline triggers levels for any Threatened or Near Threatened category (Taylor, 2016e). Further sampling (such as the survey of Monadjem *et al.* (2010c) in Mozambique) may reveal more populations of this species indicating that the species is not as rare as previously thought (Taylor, 2016e).

Assessment History
Global
2016: LC ver 3.1 (2001) (Taylor, 2016e). 2008: VU A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2008ao; IUCN, 2009). 2004: VU A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004bd; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996). 1994: VU (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
Although the natural history of this species is little known, there is considerable ongoing habitat loss within the species range (through logging, harvesting of firewood and conversion of land to agricultural use) (Mickleburgh *et al.*, 2008ao; IUCN, 2009; Taylor, 2016e).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ao) [in IUCN (2009)] report that there appear to be no direct conservation measures in place for this species. In Zimbabwe it has been recorded from the Haroni and Rusitu protected areas, but the forest has still been declining at these localities over the past three decades. Further surveys are needed to better determine the full extent of this species range. There is a need to conserve remaining lowland forest throughout much of East Africa.

GENERAL DISTRIBUTION:
Bergmans (1997) reports that the species is known from the Shimba Hills in southeast Kenya, the Usambara and Nguru Mountains in Tanzania. Several other unpublished localities in Tanzania and more recently from eastern Zimbabwe and Mozambique.

A female specimen captured in Haroni Forest (Zimbabwe) in 1973 and originally identified incorrectly as *Rousettus* (= *Lissonycteris*) *angolensis*, was re-identified as *Myonycteris relicta* (Cotterill, 1995; Bergmans, 1997).

Native: Kenya (Simmons, 2005: 328); Mozambique (Simmons, 2005: 328;: 554; Monadjem *et al.*, 2010c: 376); Tanzania (Simmons, 2005: 328; Stanley and Goodman, 2011: 40); Zimbabwe (Simmons, 2005: 328; Monadjem *et al.*, 2010d: 554).

HABITAT:
All localities known with some accuracy are in East African Zanzibar-Inhambane coastal mosaic: forest patches or in undifferentiated Afromontane vegetation bordering on East African Zanzibar-Inhambane coastal mosaic (Bergmans, 1997). The holotype specimen was caught over the Mukanda River, bordered by big thorn trees and fig trees, in the Shimba Hills, which are covered with a mosaic of open country and forest patches (Bergmans, 1997).

POPULATION:
Structure and Density
There is little known about the population of this species. Nearly all collections have been of single specimens caught in mist nets (Mickleburgh *et al.*, 2008ao; IUCN, 2009; Taylor, 2016e).

Trend
2016: Decreasing (Taylor, 2016e). 2008: Decreasing (Mickleburgh *et al.*, 2008ao; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Malawi, Mozambique, Tanzania, Zimbabwe.

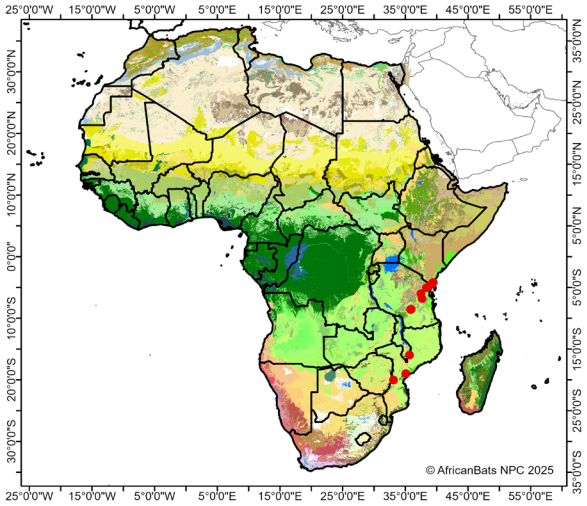

Figure 36. Distribution of *Myonycteris (Myonycteris) relicta*.

Myonycteris (Myonycteris) torquata (Dobson, 1878)

1871. *Cynopterus collaris* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 123. Publication date: 14 January 1871. Type locality: Angola: "Angola". [Goto Description]. Holotype: NHMUK 1843.9.27.2. - Comments: Not of Kolenati, 1860 [=*Rousettus leachi*] not of Geoffroy. Cat. Monkeys, Lemurs, Fruit-eating Bats Brit. Mus., p. 123. Type locality "W Africa, Lower Congo; Angola" see Allen (1939a: 58). Andersen (1912b: 581) mentions "The type was obtained 'near Congo' by one Mr. Currer, from whom it came into the hands of Dr. (afterwards Sir) J. Richardson, who presented it to the British Museum. Gray's statement that the specimen is 'young' is incorrect; his quotation of 'Gray, List Mamm. B. M. (1843),' where the specimen is stated to have been mentioned under the name *Xantharpyia collaris*, does not refer to the printed text of that book, but to a hand-written addition by Gray in his own copy of the book.".

*1878. *Cynonycteris torquata* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, xxxvii, 71, 76, pl 5, fig 1. Publication date: 15 June 1878. Type locality: Angola: N Angola: Lower Cuanza region: Golungo Alto. [Goto Description]. Lectotype: NHMUK 1866.1.20.4: ad ♂, skull and alcoholic. Collected by: Friedrich Martin Josef Welwitsch; collection date: 1853 - 1860. See Bergmans (1997: 49). - Comments: Grubb *et al.* (1998: 68) indicate "definite restriction of the type locality is not possible at present (Bergmans, 1976: 210 - 211)". Bergmans (1997: 49) indicates that Bergmans (1976) restricted the type locality to "Lower Cuanza Region" and the area was restricted to Golungo Alto by Crawford-Cabral (1989).

2014. *Myonycteris tarquata:* Ndara R., IJISR, 12 (1): 253. Publication date: November 2014. (Lapsus).

2021. *Myonycters torquuata:* Ohimain, Curr. Opin. Pharmacol., 60: 69. Publication date: 3 August 2021. (Lapsus).

2023. *Myonycteris torcata:* Vidovszky, Kapitány, Gellért, Harrach, Görföl, Boldogh, Kohl, Wibbelt, Mühldorfer, Kemenesi, Gembu, Hassanin, Tu, Estók, Horváth and Kaján, Vet. Res. Commun., xxx (x): Suppl. Publication date: 31 March 2023. (Lapsus).

? *Myonycteris (Myonycteris) torquata:* (Name Combination).

? *Myonycteris torquata:* (Name Combination).

? *Myopterus torquata:* (Name Combination, Lapsus).

TAXONOMY:
See Hayman and Hill (1971), Peterson *et al.* (1995), Bergmans (1976; 1997) and Simmons (2005: 328). Subspecies follow Koopman (1994), but see Bergmans (1997).

In their study on cytochrome *b* sequences, Nesi *et al.* (2012) concluded that West African *Myonycteris torquata* (Dobson, 1878) differed considerably from the specimens from Central African, which resulted in the recognition of *M. leptodon* as a separate species.

COMMON NAMES:
Castilian (Spain): Zorra Voladora de Collar. Czech: kaloň límcový. English: Little Collared Fruit-bat, Little Collared Fruit Bat. French: Petit Myonyctère, Petite Chauve-souris frugivore à collier. German: Kleiner Halskrausen-Flughund, Kleiner Halsbandflughund.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bb; IUCN, 2009; Bakwo Fils and Kaleme, 2016b). But due to the taxonomic changes, it is possible that in the near future, this listing might need to be re-considered in light of results of inventories within the range of the species (Bakwo Fils and Kaleme, 2016b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Bakwo Fils and Kaleme, 2016b). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bb; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bz; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There are generally no major threats to this species. It is threatened in parts of its range by severe habitat loss, presumably through general logging operations and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008bb; IUCN, 2009; Bakwo Fils and Kaleme, 2016b).

CONSERVATION ACTIONS:
The species has been recorded in the Dja Biosphere Reserve in Cameroon (Bakwo Fils, 2009) and it seems probable that it is present Central African protected areas (Mickleburgh *et al.*, 2008bb). No direct conservation measures are currently needed for this species as a whole (Mickleburgh *et al.*, 2008bb; Bakwo Fils and Kaleme, 2016b). The reduction of the home range may also influence its conservation status. Even within central Africa, the occurrence is reduced to some suitable habitats that are mostly found in protected areas.

Monitoring of populations is important, although it will be challenging in this area. Apart from larger mammals and some taxa such as birds that are mostly used in monitoring programs, bats are less considered in monitoring strategies and even for funding of some activities (Bakwo Fils and Kaleme, 2016b). Monitoring populations is critical to provide baseline information on population trends. In many countries, only tourist appealing mammals or keystone species are more on top for conservation efforts forgetting the ecosystem services of the forgotten ones.

Bakwo Fils and Kaleme (2016b) also recommend some studies such as reproduction and ecology of the species in order to provide information on how populations can grow or decline in a time span.

GENERAL DISTRIBUTION:
Myonycteris torquata used to be considered widespread in West Africa and Central Africa, ranging into western East Africa, but since the recognition of *M. leptodon* as a separate species, its distribution range starts from Nigeria and Cameroon into Equatorial Guinea (Rio Muni and Bioko), Gabon, Congo, Central African Republic, Democratic Republic of the Congo, Angola, extreme northwestern Zambia, Rwanda, Uganda and possibly southern Sudan. It is a lowland species found up to 800 m asl.

Nesi *et al.* (2012) did not include specimens from the area between the Dahomey Gap and the Niger delta, and Herkt *et al.* (2017: Appendix S9) were not able to determine a preferential habitat type in that area for either *M. torquata* or *M. leptodon*. However, they were able to determine that the Dahomey Gap was a pronounced break in the habitat suitability predictions of both species. Therefore, they considered the specimens on the western side of the Gap to belong to *leptodon* and on the eastern side to *torquata*.

Native: Angola (Bergmans, 1997; Simmons, 2005: 328; Monadjem *et al.*, 2010d: 554); Cameroon; Central African Republic (Morvan *et al.*, 1999: 1195); Congo (King and Dallimer, 2010: 65); Congo (The Democratic Republic of the) (Bergmans, 1997; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 554); Ethiopia (Lavrenchenko *et al.*, 2004b: 136); Equatorial Guinea (Bioko) (Fahr and Ebigbo, 2003: 128; Simmons, 2005: 328); Gabon; Nigeria (Capo-Chichi *et al.*, 2004: 161; Tanshi *et al.*, 2022a: 317); Rwanda; Uganda (Kityo and Kerbis, 1996: 59; Simmons, 2005: 328); Zambia (Bergmans, 1997; Simmons, 2005: 328; Monadjem *et al.*, 2010d: 554).

Presence uncertain: Sudan.

MOLECULAR BIOLOGY:
Karyotype
Haiduk *et al.* (1980; 1981: 223) reported 2*n* = 36, FN = 66, BA = 32, a subtelocentric X chromosome and an acrocentric Y chromosome for specimens from Cameroon. Identical karyotypes were reported by Primus *et al.* (2006) for specimens from Gabon.

DIET:
In Cameroon, Grünmeier (1993: 35) found the following pollen in the gut and faeces: *Mucuna flagellipes* Hook. f. (Fabaceae), *Anthocleista* sp. (Gentianaceae), *Kigelia africana* (Lam.) Benth. (Bignoniaceae), *Elaeis* cf. *guineensis* Jacq. (Arecaceae), *Musa* sp. (Musaceae), Bombacaceae indet., and Mimosaceae indet.

In Congo, Kipalu (2009: 16) reported *M. torquata* visiting/consuming fruits of *Chlorophora excelsa* (African Teak) and *Ficus mucuso*.

Gembu Tungaluna (2012: 102 - 104) reported the following fruits being eaten in the Kisangani area

(DRC) during the various seasons: First heavy rain season (September - November): *Uapaca guineensis* Müll. Arg., 1864 (Sugar Plum, Red Cedar, False Mahogany, Rikio) (19%), *Ficus leprieuri* Miq., 1867 (17%), *Carica papaya* L. (Papaya) (11%), *Musanga cecropioides* R. Br. & Tedlie (African Corkwood Tree, Umbrella Tree) (11%), *Pseudospondias microcarpa* (A. Rich.) Engl. (8%), *Persea americana* Mill., 1786 (Avocado) (8%), *Dacryoides edulis* H.J. Lam (Safou, African Pear, Bush Pear, Nsafu, Bush Butter Tree, Butterfruit) (8%), *Ficus wildemanniana* Warb. (6%), *Ficus vallis-choudae* Delile (6%), *Ficus mucoso* Welw. (3%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, Otaheite Apple, Great Hog Plum) (3%).
First mild rain/dry season (December - February): *Elaeis guineensis* Jacq. (African Oil Palm, Macaw-fat) (50%), *Myrianthus arboreus* P. Beauvois, 1805 (Giant Yellow Mulberry, Bush Pineapple, Corkwoord) (50%).
Second heavy rain season (March - May): *Pseudospondias microcarpa* (17%), *Musanga cecropioides* (14%), *Spondias cytherea* (9%), *Ficus leprieuri* (8%), *Ficus* sp1 (8%), *Uapaca guineensis* (8%), *Annonidium mannii* (Oliv.) Engl. & Diels (Junglesop) (6%), *Ficus vallis-choudae* (6%), *Ficus wildemanniana* (3%), *Ficus* sp2 (3%), *Dacryoides edulis* (3%), *Elaeis guineensis* (3%), *Parinari excelsa* Sabine (Guinea Plum) (3%), Musa sp. (3%).
Second mild rain/dry season (June - August): *Ficus leprieuri* (34%), *Myrianthus arboreus* (33%), *Annonidium mannii* (Junglesop) (33%).

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Myonycteris torquata*: *Adenia cissampeloides* (Planch. ex Hook.) Harms, 1897, *Adenia meigei*, *Ficus capensis* Thunb., 1786, *Ficus leprieuri* Miq., 1867, *Ficus polita* Vahl, 1805, *Ficus scott-eliotti* Mildbr. and Burret, 1911, *Ficus thonningii* Blume, 1839, *Ficus vallis-choudae* Delile, 1843, *Solanum verbascifolium* Kunth.

POPULATION:
Structure and Density
Although the species is infrequently caught in ground level nets, it is commonly caught in canopy nets. In Tai National Park (Côte d'Ivoire) it is one of the most common fruit bats (Mickleburgh *et al.*, 2008bb; IUCN, 2009).

Trend
2008: Stable (Mickleburgh *et al.*, 2008bb; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In Congo, Bergmans (1979a: 169) caught a female with a large foetus on 25 November, and a male with large, but not active testes on 28 November.

MATING:
This species has a polygynandrous mating system (Webber *et al.*, 2017: Suppl.)

PARASITES:
BACTERIA
Gram-negative bacterium
Of the 40 bats tested by Nowak *et al.* (2017: 6) in the Republic of Congo, 22 tested positive for *E. coli*. One isolate was identified as *E. albertii*.

HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 7 *M. torquata* specimens from East Africa and found four of them infected with *Hepatocystis* sp. Perkins and Schaer (2016: Suppl.) mention the presence of *Hepatocystis perronae* Landau and Adam, 1971 in bats from the Republic of Congo and the Central African Republic (see also Adam, 1973: 4; Miltgen *et al.*, 1977: 595).

VIRUSES:
Circoviridae
Chimpanzee associated cyclovirus 1 was reported by Vidovszky *et al.* (2023: Suppl.) from a bat from the DRC.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999 for antibodies to SARS-CoV in sera of seven individuals from Bandundu Province, DRC, one specimen tested positive (1/7, 14.3 %).

For the two Congos, Kumakamba *et al.* (2021: 7) found none of the 22 tested bats to be positive for coronaviruses.

Filoviridae - Filo viruses
Ebolavirus
Pourrut *et al.* (2007) showed that there is a homogeneous ZEBOV [Zaire Ebolavirus] infection in the wild populations of *M. torquata* in Gabon and the Democratic Republic of the Congo. Four out of 58 bats had immunoglobulin G (IgG) specific for Ebola in Gabon during a test performed by Leroy *et al.* (2005: 575). One to six out of 66 bats from the DRC tested by Lacroix *et al.* (2021: 7) were found to be positive for Ebola antibodies.

Bausch and Schwarz (2014: 1) and Pigott *et al.* (2014: 9) indicate that *M. torquata* is one of the leading candidates for introducing Ebola in

Guinea (together with *Epomops franqueti* and *Hypsignathus monstrosus*). While Vogel (2014: 140) names *M. torquata* the leading suspect for the Ebola outbreak in Guinea in the beginning of 2014. However, no proof has been provided that this was indeed the case.

Marburgvirus
Towner *et al.* (2007) tested 264 individuals from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and 55 individuals for anti-Marburg virus IgG antibodies by ELISA; no positives were found.

Nairoviridae
Orthonairovirus
Only three of the 100 specimens from Congo tested by Müller *et al.* (2016: 3) were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that three of the 111 specimens (2.7 %) they examined from Gabon, Congo and the Democratic Republic of the Congo tested positive for *Henipavirus*.

Rhabdoviridae
Kalemba *et al.* (2017: 409) reported that out of 6 bats examined from the DRC, two tested positive for Lagos Bat Virus neutralizing antibodies.

Togaviridae
Raulino *et al.* (2022: 256) found antibodies against Chikungunya virus and O'nyong nyong virus.

In their overview table, Maganga *et al.* (2014a: 8) reported that the following viruses were already found on *M. torquata*: Zaire Ebola virus (ZEBOV), Coronavirus (SARS-CoV), Henipavirus.

UTILISATION:
Contrary to what was reported in the Bats as Bushmeat review (Mickleburgh *et al.*, 2009), Bakwo Fils and Kaleme (2016b) observations in the field suggest this species is affected by hunting. Particularly notable is hunting by pygmy tribes, who are known to eat even what other people do not use as food including fruit bats (Bakwo Fils et al. *pers. comm.*). There are exceptions, in which some species that are prohibited by traditions or cause some problems in some tribes. However, for most of the local peoples, fruit bats are mostly used as food but microbats are not eaten by many tribes.

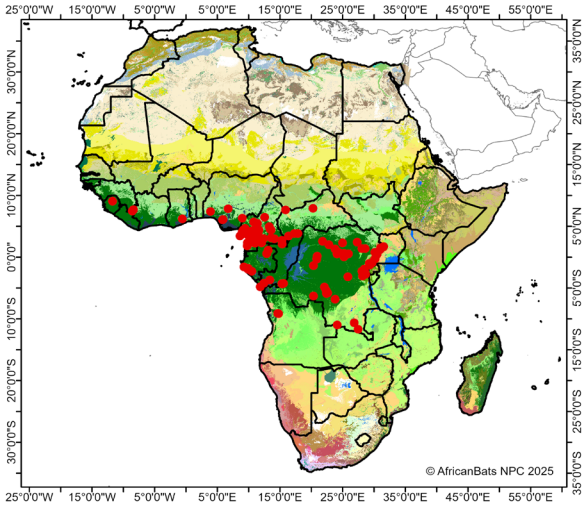

Figure 37. Distribution of *Myonycteris (Myonycteris) torquata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Gabon, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Uganda, Zambia.

Myonycteris (Myonycteris) torquata torquata (Dobson, 1878)

*1878. *Cynonycteris torquata* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, xxxvii, 71, 76, pl 5, fig 1. Publication date: 15 June 1878. Type locality: Angola: N Angola: Lower Cuanza region: Golungo Alto. [Goto Description]. - Comments: Grubb *et al.* (1998: 68) indicate "definite restriction of the type locality is not possible at present (Bergmans, 1976: 210 - 211)". Bergmans (1997: 49) indicates that Bergmans (1976) restricted the type locality to "Lower Cuanza Region" and the area was restricted to Golungo Alto by Crawford-Cabral (1989).
1971. *M[yonycteris (Myonycteris)] t[orquata] torquata:* Hayman and Hill, in: Meester and Setzer, The mammals of Africa. Order Chiroptera, 12. (Name Combination).
? *Myonycteris (Myonycteris) torquata torquata:* (Name Combination).
? *Myonycteris torquata torquata:* (Name Combination).

VIRUSES:
Nesi *et al.* (2012: 126) suggest that the high nucleotide distance between Ebola virus Côte d'Ivoire and Ebola virus Zaire can be correlated with the Plio/Pleistocene divergence between their putative reservoir host species, i.e., *Myonycteris torquata leptodon* and *Myonycteris torquata torquata*, respectively.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Cameroon.

Myonycteris (Myonycteris) torquata wroughtoni K. Andersen, 1908

*1908. *Myonycteris wroughtoni* K. Andersen, Ann. Mag. nat. Hist., ser 8, 2 (11): 450. Publication date: 1 November 1908. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Likandi river [=Litaki river] [03 20 N 26 10 E]. [Goto Description]. Holotype: NHMUK 1907.7.8.25: ad ♂, skin and skull. Collected by: The Alexander-Gosling Expedition; collection date: 18 April 1906. See Andersen (1908c: 450); Bergmans (1997: 50). Paratype: NHMUK 1907.7.8.26: ♂. - Etymology: In honour of Mr. Robert Charles Wroughton, who assisted in working out the mammals collected during the Alexander-Gosling Expedition: see Andersen (1908c: 450).
1971. *M[yonycteris (Myonycteris] t[torquata] wroughtoni:* Hayman and Hill, in: Meester and Setzer, The mammals of Africa. Order Chiroptera, 13. (Name Combination).
1971. *Myonycteris torquata wroughtoni:* Jones, J. Mamm., 52 (1): 129. Publication date: February 1971. (Name Combination).
? *Myonycteris (Myonycteris) torquata wroughtoni:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

Subgenus *Myonycteris (Phygetis)* K. Andersen, 1912

*1912. *Phygetis* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, 579. Publication date: 23 March 1912. - Comments: Type species: *Cynonycteris brachycephala* Bocage, 1889.
1993. *Phylletis* Juste and Ibáñez, 222.
? *Myonycteris (Phygetis):* (Name Combination, Current Combination).

Myonycteris (Phygetis) brachycephala (Bocage, 1889)

*1889. *Cynonycteris brachycephala* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (3): 198. Publication date: December 1889. Type locality: São Tomé and Príncipe: São Tomé Island. Holotype: MLZA 449a: ad ♀, mounted skin and skull. Collected by: F. Newton and Pires; collection date: 1868. Holotype number "T114"; destroyed by fire in 1978: see Bergmans (1997: 53).
1898. *Cynonycteris brachycephalus:* Seabra, J. Sci. mat. phys. nat., ser 2, 5: 170. (Alternate Spelling).
1995. *M[yonycteris] brachyptera:* Peterson, Eger and Mitchell, : 48. - Comments: Mentioned by Peterson *et al.* (1995: 48) only with the remark "La situation exacte de ce taxon suppose une étude plus poussée". [The exact situation of this taxon needs a more thorough study]. (Lapsus).
? *Myonycteris (Myonycteris) brachyptera:* (Lapsus).
? *Myonycteris (Phygetis) brachycephala:* (Name Combination).
? *Myonycteris brachycephala:* (Name Combination).

TAXONOMY:
Reviewed by Bergmans (1997). See Simmons (2005: 328).

COMMON NAMES:
Czech: kaloň tomášský. English: Sao Tomé Collared Fruit Bat. French: Myonyctère de São Tomé, Chauve-souris frugivore à collier de São Tomé. German Halskrausen-Flughund, São Tomé Halskrausen-Flughund.

CONSERVATION STATUS:
Global Justification
It is assessed Endangered because its extent of occurrence (EOO) is 750 km^2, it is known from less than five locations, and there is continuing decline in habitat quality inferred due to intense logging activities and the conversion of land to agricultural use (Juste, 2016b). This is a is range-restricted species. It is endemic to the island of São Tomé, where it is known from a single location (Juste *et al.*, 2008a; IUCN, 2009). Juste (2016b) mentions three localities, but no colonies.

Assessment History
Global
2016: EN B1ab(iii) ver 3.1 (2001) (Juste, 2016b). 2008: EN B1ab(iii) ver 3.1 (2001) (Juste *et al.*, 2008a; IUCN, 2009). 2004: EN B1ab(iii) ver 3.1 (2001) (Juste *et al.*, 2004b; IUCN, 2004). 2000: EN (Hilton-Taylor, 2000). 1996: VU (Baillie and Groombridge, 1996). 1994: VU (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
Within the species' relatively limited range it is threatened by ongoing habitat loss, presumably

related to logging activities and the conversion of land to agricultural use (Juste *et al.*, 2008a; IUCN, 2009; Juste, 2016b).
Rainho *et al.* (2010b: 257) indicate that hunting might also be a problem for this island endemic.

CONSERVATION ACTIONS:
Juste *et al.* (2008a) [in IUCN (2009)] report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas, although is expected in mountain forest within the protected area of Lagoa Amelia (Juste, 2016b). There is a need to protect suitable areas of remaining natural habitat for this species, with additional research required into the persistence of populations in modified habitats (such as cocoa plantations). Further surveys are needed to identify additional localities for this species, and to better understand its natural history (Juste *et al.*, 2008a; Juste, 2016b).

GENERAL DISTRIBUTION:
Myonycteris brachycephala is endemic to the uplands of São Tomé Island of São Tomé and Príncipe. It is absent from the northern part of the island. It has only been recorded from three localities, and no colonies have been reported. Individuals have been recorded between 300 and 1,200 m asl.

Native: São Tomé and Príncipe (Bergmans, 1997; Simmons, 2005: 328; Rainho *et al.*, 2010a: 18).

DENTAL FORMULA:
Juste and Ibáñez (1993a: 221) report on an asymmetric dental formula in *M. brachycephala*, which resulted from the absence of a lower internal incisor, either in the left or right mandible. They indicate that this might be related to a developmental instability associated with the colonization by the island species.

POPULATION:
Structure and Density
It appears to be a naturally rare species (Juste *et al.*, 2008a; IUCN, 2009). Nothing is known about the social structure of the species and it seems to show no sexual dimorphism. Individuals were always captured in mountain passes along most possibly commuting flights. Recent bat surveys with mist nets in primary and secondary forests as well as in cocoa plantations have failed to capture the species again (C. Meyer, pers. comm in Juste (2016b)).

Trend
2016: Decreasing (Juste, 2016b). 2008: Decreasing (Juste *et al.*, 2008a; IUCN, 2009; Rainho *et al.*, 2010b: 257).

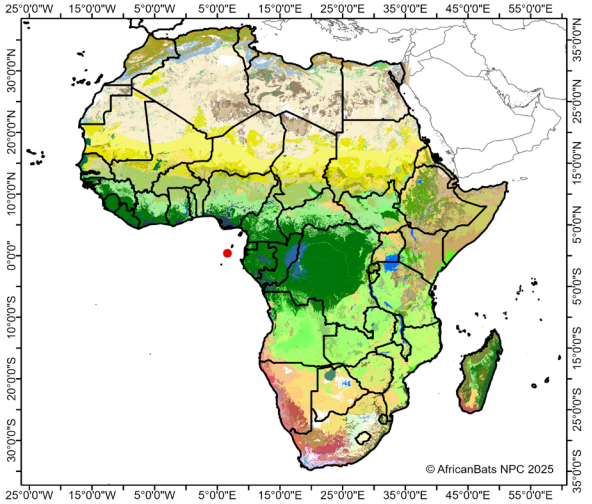

Figure 38. Distribution of *Myonycteris (Phygetis) brachycephala*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
São Tomé and Príncipe.

TRIBE Plerotini Bergmans, 1997

*1997. *Plerotini* Bergmans, Beaufortia, 47 (2): 69. Publication date: 20 June 1997.

TAXONOMY:
Includes only the genus ***Plerotes*** K. Andersen, 1910 (Almeida *et al.*, 2020: 11).

Genus ***Plerotes*** K. Andersen, 1910

*1910. *Plerotes* K. Andersen, Ann. Mag. nat. Hist., ser 8, 5 (25): 97. Publication date: 1 January 1910. - Comments: Type species: *Epomophorus anchietæ* Seabra, 1900. - Etymology: From the Greek "*πλεροτες*", meaning one who renders full or complete. (Current Combination).
2014. *Plerote:* Ndara R., IJISR, 12 (1): 253. Publication date: November 2014. (Lapsus).

TAXONOMY:
Revised by Bergmans (1989). See Simmons (2005: 333).

Included in the Plerotini tribe by Bergmans (1997: 69) and Almeida *et al.* (2016: 83), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter. Hassanin *et al.* (2020: 5) include it in the Epomophorini tribe and Plerotina subtribe.

Currently (Simmons and Cirranello, 2023b) recognized species of *Plerotes*: ***anchietae*** (Seabra, 1900).

COMMON NAMES:
Czech: pyložraví kaloni. English: Plerote Fruit-bats, Plerotes Fruit-bats. French: Plérotes. German: Breitgesicht-Flughunde.

Plerotes anchietae (Seabra, 1900)

*1900. *Epomophorus anchietæ* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 116. Publication date: August 1900. Type locality: Angola: Benguela district: East of Hanha: Galanga [12 04 S 15 09 E]. Holotype: MLZA 481a: ♀, mounted skin and skull. Collected by: José Alberto de Oliveira Anchieta. Neotype: CZL 31-59026: imm ♀. Collected by: Jaime V. Santos; collection date: 8 December 1959. Designated by Bergmans (1989: 144). - Comments: Andersen (1912b: 487) mentions: "Type, in the Lisbon Museum, an adult female, mounted, skull extracted, obtained by Sr. Anchieta.".
2014. *Plerote anchetae:* Ndara R., IJISR, 12 (1): 253. Publication date: November 2014. (Lapsus).
? *Epomophorus anchietae:* (Name Combination).
? *Epomophorus n. sp.:*
? *Nanonycteris veldkampii:* - Comments: Not of Jentink, 1888. (Lapsus).
? *Plerotes ancheilae:* (Lapsus).
? *Plerotes anchietae:* (Name Combination, Current Combination).
? *Plerotes anchietai:* (Lapsus).

TAXONOMY:
Koopman (1993a: 145) mentions this name as *anchietai*, whereas Allen (1939a: 59) and Kock (1969a: 114) use *anchietae*. See Simmons (2005: 333).

Almeida *et al.* (2016: 82) found that the only adult male specimen (SMF 85744 from Malawi) showed some interesting morphological features (i.e. a ruff of enlarged, clustered glandular hairs) that link *Plerotes* to the myonycterines (*Megaloglossus* and *Myonycteris*).

COMMON NAMES:
Czech: kaloň pyložravý. English: Anchieta's Plerote Fruit-bat, Benguela Fruit-bat, D'Anchieta's Fruit Bat, Anchieta's Fruit Bat. French: Plérote d'Anchieta, Chauve-souris frugivore d'Anchieta. German: Anchietas Breitgesicht-Flughund. Kiluba (DRC): Mulima. Malawian: Lichinji, Mleme.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Mickleburgh *et al.*, 2008br; IUCN, 2009).

Assessment History
Global
2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008br; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004ch; IUCN, 2004). 2000: DD (Hilton-Taylor, 2000). 1996: VU (Baillie and Groombridge, 1996). 1994: Rare (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
Within the Angolan and Malawian parts of the species range it may be threatened by habitat destruction resulting from agricultural development, collection of timber and firewood, and setting of fires by poachers (Mickleburgh *et al.*, 2008br; IUCN, 2009).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008br) [in IUCN (2009)] report that although there appear to be no direct conservation measures in place, it has been recorded from a number of protected areas in Malawi and the Democratic Republic of the Congo. Further field surveys are needed to better determine the current status of this poorly known species.

GENERAL DISTRIBUTION:
Plerotes anchietae is largely known from scattered records in Central Africa. Most reports of this species are from the 1950's in Angola, the Democratic Republic of the Congo, Malawi and Zambia. A single specimen was collected in Malawi in 1997. It has been recorded between 1,000 and 2,000 m asl (Bergmans, 1989).

Native: Angola (Bergmans, 1989; Monadjem *et al.*, 2010d: 555; Taylor *et al.*, 2018b: 60); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Bergmans, 1989; Monadjem *et al.*, 2010d: 555); Malawi (Kock *et al.*, 1998a; Monadjem *et al.*, 2010d: 555); Zambia (Bergmans, 1989; Monadjem *et al.*, 2010d: 555).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Harrison (1960c: 68) described the colour of the hairs on the dorsal surface of a subadult male from Zambia as "terminally a uniform light brown (nearest to Suntan Merida+Mayfair Tan-, Plates 13 and 7B, Maerz and Paul, 1950), becoming a little more rufous on the tibiae. The bases of the hairs are paler, buffy coloured". On the ventral surface, the pelage is "pale greyish buff, without any indication of a darker neck band".

DENTAL FORMULA:
The permanent dental formula is as follows: $I^1/_2$ $C^1/_1$ $PM^3/_3$ $M^1/_3$ = 30.

Harrison (1960c: 69) also indicates that almost all known specimens of the genus *Plerotes* have some difference in the dental formula.

FUNCTIONAL MORPHOLOGY:
Harrison (1960c: 69) indicates that the tongue is 20 mm long (sub-equal to the mandibular length) and 9.5 mm wide at the base of the epiglottis. The dorsal tip and anterior quarter is covered with filiform papillae.

POPULATION:
Structure and Density
It appears to be a rare, or at least a rarely recorded, species (Mickleburgh *et al.*, 2008br; IUCN, 2009).

Trend
2008: Unknown (Mickleburgh *et al.*, 2008br; IUCN, 2009).

VIRUSES:
Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that single specimen they examined from Gabon did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

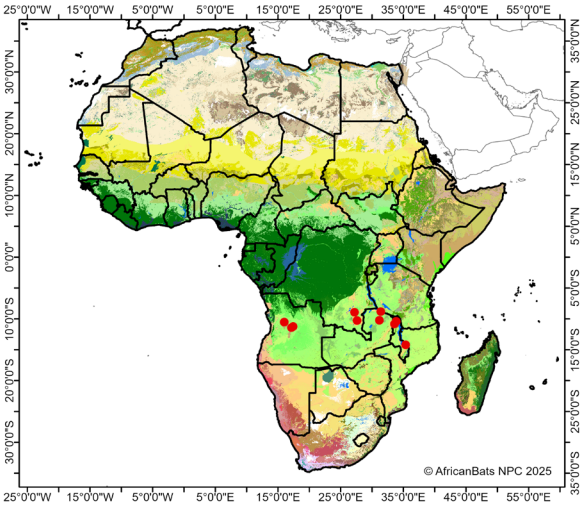

Figure 39. Distribution of *Plerotes anchietae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Congo (Democratic Republic of the), Malawi, Zambia.

TRIBE Rousettini Andersen, 1912

*1912. *Rousettini* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, xxx. Publication date: 23 March 1912.

TAXONOMY:
Includes only the genus ***Rousettus*** Gray, 1821 (Simmons and Cirranello, 2020: 11).

Genus ***Rousettus*** J. E. Gray, 1821

*1821. *Rousettus* J. E. Gray, London Med. Repos., 15: 299. Publication date: 1 April 1921. - Comments: Type species: *Pteropus Egyptiacus* E. Geoffroy Saint-Hilaire, 1810. Not *Pteropus aegyptiacus* Geoffroy, 1818 (see Corbet and Hill, 1992: 67). - Etymology: From the French "*rousette*" for the rosette of glandular hairs on the neck of males (see Flannery, 1995a: 304) or from the French "*rousse*" for reddish or reddish brown, referring to the fur colour of the earliest specimens taken in Egypt (see Kwiecinski and Griffiths, 1999: 7). - Phonetics: rue-set'-us. (Current Combination).

1829. *Cercopteropus* Burnett, Quart. J. Sci., Lit. and Art, pt 1, art 5, p 269. Publication date: April - June 1829. - Comments: Type species: *Pteropus aegyptiacus* E. Geoffroy Saint-Hilaire, 1818 (Designated by Andersen, 1912b: 23). Burnett (1829: 269) did mention both *Ægyptiacus* and *Amplexicaud* [for *amplexicaudata*] as being

included in his genus. - Etymology: From the Greek "*κέρκος*", meaning tail and "*Pteropus*" (see Palmer, 1904: 172).

1843. *Xantharpyia* J. E. Gray, Catalogue of the species of mammals of the British Museum, xix, 37. Publication date: 13 May 1843. - Comments: Type species: *Pteropus amplexicaudatus* E. Geoffroy Saint-Hilaire, 1810. - Etymology: From the Greek "*ξανθός*", meaning yellow and *Harpyia* from the characteristic colour (see Palmer, 1904: 710).

1844. *Eleutherura* J. E. Gray, Mammalia, in Voyage "Sulphur", Zool, 1: 29. - Comments: Type species: *Pteropus leachii* A. Smith, 1829 (=*Pteropus aegyptiacus* E. Geoffroy Saint-Hilaire, 1810). Andersen (1912b: 24) mentions *Pteropus hottentotus* Temminck, 1832 as type species, which is a synonym of *P. leachi* A. Smith 1829. Preoccupied by *Eleutherura* Gray, 1843; nom. nud. (Andersen, 1912b: 16; Meester *et al.*, 1986: 28; Pavlinov *et al.*, 1995: 61). Allen (1939a: 61) indicates that Gray (1843 - List. Spec. Mamm. Brit. Mus., p. xix) is a nomen nudum, but that it is redescribed in the 1844 publication. - Etymology: From the Greek "*ἐλεύθερος*", meaning free and "*οὐρά*", meaning tail, referring to having the tail free from the interfemoral membrane (see Palmer, 1904: 255).

1852. *Cynonycteris* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 25 [Goto Description]. - Comments: Type species: *Pteropus collaris* Liechtenstein [not Illiger] (=*Pteropus aegyptiacus* E. Geoffroy Saint-Hilaire, 1810). - Etymology: From the Greek "*κύων*" or "*κυνός*", meaning dog and "*νυκτερις*", meaning bat, probably referring to the dog-like head (see Palmer, 1904: 212).

1871. *Senonycteris* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 115. Publication date: 14 January 1871. - Comments: Type species: *Pteropus seminudus* Kelaart, 1850 (=*Pteropus lechenaulti* Desmarest, 1820). Described as subgenus of *Xantharpyia*.

1906. *Roussettus (Xantharpyia):* Johnston, Liberia, Volume II: 690. (Name Combination, Lapsus).

1906. *Roussettus:* Johnston, Liberia, Volume II: 688. (Lapsus).

1992. *Rosetus:* Agrawal, Das, Chakraborty, Ghose, Mandal, Chakrabo, Zoological Survey of India, State Fauna Series 3, 49. - Comments: Lapsus. See Bergmans (1994: 82). (Lapsus).

1999. *Rosettus:* Buffenstein, Maloney and Bronner, S. Afr. J. Zool., 34 (1): 16. (Lapsus).

2007. *Rousetus:* Nel and Markotter, Crit. Rev. Microbiol., 33 (4): 308. (Lapsus).

2015. *Rousettes:* Lee, Kulcsar, Elliott, Khiabanian, Nagle, Jones, Amman, Sanchez-Lockhart, Towner, Palacios and Rabadan, BMC Genomics, 16 (1033): 1. Publication date: 7 December 2015. (Lapsus).

TAXONOMY:

Meester *et al.* (1986) mention that the inclusion of *Lissonycteris* as a subgenus of *Rousettus* is open to question. Lawrence and Novick (1963) maintain that *Lissonycteris* should be regarded as a valid genus, more closely related to *Myonycteris* Matschie, 1899, than to *Rousettus*. In this, they are followed by Rosevear (1965), Ansell (1978), Corbet and Hill (1980), Almeida *et al.* (2011a), and Patterson and Webala (2012). Koopman (1975), on the other hand, concludes that although there is a close relationship between *Lissonycteris* and *Myonycteris*, the relationship of *Lissonycteris* with *Rousettus* is sufficiently close for it to be retained as subgenus. Koopman (1982) again treats *Lissonycteris* as a subgenus, as is done also by Hayman and Hill (1971). Bronner *et al.* (2003), following Lawrence and Novick (1963), separated *Lissonycteris* from *Rousettus* because of ethological differences concerning the use of the limbs, and the absence of echolocation in *Lissonycteris*. Juste B. *et al.* (1997) presented allozyme evidence corroborating earlier chromosome studies (Haiduk *et al.*, 1980, 1981), DNA-hybridisation results (Kirsch *et al.*, 1995) and cladistic analysis (Springer *et al.*, 1995) that support the recognition of *Lissonycteris* as a distinct genus. Three subgenera are often recognized (*Rousettus*, *Boneia*, and *Stenonycteris*), although Bergmans (1994), rejected the use of subgenera for the African species (Simmons, 2005: 347).

A key to the species is provided by Kwiecinski and Griffiths (1999: 1, Mammalian Species, 611).

Included in the Rousettini tribe by Almeida *et al.* (2016: 83) and Hassanin *et al.* (2020: 5).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Rousettus*: ***aegyptiacus*** (E. Geoffroy Saint-Hilaire, 1810); *amplexicaudatus* (E. Geoffroy Saint-Hilaire, 1810) – Cambodia, Thailand, Burma, and Laos, Peninsular Malaysia through Indonesia, Java, and Bali, Philippines; New Guinea, Bismarck Archipelago, Solomon Islands (Simmons, 2005: 347); *leschenaultii* (Desmarest, 1820) – Sri Lanka, Pakistan to Vietnam and southern China, Peninsular Malaysia, Sumatra, Java, Bali, and Mentawai Islands (Indonesia) (Simmons, 2005: 348); *linduensis* Maryanto and Yani, 2003 – central Sulawesi (Simmons, 2005: 348); ***madagascariensis*** G. Grandidier, 1929; ***obliviosus*** Kock, 1978; *spinalatus* Bergmans and Hill, 1980 – Sumatra, Borneo (Simmons, 2005: 348).

COMMON NAMES:

Czech: egyptští kaloni, noční kaloni, psi noční. English: Rousettes, Rousette Fruit-bats. French: Roussettes. German: Höhlenflughunde. Italian: Rossétti.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Horáček *et al.* (2013b: 1) report on two tooth fragments from the Middle Pleistocene Israeli site Qesem Cave, which they tentatively attribute to

cf. *Rousettus* sp. If this identification is confirmed, they suggest that the current Mediterranean population of *R. aegyptiacus* could be seen as a paleochoric element. However, the teeth they report on are larger than similar teeth in extant *R. aegyptiacus* specimens, so they might be from a different species or there might have been phenotypic rearrangements such as increased body size (as they suggest on page 13).

GENERAL DISTRIBUTION:
Stribna *et al.* (2019: 2337) indicate that the genus probably originated in Asia and that the colonisation of Africa occurred in the late Pliocene or early Pleistocene (ca. 2.6 to 1.7 mya).

BIOGEOGRAPHY:
Several hypotheses have been proposed about the origin of the genus *Rousettus* on the phylogenetic inference, and centers of diversity pinpoint a southeastern Asian origin (Juste B. *et al.*, 1999). Three separate routes have been suggested for western expansion of pteropodids into Africa, via a middle Asian-European-Gibraltar route, a middle-Asian, Middle Eastern route, and an Indian subcontinent-western Indian Ocean, east African route (Juste B. *et al.*, 1999). Giannini and Simmons (2003, 2005) support the Middle Eastern route with the Afrotropical clade composed of *R. aegyptiacus* and *R. madagascariensis* being the sister group to *R. leschenaulti*.

Almeida *et al.* (2016: 82) indicate that *Rousettus* expanded from Asia into Africa in the late Pliocene or early Pleistocene, where the continental *R. aegyptiacus* already split off in the early Pleistocene, slightly later followed by a split of the two island forms.

PARASITES:
BACTERIA
Di Cataldo *et al.* (2020: 2) examined 6 Nigerian *Rousettus* bats and found 2 to be infected by hemoplasma bacteria.

ACARI
Trombiculidae
Stekolnikov (2018a: 50) reported *Rousettus* sp. to be the type host of *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957.

DIPTERA
Nycteribiidae
Tripselia blainvillii (Leach 1817) single record (Haeselbarth *et al.*, 1966: 113). Morse *et al.* (2013: Suppl. 1) refer to *Dipseliopoda biannulata* collected from a non-specified Kenyan *Rousettus* specimen. This bat fly was itself infected by an *Arsenophonus* sp. bacteria (Szentiványi *et al.*, 2019a: Suppl.).

Dick *et al.* (2023) mentioned that the bat flies *Dipseliopoda biannulata* (Oldroyd, 1953) and *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817), have been found on *Rousettus* sp.:

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Kenya, South Africa, Tanzania, Uganda.

Rousettus aegyptiacus (E. Geoffroy St.-Hilaire, 1810)

*1810. *Pteropus Egyptiacus* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 15: 96. Type locality: Egypt: Giza province: Giza: Great Pyramid [30 01 N 31 13 E]. Holotype: MNHN ZM-MO-1996-2119: ad ♀, skull and alcoholic. Collected by: Etienne Geoffroy-Saint-Hilaire. See Qumsiyeh (1985: 13). Numbers "167" and "A.70" in Rode (1941).
Previously mentioned as MNHN A.70. Allotype: MNHN ZM-MO-1996-2120: ♂, mounted skin (skull not removed). Collected by: Etienne Geoffroy-Saint-Hilaire. Rode (1941: 234) also mentions numbers 762A and 167a. Andersen (1912b: 32) mentions that there were several specimens, but only one was still present: an adult male (A.69). - Comments: Type locality originally "la basse Egypte - le plafond d'une des chambres de la grande Pyramide". See Kwiecinski and Griffiths (1999: 1). Type MNHN A.70 (ad ♀, alcoholic and skull: Qumsiyeh, 1985: 13). - Etymology: The name is derived from the fact that the species was originally described from a specimen from the Great Pyramid of Giza in Egypt (see Smithers, 1983: 63).

1818. *Pteropus aegyptiacus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 134, pl 3, No 2. - Comments: Emendation of *egyptiacus*. Unjustified according to Corbet and Hill (1992: 67), justified according to Kock (2001c). - Etymology: From the scientific Latin masculine adjective *aegyptiàcus*, meaning "Egyptian", as the species was described from an Egyptian specimen (see Lanza *et al.*, 2015: 69). (Emendation).

1823. *Pteropus collaris* Lichtenstein, Verzeichniss der Doubletten des Zool. Mus. K. Univ. Berlin, 3, 5. Type locality: South Africa: "Terra Caffrorum". - Comments: Preoccupied by *Pteropus collaris* Illiger, 1815; see Kwiecinski and Griffiths (1999: 1).

1825. *Pteropus geoffroyi* Temminck, Monogr. Mamm, 1 (5): 197, pl 15, f 14, 15. Publication date: 1825. Type locality: Senegal: Senegal and north coast of Africa. - Comments: Meester *et al.* (1986: 29) mention that the type locality is restricted to Giza, Egypt by Koopman (1975: 361). Andersen (1912b: 32) mentions it as a replacement name for *R. aegyptiacus*, since "vu que l'espèce se trouve au Sénégal, et probablement sur toute la côte septentrionale d'Afrique," [= "in view of the fact that the species occurs in Senegal and probably over the the entire northern coast of Africa."].

1829. *Pteropus Leachii* A. Smith, Zool. Journ., 4 (16): 433. Publication date: May 1829. Type locality: South Africa: Gardens about Cape Town [ca. 33 56 S 18 28 E]. [Goto Description]. Paratype: SMF 891: juv ♂, skin and

skull. Cotype: NHMUK 1875.11.3.2: ad ♀, alcoholic (skull not removed). Collected by: Sir Andrew Smith. Exchanged by G.E. Dobson (see Andersen, 1912b: 28).
Smith (1829: 433) does not mention a specific specimen as the type specimen, nor on how many specimens his description is based. Therefore it is not clear whether this specimen is a syntype or a paratype. - Etymology: In honour of the celebrated naturalist, Dr. Leach, F.R.S. (see Smith, 1829: 433).

1832. *Pteropus hottentottus* Temminck, in: Smuts, Enumer. Mamm. Capensium, 3. Type locality: South Africa: Cape province: originally ""circa urbem apensem" see Andersen (1912b: 28), restricted to Capt Town.: Cape Town [33 56 S 18 28 E]. [Goto Description]. - Comments: Mentioned as "*hottentotus*" by Koopman (1993a), Simmons (2005), but as *hottentottus* by Allen (1939a: 62), Roberts (1951: 55), Meester *et al.* (1986: 29), Kwiecinski and Griffiths (1999). Andersen (1912b: 29) mentions that the type is in the RMNH, but also indicates that there are "authentic specimens" in the NHMUK: 1837.4.28.33-34, 38, 40, 67 (4 ad + 1 imm; sks and skulls), from "near Cape Town" (J. Smuts), and purchased from the Leyden Museum.

1862. *Xantharpyia ægyptiaca:* Gerrard, Catalogue of the bones of Mammalia in the collection of the British Museum, 57. Type locality: Egypt. (Name Combination).

1862. *Xantharpyia leachii:* Gerrard, Catalogue of the bones of Mammalia in the collection of the British Museum, 57.

1871. *Eleutherura unicolor* J. E. Gray, Catalogue of Monkeys, Lemurs and Fruit-eating bats in the collection of the British Museum London, 117. Publication date: 14 January 1871. Type locality: Gabon: "Gabon". [Goto Description]. Holotype: NHMUK 1862.8.26.1: ad ♂, skin and skull. Purchased Verreaux: see Andersen (1912b: 32).

1906. *R[oussettus (Xantharpyia)] collaris:* Johnston, Liberia, Volume II: 690. (Lapsus).

1908. *Rousettus sjöstedti* Lönnberg, Wiss. Ergebn. Swedischen Zool. Exp. u. Leitung Sjöstedt, Kilimandjaro-Meru, 1 (2): 7. Type locality: Tanzania: near Tanga: Mkulumusi caves. [Goto Description]. Holotype: NRM 642170: ad ♀, alcoholic (skull not removed). Collected by: Bror Yngve Sjöstedt; collection date: 4 May 1905.
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1911. *Cynonycteris collaris:* Mitchell, Proc. zool. Soc. Lond., 1911, II: 444. Publication date: 6 July 1911.

1951. *Pteropus amphiplexicaudatus:* Roberts, The mammals of South Africa. Type locality: South Africa: Cape. - Comments: Probably a lapsus. Roberts (1951: 55) attributed the name to Temminck (1827) and mentions it as "not of Geoffroy", which would probably refer to *amplexicaudatus*. However, Temminck (1827) did not use this erroneous spelling. (Lapsus).

1958. *Rousettus aegypticus:* Griffin, Novick and Kornfield, Biol. Bull., 115 (1): 107. Publication date: August 1958. (Lapsus).

1960. *Rousettus aegyptiacus occidentalis* Eisentraut, Bonn. zool. Beitr., 10: 231, figs 8, 13 (for 1959). Publication date: 10 January 1960. Type locality: Cameroon: N side of Mount Cameroon: Mueli [04 23 N 09 07 E, ca. 600 m]. Holotype: ZFMK MAM-1959.0450: ad ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: 20 February 1958; original number: 648. Paratype: MHNG 950.095: ♂, alcoholic (skull not removed). Collected by: Jean-Luc Perret; collection date: 18 November 1956. Paratype: MHNG 950.096: ♂, alcoholic (skull not removed). Collected by: Pierre Strinati and Villy Aellen; collection date: 6 August 1957; original number: 1833. Paratype: MHNG 950.097: ♂, alcoholic (skull not removed). Collected by: Pierre Strinati and Villy Aellen; collection date: 6 August 1957; original number: 1834. Paratype: MHNG 950.098: ♀, alcoholic (skull not removed). Collected by: Pierre Strinati and Villy Aellen; collection date: 6 August 1957; original number: 1835. Paratype: MHNG 950.100: ♀, alcoholic (skull not removed). Collected by: Pierre Strinati and Villy Aellen; collection date: 6 August 1957; original number: 1836. Paratype: ZFMK MAM-1961.0575: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: January 1958. Lager IV [= Camp IV], near lake Koto Barombi, 120 m, N side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0576: ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0577: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0578: ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0579: ♀, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: January 1958. Lager IV [= Camp IV], near lake Koto Barombi, 120 m, N side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0580: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0581: ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0582: ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0583: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0584: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0585: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0586: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0587: juv ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0588: juv ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0589: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0590: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and

Peters, 2010: 10). Paratype: ZFMK MAM-1961.0591: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0592: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0593: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0594: juv ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0595: ♀, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0596: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0597: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0598: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0599: ♀, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0600: ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0601: ♂, skull only. Collected by: Prof. Dr. Martin Eisentraut; collection date: January 1958. Lager IV [= Camp IV], near lake Koto Barombi, 120 m, N side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1961.0602: ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: February 1958. Lager V [= Camp V], above Mueli, 600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0208a: ♀, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0208b: ♂, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0208c: Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0208d: ♂, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0208e: ♂, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: March 1958. Lager VI [= Camp VI], Isobi, 30 m, W side Mount Cameroon (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209a: ♀, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209b: Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209c: ♀, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209d: ♀, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209e: ♀, skin only. Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10). Paratype: ZFMK MAM-1963.0209f: Collected by: Prof. Dr. Martin Eisentraut; collection date: November 1957. Lager I [= Camp I], above Buea, 1,600 m (see Hutterer, 1984: 29; Hutterer and Peters, 2010: 10).

1974. *Rousettus aegyptiacus unicolor:* Bergmans, Bellier and Vissault. (Name Combination).

1993. *Rousettus aegyptiacus princeps* Juste and Ibáñez, Zool. J. Linn. Soc., 107 (2): 123. Publication date: February 1993. Type locality: São Tomé and Príncipe: Principé Island: 2 km S of Santo Antonio de Principé: Roça Bela Vista [ca. 01 37 N 07 27 E]. [Goto Description]. Holotype: EBD 18208M: ad ♂, skin and skull. Collected by: Javier Juste, Carlos J. Ibáñez Uargui and Antonio Ayong; collection date: 31 March 1988.

1993. *Rousettus aegyptiacus thomensis* Feiler, Haft and Widmann, Faun. Abh. Mus. Tierk. Dresden, 19 (4): 22. Publication date: 1 July 1993. Type locality: São Tomé and Príncipe: São Tomé Island: Generosa. [Goto Description]. Holotype: SMTD B16753: ad ♂, skin and skull. Collected by: Alfred Feiler, Jan Haft, Peter Widmann, Jakob Fahr, Tilo Nadler, Carsten A. Brühl, T. Nill and P. Schütz; collection date: 26 March 1991. See Feiler *et al.* (1993: 22 - 23). Paratype: SMTD B16750: ad ♂, skin and skull. Collected by: Jakob Fahr and Jan Haft; collection date: 28 March 1989. See Feiler *et al.* (1993: 22 - 23). Paratype: SMTD B16751: ad ♂, skin and skull. Collected by: Alfred Feiler, Jan Haft, Peter Widmann, Jakob Fahr, Tilo Nadler, Carsten A. Brühl, T. Nill and P. Schütz; collection date: 28 March 1991. Paratype: SMTD B16752: ad ♀, skin and skull. Collected by: Alfred Feiler, Jan Haft, Peter Widmann, Jakob Fahr, Tilo Nadler, Carsten A. Brühl, T. Nill and P. Schütz; collection date: 20 April 1991. See Feiler *et al.* (1993: 22 - 23). Paratype: SMTD B16754: ad ♀, skin and skull. Collected by: Alfred Feiler, Jan Haft, Peter Widmann, Jakob Fahr, Tilo Nadler, Carsten A. Brühl, T. Nill and P. Schütz; collection date: 19 April 1991. Paratype: SMTD B16755: ad ♀, alcoholic (skull not removed). Collected by: Alfred Feiler, Jan Haft, Peter Widmann, Jakob Fahr, Tilo Nadler, Carsten A. Brühl, T. Nill and P. Schütz; collection date: 26 March 1991.

1993. *Rousettus aegyptiacus tomensis* Juste and Ibáñez, Zool. J. Linn. Soc., 107: 124. Type locality: São Tomé and Príncipe: São Tomé Island: Bindá (Santa Catarina) [00 16 N 06 29 E]. [Goto Description]. Holotype: EBD 17495M: ad ♂, skin and skull. Collected by: Javier Juste and Carlos J. Ibáñez Uargui; collection date: 7 April 1988.

2006. *Rousettus egyptiacus:* Nogales, Rodríguez-Luengo and Marrero, Mammal Rev., 36 (1): 49. Publication date: January 2006. (Lapsus).

2008. *Rousettus aegyptiacu:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 249. (Lapsus).

2008. *Rousettus occidentalis:* Benda, Vespertilio, 12: 109. (Name Combination).
2011. *Rousettus aegyptiacusi:* Hickey, Jüllig, Aitken, Loomes, Hauber and Phillips, Ageing Res. Revs, 11 (2): 249 (for 2012). Publication date: 13 December 2011. (Lapsus).
2012. *R[ousettus] a[egyptiacus] egyptiacus:* Hulva, Marešová, Dundarova, Bilgin, Benda, Bartonička and Horáček, Mol. Ecol., 21 (24): 6105. Publication date: 24 October 2012. (Lapsus).
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2015. *Rousettus aegypticus occidentalis:* Sylla, Pourrut, Diatta, Diop, Ndiaye and Gonzalez, Afr. J. Microbio. Res., 9 (22): 1468. Publication date: 3 June 2015. (Lapsus).
2019. *Rousettus aegypti:* Siya, Bazeyo, Tuhebwe, Tumwine, Ezama, Manirakiza, Kugonza and Rwego, BMC Public Health, 19 (136): 1. Publication date: 31 January 2019. (Lapsus).
2019. *Rousettus aegyptiacusi:* Malmlov, Bantle, Aboellail, Wagner, Campbell, Eckley, Chotiwan, Gullberg, Perera, Tjalkens and Schountz, PLoS Negl. Trop. Dis., 13 (2) e0007071: 3. Publication date: 4 February 2019. (Lapsus).
2020. *Rosettus Aegiptiacus:* David, Davidson, Berkowitz, Karniely, Edery, Bumbarov, Laskar and Elazari-Volcani, Vet. Med. Sci., xxx (x): xxx. Publication date: 25 February 2020. (Lapsus).
2024. *Rousettus aegyptiacuse:* Franco, dos Santos, de Sousa Verde, Calchi, de Mello, Lee, Días, Machado, Carvalho and André, Vet. Res. Commun., xxx (x): 8. Publication date: 24 September 2024. (Lapsus).
2025. *Roussettus aegyptiacus:* Tolovou and Lenga, Biod. J., 16 (1): 52. Publication date: 30 March 2025. (Lapsus).
? *Cynonycteris ægyptiaca:* - Comments: see: Günther (1880: 741) as synonym of *Cynonycteris collaris*. (Name Combination).
? *Pteropus ægyptiacus* - Comments: Günther (1880: 741) refers to a list by Kotschy and published in Unger and Kotschy's 'Die Insel Cypern'. (Alternate Spelling).
? *Rousettus (Rousettus) aegyptiacus leachii:* (Name Combination).
? *Rousettus (Rousettus) aegyptiacus:* (Name Combination).
? *Rousettus aegyptiacus aegyptiacus:* (Name Combination).
? *Rousettus aegyptiacus arabicus:* (Name Combination).
? *Rousettus aegyptiacus leachi:* (Name Combination).
? *Rousettus aegyptiacus leachii:* (Name Combination).
? *Rousettus aegyptiacus leacii:* (Lapsus).
? *Rousettus aegyptiacus:* (Name Combination, Current Combination).
? *Rousettus arabicus:*
? *Rousettus collaris:* - Comments: .
? *Rousettus leachi:*

TAXONOMY:



Figure 40. *Rousettus aegyptiacus*, Pufuri, Kruger NP, South Africa.

Andersen (1912b) recorded *R. aegyptiacus*, *R. arabicus* and *R. leachii* as species in the genus *Rousettus*. Miller (1912) and Ellerman and Morrison-Scott (1951) recognized *R. arabicus* as a valid species. Harrison (1964a) stated that *R. aegyptiacus* is represented by the subspecies *R. a. aegyptiacus* and *R. a. arabicus*. Bergmans (1994) recognised *R. a. aegyptiacus*, *R. a. leachii*, *R. a. unicolor*, and *R. a. arabicus* as valid subspecies. Rainho *et al.* (2022: 604) recognize *R. a. princeps* Juste and Ibáñez, 1993 from Príncipe and *R. a. tomensis* Juste and Ibáñez, 1993 from Sáo Tomé as valid subspecies, where they consider the former to be a classic example of island dwarfism and the latter of island gigantism.

Corbet and Hill (1992) corrected Geoffroy Saint-Hilaire's spelling of *Rousettus aegyptiacus* to *R. egyptiacus*, a change endorsed by Koopman (1993a: 152) and Bergmans (1994). Kock (2001c), however, has presented a detailed and convincing case for regarding *egyptiacus* as an incorrect original spelling and treating *aegyptiacus* as the valid name (Bronner *et al.* (2003). Kock (1969a: 16), Qumsiyeh *et al.* (1992: 104) and Horáček *et al.* (2000) state that Geoffroy Saint-Hilaire (1818: 134) already corrected the spelling to *aegyptiacus*. Allen (1939a: 62) also indicates that it was a misprint in the 1810 publication, which was corrected in the 1818 publication.

Meester *et al.* (1986) state that, while *leachii* is clearly the Southern African subspecies extending well beyond the limits of this subregion, Hayman and Hill (1971) mention that intergradation with *aegyptiacus* may occur in the equatorial zone. Koopman (1975: 361) indicates that in the Sudan there is a hiatus between the ranges of these two sub-species, and he remarks that if they make contact it will be in Ethiopia, north of the equator. See Simmons (2005: 347).

Horáček *et al.* (2010: 175) indicate that the specimens from the Mediterranean area differ with more than 10 % in their mtDNA from the Sub-Saharan populations, which might suggest that these specimens represent a different species. Benda *et al.* (2012b: 1230) showed that, although two size morphotypes were found, the Palaearctic populations of *R. aegyptiacus* represent only one form, which is uniform in genetic traits (mitochondrial genome [nd1 and cyt *b*]) but plastic in metric traits.

Avery and Avery (2011: 539 - 540) report that a separation between the ancestor of *R. aegyptiacus* and those of genera such as *Myotis* and *Kerivoula* occurred some 64 million years ago. The separation with *Rhinolophus* and *Hipposideros* occurred slightly less than 60 million years ago, and that with *Pteropus* some 22 million years ago.

COMMON NAMES:
Afrikaans: Egiptiese vrugtevlermuis. Albanian: Lakuriq nate egjiptian i frutave. Arabian: Khafash El Fawakeh, Khafash Masri, Khaffash, Wat-Wat. Armenian: Եգիպտական մեծաչղջիկ. Azerbaijani: Misir meyvə yarasası. Basque: Fruitu-saguzar egiptoar. Belarusian: Крылан егіпецкі. Bosnian: Egipatski letipas. Breton: Lgodenn-dall rous Egipt. Bulgarian: Египетски плодояден прилеп. Castilian (Spain): Murciélago de la fruta egípcio, Ruseta Egipicia. Catalan (Spain): Ratpenat egipci. Chewa (Malawi): Karuru. Chinese: 北非果蝠. "Congolese": Kubukubo, Papo. Croatian: Egipatski plodojedi šišmiš. Czech: Kaloň egyptský, Upír egypecký, Kaloň nilský. Danish: Egyptisk flyvehund. Dutch: Nijlrousette, Nijlrousettus. English: Egyptian Fruit Bat, Egyptian Rousette, Egyptian Rousette Bat, West African Rousette, Egyptian Xantharpy. Estonian: Egiptuse öötiibur. Finnish: Ronkko. French: Roussette egyptienne, Roussette d'Égypte. Frisian: Nylrûsette. Galician (Spain): Morcego exipcio. Georgian: ეგვიპტური მფრინავი ძაღლი. German: Nilflughund (Ägyptischer Höhlenflughund), Egyptischer fliegender Hund. Greek: Αιγυπτιακή φρουτονυχτερίδα. Hebrew: Atalef Perot. Hungarian: Nílusi repülőkutya. Italian: Rossétto egiziàno, Rossétto del Nìlo, Rossetta. Irish Gaelic: Ialtóg meas Éigipteach. Kikongo (Angola): Ngembe. Kinande (DRC): Mulima. Kiswahili: popo-mgomba. Latvian: Ēģiptes augļsikspārnis. Lithuanian: Egiptinis vaisėdis. Luxembourgish: Nilfluchhond. Macedonian: Египетски овошен лилјак. Malawian: Lichinji, Mleme. Maltese: Farfett il-Lejl tal-Frott ta' L-Eġittu. Montenegrin: Egipatski letipas. Norwegian: Afrikagrotteflygehund. Polish: Rudawka nilowa. Portuguese: Morcego-frugívoro-egípcio, Morcego frugivoro do Egipto. Rhaeto-Romance: Chaun sgulant da l'Egipta. Romanian: Liliacul fructivor egiptean. Russian: Крылан египетский. Serbian: Обични пећински летипас [= Obični pećinski letipas]. Scottish Gaelic: Ialtag meas Èipheiteach. Slovak: Kaloň egyptský. Slovenian: Egipčanski leteči pes. Swedish: Nilflyghund. Turkish: Mısır Meyve Yarasası. Ukrainian: Крилан єгипетський. Welsh: Ystlum-ffrwythau yr Aifft.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Hildebrand *et al.* (2010: 268) recorded this species from the Kumali site in southern Ethiopia.

Van Neer (1990) reported on the presence of archeozoological material from this species in a number of localities in Central Africa.

Van Damme *et al.* (2018) report on a Holocene specimen retrieved from a cave on Socotra (Yemen), which seems closer related to current day Egyptian and West African *R. aegyptiacus* than to animals from eastern Africa and Arabia. As the species is currently missing in the Horn of Africa, this suggests that the early Holocene in Socotra likely corresponded to a wet period with high precipitation, which gradually decreased towards the late Holocene (Van Damme *et al.*, 2018: 2016).

CONSERVATION STATUS:
Global Justification
This species is broadly distributed and abundant, and is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category, hence is listed as Least Concern (LC ver 3.1 (2001)) (Benda *et al.*, 2008a; IUCN, 2009; Korine, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Korine, 2016). 2008: LC ver 3.1 (2001) (Benda *et al.*, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ct; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Markotter *et al.*, 2016). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).
Sáo Tomé: VU. Due to the small range and projected habitat degradation (for "*R. a. tomensis*") (Rainho *et al.*, 2022: 604).

MAJOR THREATS:
This species faces several threats, but none of them are considered a serious threat to the species at the global level. Hunted for food in

some cave systems in Africa. Cave disturbance and persecution are also a problem in parts of the range. The species is considered as a pest by fruit farmers and consequently cave roosts have been fumigated and destroyed in Israel, Turkey and Cyprus, resulting in incidental killing of many insectivorous bats of the genera *Rhinolophus* and *Myotis* (Benda *et al.*, 2008a; IUCN, 2009; Korine, 2016). The Israeli Nature Conservation Society is trying to prevent this lethal control (D. Kock, *pers. comm.*, in Benda *et al.*, 2008a, in IUCN, 2009), as campaigns during the 1950s led to the unintended death of 90 % of the insectivorous bats that roosted in the same caves (Makin and Mendelssohn, 1985 [in Guyton and Brook, 2014: 77]).

Sherwin *et al.* (2012: 174) identified that *R. aegyptiacus*'s frugivory and long-distance dispersal are major risk factors linked with climatic change. Weinberg *et al.* (2022: 5) found that during the winter in Israel, the bats needed to visit more fruiting trees (carrying less fruits) during the winter, which resulted in higher foraging effords and higher morbidity.

MacEwan (2016: 3) reports on *R. aegyptiacus* as fatalities of wind turbine blades. Cistrone *et al.* (2025: 1) furthermor indicated that although *Rousettus aegyptiacus* populations in South Africa might withstand low to medium levels of turbine-related mortality, these nevertheless pose a significant risk for long-term population declines.

Monadjem *et al.* (2016y: 364) report that the species has disappeared from the Liberian side of Mount Nimba, possibly as a result of hunting.

Bolognino de Orth *et al.* (2025: 3, 8) found that in Uíge (Angola) *Rousettus aegyptiacus* accounted for about two-thirds of the animals offered as bushmeat and they were sold in units of five to eight bats due to their relatively small size. During the two months of their study, they counted 990 bats being sold.at the central market of Uíge alone, which also makes this a major factor in disease transmission.

CONSERVATION ACTIONS:
Benda *et al.* (2008a) [in IUCN (2009)] and Korine (2016) report on International legal obligations for protection through the Bonn Convention (Eurobats) in areas where this applies. Included in Annex IV of the EU Habitats Directive in areas where this applies. Occurs in a number of protected areas. There is a need to enforce measures to protect this species, especially to prevent the fumigation of caves.

Pakenham (1984: 27) mentioned that, on Pemba, these bats were considered guardians of the spirits of the caves ("askaris"). Disturbing them would bring bad luck to the village.

GENERAL DISTRIBUTION:
Rousettus aegyptiacus is patchily distributed across sub-Saharan Africa and North Africa; also ranges outside of Africa through south-west Asia to Iran, Pakistan and India; also on Cyprus.
In the Western Palaearctic it occurs as two forms: *R. a. arabicus* (Iran, southern Arabia, Pakistan), *R. a. aegyptiacus* (rest of range). For more details on the Palaearctic distribution, see Benda *et al.* (2011a). In sub-Saharan Africa occurs as four forms: subspecies *leachi* is found in SW Ethiopia, S Sudan, E and S DR Congo, Uganda, Kenya, Tanzania (including the islands of Pemba and Unguja [see O'Brien (2011: 286]), Zambia, Malawi, Zimbabwe, Mozambique, and the extreme E and south of South Africa, including Swaziland and Lesotho; subspecies *princeps* is endemic to Príncipe Island in the Gulf of Guinea; subspecies *tomensis* is endemic to São Tomé; and subspecies *unicolor* is found from Senegal and the Gambia east to Liberia, Côte d'Ivoire, Ghana, Togo, south to northern central Nigeria and W Cameroon and Bioko Island, then south from Gabon and Congo to western DRC and W Angola. Elevational range: from sea level to 4,000 m asl, although Dongmo *et al.* (2020: 51) only reported it in Cameroon from elevations below 1,250 m.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 692,896 km^2. In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

For Ethiopia, Ahmed *et al.* (2023: 1) calculated the current suitable habitat to cover 60,271.4 km^2, and they predict it might increase with 24.4 % by 2050 and with 22.8 % by 2070 due to more favorable climate conditions.

Nogales *et al.* (2006: 52) report on a population of *R. aegyptiacus*, which escaped in 2000 from two zoos on Tenerife, where they were kept from around 1992. This population was eradicated in 2009 (see Simons *et al.*, 2014: 2091).

González-Gutiérrez *et al.* (2025: Suppl.) calculated the entire distribution area for this species to cover 4,315,563.33 km.

Native: Angola (Crawford-Cabral, 1989; Bergmans, 1994; Monadjem *et al.*, 2010d: 555); Burkina Faso (Kangoyé *et al.*, 2012: 6024; 2015a: 607); Burundi; Cameroon; Central African

Republic (Morvan *et al.*, 1999: 1195); Congo; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 555); Côte d'Ivoire; Cyprus; Egypt (Benda *et al.*, 2008f: 1); Equatorial Guinea (Fahr and Ebigbo, 2003: 128); Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 135; Benda *et al.*, 2020: 2582); Gabon; Gambia; Ghana; Greece (Strachinis *et al.*, 2018: 611); Guinea (Denys *et al.*, 2013: 281; Decher *et al.*, 2016: 263); Guinea-Bissau (Rainho and Ranco, 2001: 33; Lopes-Lima *et al.*, 2024: 410); India (Rainho *et al.*, 2010a), Iran, Islamic Republic of; Israel; Jordan; Kenya; Lebanon; Lesotho; Liberia (Monadjem and Fahr, 2007: 50); Libyan Arab Jamahiriya; Macaronesian islands (Tenerife island (Fajardo, 2002; Rodriguez-Luengo and Garacia Casanova, 2002; Trujillo, 2003; Nogales *et al.*, 2006; Masseti, 2010)); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 28; Bergmans, 1994; Monadjem *et al.*, 2010d: 555); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 555; Monadjem *et al.*, 2010c: 377); Nigeria (Capo-Chichi *et al.*, 2004: 161); Oman; Pakistan; Palestinian Territory, Occupied; Rwanda; São Tomé and Príncipe (Juste and Ibáñez, 1993c: 906; Rainho *et al.*, 2010a: 19 as *R. a. tomensis*); Saudi Arabia; Senegal; Sierra Leone; South Africa (Monadjem *et al.*, 2010d: 555); Sudan; Syrian Arab Republic; Tanzania (Stanley and Goodman, 2011: 40); Togo; Turkey; Uganda (Kityo and Kerbis, 1996: 59); United Arab Emirates (Anonymus, 2008: 38); Yemen (Benda *et al.*, 2011b: 26) ; Zambia (Ansell, 1969; Bergmans, 1994; Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 555); Zimbabwe (Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 555).

BIOGEOGRAPHY:
Horáček *et al.* (2013a: 71) suggest a few hypotheses about the presence of *R. aegyptiacus* in the eastern Mediterranean. These populations might be the result of immigration from sub-Saharan Africa or southern Arabia, although they also indicate that the Mediterranean form might have been the source population for the spread of *R. aegyptiacus* towards Africa.

Hulva *et al.* (2013: 74) indicate that the colonisation of northeastern Africa and the Middle East was connected with the spread of agricultural plants and might therefore have an anthropogenic component.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Sterbing and Moss (2017: 125) mention an average body mass of 140 g and a wingspan of 57 cm. The wings have an aspect ratio of 5.9 and a wing load of 24.6 N/m^2. The wing membranes bear small hairs of up 3 mm in length, with a diameter at the base of about 11.04 ± 3.31 µm, and about 4.68 µm at the blunt tip. The density of these hairs is 1 to 3 per square mm on the dactylopatagium and plagiopatagium, but can be much higher on the propatagium close to the arm.

DENTAL FORMULA:
Three out of 63 skulls examined by Esquivel *et al.* (2021: Suppl.) had extra teeth.

DETAILED MORPHOLOGY:
Baculum
See Albayrak *et al.* (2008) for samples from Turkey.

Brain
Chawana *et al.* (2013: 160) reported the average brain mass for two specimens to be 2.01 g, whereas Tambusso and Fariña (2015: Suppl.) mention a mass of 2.6 g for an average body mass of 130 g. Bhagwandin *et al.* (2020: 3027) found that the bat's brain contained 360,503 white matter interstitial cells (WMICs) for a brain mass of 2.1 g. Maseko *et al.* (2007) used immunohistochemical techniques to describe the nuclear parcellation and neuronal morphology of the cholinergic, catecholaminergic and serotonergic systems within the brain of three adult female *R. aegyptiacus*, captured from a cave adjacent to Legalametse Nature Reserve, Limpopo Province, South Africa. Naumann *et al.* (2015) investigated the medial entorhinal cortex architecture in layer 2 of the bat's brain.

Chawana *et al.* (2020: 2999) found a brain mass which seem to be linked to the bat's environment: in fifth-generation captive-bred animals the mass was on average 1.84 g, in bats from the Central African rainforest: 2.04 g and in bats from the subtropical woodlands in South Africa: 2.42 g.

The cytoarchitecture of *R. aegyptiacus*'s brain was investigated by Rodenas-Cuadrado *et al.* (2018: 1237) to determine the expression patterns of *FoxP2, FoxP1*, and *Cntnap2*, which are implicated in human speech and language phenotypes.

Schönenberger and Lane (1971: 653) studied the peripherical nervous system in the wings of *R. aegyptiacus*. The nerve bundle consists of a number of fascicles and each of these contains both myelinated and non-myelinated fibres. They also found that some of these nerves react positively to an histochemical test for catecholamine. The accompanying veins and arteries were studied by Lane *et al.* (1971).

Noll (1979a: 79) found that *R. aegyptiacus* shows a distinct circadian rhythm of body temperature, O_2 consumption and heart rate.

Tongue

The tongue of *R. aegyptiacus* is rectangular in shape and has an elongated body and widened root (Haggag *et al.*, 2020: 496). The arrangement of mechanical filiform papillae and gustatory papillae is regarded as being useful for the efficient uptake of semiliquid food and also an adaptation to a fruit diet (Jackowiak *et al.*, 2009). Abumandour and El-Bakary (2013: 230) report four types of lingual papillae: two mechanical (filiform and conical)l and two gustatory (fungiform and circumvallate) in which the shape, size, number, distribution, nomenclature and orientation of these lingual papillae are region specific according and in relation to feeding habits and food types. Abumandour (2014: 1407) distinguishes four types of lingual papillae, of which the filiform papillae can be subdivided into six subtypes: three on the anterior part (small, conical and giant), two on the middle part (cornflower and leaf-like papillae), and rosette shape filiform papillae on the posterior part. El-Mansi *et al.* (2019: 24, 29) subdivided the mechanical papillae in conicals (small and large) and filiforms (giant, rousette, leaf-like and spear-like filiforms). The gustatory papillae are either fungiform (with one or two taste buds) or vallate (with a single, barrel-shaped taste bud). Haggag *et al.* (2020: 496) only distinguish two types of filiform papillae on the dorsal side of the tongue: flower-like (which aid in food retention and gripping fruit) and leaf-like.
Kandyel *et al.* (2022: 400) distinguished three types of lingual papillae: one mechanical (filiform) - further subdivided in seven subtypes (one for each lingual region) - and two gustatory (fungiform and circumvallate)

See also Massoud and Abumandour (2020).

Stomach

The histomorphological characters of the stomach were studied by Abumandour and Pérez (2017), who concluded that this had special characters different to other mammals. The C-shaped stomach is divided into three parts: an elongated fundic cecal region with a blunt end, a long and narrow tubular pyloric part, and a small cardiac vestibular part. These characteristics of frugivorous species will help in their adaptations to accumulate large quantities of bulky food material.

Eye

Bojarski and Bernard (1988: 155) found that the retina shows a marked folding due to papillae projecting inwards from the inner choroid layer. These papillae are directed towards the nodal point of the dioptric apparatus, which makes that light coming in from an angle onto the papillae produces no shadow on the retina, which would otherwise result in the formation of an incomplete image. The eye of *R. aegyptiacus* possesses a tapetum lucidum, which increases the visual sensitivity by reflecting more light onto the retina and causes a faint red eyeshine observed while collecting the specimens. Aboelnour *et al.* (2020: 1391) confirmed the presence of the protruding projections and furthermore established that the outer plexiform layer was arranged into islets between the outer nuclear layer resulting in differences in its thickness

The eyes of this bat contain an average of 160,000 retinal ganglion cells (Coimbra *et al.*, 2016: 191). These authors also calculated the minimum angle of resolution as about 0.167° (ca. 5-6 mm at 1 m distance). Surprisingly, the eye of *R. aegyptiacus* contained a horizontal streak, which is generally found in species which roost in open environments (e.g., *E. helvum, E. franqueti* or *E. wahlbergi*. The horizontal streak of high retinal ganglion cell density in megachiropterans may afford increased resolution across the horizon, potentially assisting with predator surveillance (Coimbra *et al.*, 2016: 195).

El-Mansi *et al.* (2020: 1) found that the eyes of *R. aegyptiacus* are well equipped to discriminate colours efficiently.

The structure of the eye lens was examined by Aboelnour *et al.* (2024).

Skull

Curtis and Simmons (2018: 1390) described the extensive calcification of the external rostral cartilages surrounding the dorsolateral sides of the nostrils. These elements do not seem to be composed of bone as no porosity nor trabeculae were found.

Muscles

Luziga *et al.* (2021: 1) studied the muscle fibres in trunk, forelimb and hindlimb muscles.

Michelmore *et al.* (1998: 319) and Meng *et al.* (2016: 1) reported that the endocrine component of the pancreas occupied 9.1 % of the total volume, which is at least nine times higher than in humans. The former authors (p. 324) also indicated that the endocrine structure of the pancreas is more like that of snakes than that of other mammals.

FUNCTIONAL MORPHOLOGY:
Holland and Walters (2005: 83) report on the movements of the pinnae in free flight and demonstrated that the ears have a greater sensitivity to click stimuli in front of the animal when directed forwards than when directed back and to the side. They also indicated (p. 87) that echolocation signals are significantly more likely to be emitted during the forward sweep of the ears.

Tarnovsky *et al.* (2023: 1) investigated the possible hearing loss in *R. aegyptiacus* and found that this bat's hearing deteriorated by about 1 dB per year, especially at higher frequencies.

Lancaster *et al.* (1997: 110) studied the wing temperature during flight and found that, on average, the wing surface temperatures were about 15 °C below the body temperature, and only some 1.8 (± 0.5) °C above the ambient temperature. Barclay *et al.* (2017: 572) found that the bat's body temperature exhibited a circadian cycle, with an average temperature of 37.7 °C when returning from foraging and decreasing to 35.5 °C by mid-day. Just before leaving for foraging, the temperature was on average 37 °C. Rissmann *et al.* (2022: 1) investigated the core temperature of captive bats and found this to have a circadian cycle with temperatures between 34° and 41.5 °C. Korine and Arad (1993: 61) indicated that thermoneutral zone ranged between 31 and 36 °C, and that the bat's oxygen consumption in this range averaged 0.95 ± 0.15 ml g^{-1} h^{-1}. Experiments executed by Czenze *et al.* (2020: 4) indicated that *R. aegyptiacus* started to show signs of severe heat stress once the body temperature reached about 38 °C, which was 2 °C lower than the value reported for the tree roosting *Epomophorus wahlbergi*.

In their study on the kinematics of the chiropteran shoulder girdle in flight, Panyutina *et al.* (2013: 393) found that the scapula and clavicle are making a very minor contribution to the wing movement as compared to the input of humerus movements relative to scapula in the shoulder joint. The shoulder girdle moves relative to thorax as a crank mechanism, where the clavicle plays the role of crank, and the scapula the role of connecting rod.

Amador *et al.* (2015: 447) refer to Norberg (1972), who provided a detailed description of the left wrist of *R. aegyptiacus*. From this (and their own study of the handwing of a number of yangochiropteran bats), they concluded that the "dactylopatagium brevis" (the small piece of wing between the thumb and the second digit) functionally belongs to the propatagium (the piece of wing in front of the arm, between the thumb and the body).

Greville *et al.* (2018: 974) studied the flight membrane healing in *R. aegyptiacus* and found that wounds in the plagiopatagium took about 50 % longer to heal than wounds in the chiropatagium.

Kissane *et al.* (2024: 5, 6) investigated the muscle properties and architecture of the bat's flight muscles and found that hat the Egyptian fruit bat is more similar to flying birds than non-flying mammals, especially by the enlarged pectoralis muscles (accounting for 60 % of the forelimb muscles) and elbow flexion and extension muscles (bicep brachii and triceps brachii - accounting for 20 % of the remaining flight muscles), which aid powered flight.

The interaction between vision and echolocation was investigated by Danilovich and Yovel (2019), who found that the bats learn the 3D shape of objects through vision and that they can classify objects using echolocation. During navigation, both senses are used: vision to decide where to fly and echolocation when approaching an obstacle.

Cechetto *et al.* (2020: 58, 62) reported that the eyes of *R. aegyptiacus* contain about 200,000 retinal ganglion cells (RGCs), which is about similar in numbers and distribution as they found in the two other (non-echolocating) pteropid bats they examined. They also found a spatial resolving power (SRP) value of about 4 cycles per degree. These values suggests that these bats rely as much on their eyes as other Old World fruit bats.

Hostnik *et al.* (2020: 897) used CT scans to investigate the differences in lung volume between bats in their natural (head-down) and inverted (head-up) position. In head-up position, the lung volume was significantly larger. CT scans were also used by Carter (2020: 299) to investigate the reinforcement of the larynx and the trachea, and he found extensively calcified or ossified cricoids and ossified thyroids, but no evidence of reinforcement (calcification or ossification) of the arytenoids or lateral expansions of the cricoid.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 24.6 Pa, aspect ratio 5.9 and tip shape index of 1.45 for a wingspan of 88 cm and a wing area of 558 cm^2 and a body mass of 140 g.

Rossborough *et al.* (2021: 757) studied the head stabilization during flight in relation to wingbeat cycle and sonar emissions. They found that inflight head and body accelerations were uncoupled, which appears to be consistent with mechanisms that limit vertical head acceleration during wing downstroke.

Jacobsen *et al.* (2023: 1) investigated the entorhinal-hippocampal projections, which appeared to be specialized to this species behavioral needs, including 3D flight and long-distance navigation.

SEXUAL DIMORPHISM:
See Albayrak *et al.* (2008) for samples from Turkey.

In South Africa, Jacobsen and Du Plessis (1976: 272) found that females were on average 18 g lighter than males during winter and spring. Females had a slightly larger average forearm length (92.3 versus 89 mm).

ECHOLOCATION:
Griffin *et al.* (1958: 112) performed a number of experiments in total darkness where *R. aegyptiacus* bats were able to avoid vertically placed metallic wires of 3 mm diameter in 85 % of the time. For 1.07 mm wires, the success percentage was reduced to 68 %, and for 0.46 mm wires it dropped to 45 %, which was still better than chance.

Rainho *et al.* (2010a: 21) and Rainho *et al.* (2022: 605) reported the calls for 8 individuals from São Tomé with the following characteristics: F_{min}: 9.3 ± 2.4 (4.1 - 11.9) kHz, F_{max}: 110.5 ± 48.0 (44.0 - 150.0) kHz, duration: 0.33 ± 0.12 (0.2 - 0.5) ms and interpulse interval: 122.5 ± 28.7 (81.7 - 165.0) ms.

Waters and Vollrath (2003: 209) found that the sonar clicks have a duration of about 250 microseconds, with most of its energy occurring during the first 100 microseconds. With these clicks, the bats can detect and avoid wires of at least 6 mm in diameter.

Yovel *et al.* (2011b: 515, 522) indicate that the sonar clicks produced by *Rousettus* species do not have a long duration as was generally believed, but are actually extremely short: 50 - 100 microseconds. The peak energy of the click is at 30 kHz, and the bandwidth is about 57 kHz. These signals could be, in some parameters, as good or even better than the signals used by *Eptesicus fuscus* (see Geva *et al.*, 2010: 147). Davies *et al.* (2013b: Table S8) report a peak energy frequency of 35.03 kHz and a range between 12 and 70 kHz. Heffner *et al.* (2019: 584) mention a frequency range from 14 to 60 kHz, with peak energy between 25 and 30 kHz. At 60 dB, the hearing range for these bats extends from 2.25 to 64 kHz.

Benda *et al.* (2012a: 182) report the following data for Iranian specimens: Start frequency: 29.7 ± 3.5 (25.7 - 31.8) kHz, end frequency: 23.4 ± 4.0 (19.1 - 26.9) kHz, FMAXE: 30.7 ± 3.9 (23.3 - 35.0) kHz, pulse duration: 1.4 ± 0.2 (1.0 - 1.5) ms, interpulse interval: 29.8 ± 16.5 (7.0 - 66.3) ms.

Yovel *et al.* (2011a: 2) found that the intensity of the click emissions alters when they approach and lock their sonar on a target, and that *R. aegyptiacus* uses an undescribed strategy to change the spatial region ("field-of-view") their sonar covers: They increase the angle between the sonar beam axes of the click-pairs they emit. Lee *et al.* (2017) studied this further and concluded that the observed beam features can be captured by inducing changes to the pattern of phase differences through moving tongue location (see also Kling, 2018).

Danilovich *et al.* (2015: R1124) also found that the click rate increases prior to landing, indicating that they adjust biosonar sampling in a task-dependent manner.

From tests in a laboratory environment, Danilovich *et al.* (2014: S32) found that *R. aegyptiacus* can transfer information acquired using echolocation to the visual modality, suggesting they can create an echo-based representation of the world that is accessible to other sensory modalities.

As to the value of echolocation for fruit-eating bats, Fenton (1994: 27) suggests it permits access to the relative safety of dark, underground roosts, a situation analogous to the nesting situations of the echolocating birds. However, Danilovich *et al.* (2015: 1124) found that *R. aegyptiacus* not only relies on echolocation in dark caves, but also during orientation and foraging in diverse light environments. The click rate and intensity increased at lower light levels, where visual information was limited.

Fenton (2013: 1) indicated that it remains to be determined if the tongue click signals can be used to monitor the activities of this species as these calls are much less conspicuous than the high intensity call used by other bats.

Boonman *et al.* (2014: 2965) mentioned that they recently recorded wing clicks produced by wild *R.*

aegyptiacus bats while they were flying in the field.

Burchardt *et al.* (2019: 2) indicate that wingbeat and echolocation calls in *R. aegyptiacus* are tightly coupled around 5 - 12 Hz (the so-called theta frequencies: brain wave frequencies which are known to play a role in active movement and stimulus intake), suggesting a neuronal correlation. See also Forli *et al.* (2025).

Smarsh *et al.* (2021: 4) found that Egyptian fruit bats hear and produce clicks from birth, and they are also able to steer their echolocation beam from day 0. The clicks produced by the pups are very short (36 µs).and also higher in frequency than in adults.

A large number of vocalizations was collected by Prat *et al.* (2017b) (for samples see: https://doi.org/10.6084/m9.figshare.c.3666502).

MOLECULAR BIOLOGY:
Karyotype
2*n* = 36, FNa = 66, BA = 32, and a submetacentric X chromosome (Đulić and Mutere, 1973b; 1977; Haiduk *et al.*, 1981: 223 from South Africa; Albayrak *et al.*, 2008 for samples from Turkey). Albayrak *et al.* (2008) reported FN = 70 for a female and Fna = 66 from Turkey. Sayed (2011: 658) reported FN = 68 for Egyptian specimens and indicates the X chromosome is a medium sized submetacentric and the Y is a minute acrocentric one. She also reported that the metacentric autosomal pair 10 has a secondary constriction near its centromere and is of variable size within the same genome. Pairs 7 and 8 also show polymorphism. Pairs 9, 14, and 15 show a G-negative band in their short arm, and pair 10 has a broad G-negative band around its centromere. Pair 17 has complete heterochromatin, and displays polymorphism, with sometimes one autosome being subacrocentric and the other submetacentric.
Denys *et al.* (2013: 281) report the karyotype of four specimens from the Guinean Mount Nimba area as 2*n* = 36, Fna = 66, with 12 metacentric pairs, two subtelocentric pairs and one small acrocentric pair. The Y chromosome is the smallest in the set.

Genetics
See Ali (2011).

Teeling *et al.* (2017: 32) mention the estimated genome size for *R. aegyptiacus* to be 2.11 C, and the assembly size 1.91 Gbp. Nikaido *et al.* (2020: 4) mention as slightly smaller size of 1.90 Gbp with 4,974 scaffolds.

Szcześniak *et al.* (2013) presented the complete sequence of the mitochondrial genome of "*R. leschenaulti*" (16,704 nt, GenBank record KC702803). However, as pointed out by Botero-Castro *et al.* (2014), the sequence actually pertains to *R. aegyptiacus*.

Lee *et al.* (2015: 2) reported on a "de novo transcriptome assembly of *R. aegyptiacus*" and assessed its quality and biological validity.

In their phylogenetic study, Hassanin *et al.* (2016: 524) found that the *Cytb* from individuals collected in the eastern Mediterranean region (Cyprus and Egypt) differed by 13 mutations from populations of sub-Saharan Africa. Additionally, some *Cytb* haplotypes of southeastern Africa were found to be highly divergent from the others, whereas the population from West Africa did not differ significantly from that of Central Africa. Stribna *et al.* (2019: 2336) distinguished two mitochondrial haplotypes: Type I is widespread in regions where there is an extensive tree cover (e.g., tropical rain forests) and has close relationships to isolated lineages in the Middle East and islands in the Gulf of Guinea. The second type or haplogroup is sister to the rest of the *R. aegyptiacus* radiation and occurs in southern and eastern Africa, northwards to the Sudanian savanna, where it is found in habitats with semi-open land cover.

Wang *et al.* (2025b: 7) report that the total length of the genome is 1.89 Gb.

Other
Hoenerhoff and Williams (2004: 592) reported hepatic copper values for 7 individuals, which ranged from 5.42 to 99.20 parts per million on dry weight basis.

Águeda-Pinto *et al.* (2019: 4) studied the *S100A7* (S100 Calcium Binding Protein A7 = psoriasin) gene in a number of bats and found that *R. aegyptiacus* possessed three copies of this gene, which might contribute to the bat's enhanced tolerance for infections.

Stasiak *et al.* (2018: 683) indicate that hemochromatosis (iron storage disease or iron overload) is a frequent cause of liver disease and mortality in captive Egyptian fruit bats. They found that Hepcidin mRNA expression increased in response to iron administration in healthy bats. The excessive iron can also be stored in the spleen, the heart, skeletal muscle, pancreas, kidneys, and various other tissues (Farina and Lankton, 2018: 610).

Haematological data were also collected by Moreno *et al.* (2021), including: erythrocyte count (RBC - 9.41 ± 0.68 10^{12}/l), total leukocyte count (WBC - 4.2 ± 1.4 10^{9}/l), platelet count (PLT - 186 ± 61 10^{9}/l), haemoglobin concentration (12.4 ± 1.0 g/dl), mean corpuscular volume (MCV - 37.7 ± 1.5 fl), haematocrit (HCT - 35.5 ± 3.1 %), mean corpuscular haemoglobin (MCH - 13.2 ± 0.3 pg), mean corpuscular haemoglobin concentration (MCHC - 35.1 ± 1.5 g/dl) and red cell distribution width (RDW - 11.0 ± 1.2 %).

Takeda *et al.* (2022: 1) experimentally studied the influence of some rodenticides on captive *R. aegyptiacus* and found that diphacinone had a similar effect on the bats as on the rats, but for warfarin, they found that this was excreted much faster in the bats than in the rats and the bats recovered much quicker from the toxic effects.

Gal *et al.* (2025: 4) found that *R. aegyptiacus* bats living in urban areas have lower blood hemoglobin (HGB) values than bats living in rural areas, which they attribute to higher levels of polution in the urban areas. None of the other blood parameters they examined (red blood cell count, white blood cell count, mean corpuscular varlue and hematocrits) showed any correlation with the polution levels.

HABITAT:
Sclater (1868: 404) reported on a "*Cynonycteris collaris*" specimen that was captured at sea off the St. John's River in Natal on 1 March 1868.

Arumoogum *et al.* (2019: 188) simulated the role of biotic and a-biotic factors in view of climate change and found that the current suitable habitat is primarily mediated by temperature, but under both moderate and extreme future climate change scenarios the most influential factor would be the distribution of freestanding fig trees.

Weinberg *et al.* (2022: 6) indicated that bats in Israel (but probably also in Egypt, Jordan, Lebanon and Turkey) are attracted to cities due to its accessible and versatile diet, the higher temperature in cities, and the availability man-made roosting structures.

Becker *et al.* (2025: 2) indicate that *Rousettus aegyptiacus* occupies seven distinct habitat types as defined by the IUCN.

HABITS:
Jacobsen and Du Plessis (1976: 271) report that, in South Africa, radio-tracked *R. aegyptiacus* specimens travelled 24 km between their roost and foraging sites, which took them about 1 hour and 29 minutes at an average speed of 16.2 km/h (see Jacobsen *et al.*, 1986: 207). They also found that these bats foraged on *Ficus* spp. inside the forest canopy and that seeds were dispersed while flying and consuming fruit on perches. The bats left their roosts between 20 and 40 minutes after sunset and started to return at 2 a.m., with a peak around 3.45 a.m. and most were back at 5 a.m.

In Cape Town, Barclay and Jacobs (2011: 468) report that individuals left the roost cave between 21 and 183 minutes after sunset, and that bats left their roosts later when it was raining at their usual emergence time. Furthermore, males left later than females in September - October (during early pregnancy), but not in November - January (during late pregnancy and lactation). The difference in emergence time between females and males in September - October is attributed to the males having to defend their roosting territory (Barclay and Jacobs, 2011: 471), and not to females having to reach fruit resources before males, or to travel to more distant fruit patches, because of the greater energy demands as was also suggested by Korine *et al.* (1994) for *R. aegyptiacus* in Israel. Barclay and Jacobs (2011: 469) also observed that the individuals left their roost in a consistent order. The bats returned to their roost between 217 and 21 minutes before sunrise, without any differences among the sexes. Barclay and Jacobs (2011: 469) furthermore found that native forest was preferred over residential areas (59.1 % versus 40.9 %) to forage in, but there were great individual differences.

Tsoar *et al.* (2010: 300) report that tracked fruit bats flew over relatively long distances (14.6 ± 3.7 km) at a speed of 33.0 ± 5.2 km/hr and at relatively high altitudes (108 ± 52.6 m) to commute between their roosting and feeding sites. Geva-Sagiv *et al.* (2015: 99) indicate that there are five main types of navigational strategies: beaconing, route following (or route guidance), path integration, cognitive map, map and compass. They also suggest that combinations of these strategies can be used.

In the Dakhla Oasis in Egypt; Lučan *et al.* (2011: 36) reported that some individuals made quite long flights of about 60 km at the beginning of their night activity. They also found that spatial activities (e.g., roost changes and night exploration of foraging grounds) was strongly reduced by the end of winter, when few food resources remained available. Bachorec *et al.* (2020b: 1), however, observed a decrease in home range size during spring, when food availability was lowest. Using an automated tracking system, Řeřucha *et al.* (2014: 14) found

that the feeding time showed a much larger variation in summer than in spring or winter, whereas the search time per night remained more or less stable. The opposite was true for winter, where the total feeding time remained more or less stable, but the total search time showed a large variation. Bachorec *et al.* (2020b: 11) also found that, when food was abundant, Egyptian fruit bats choose to forage with more related individuals.

Jahelková and Vašíčková (2010: 182) describe some social calls and social behaviour (e.g., protection of mother and juvenile by a male during lactation) in a captive population. Prat *et al.* (2016: 1) examined the vocalizations of these bats and found that these contained information about identity of the emitter, the context of the call, the behavioural response to the call, and even the call's addressee. These vocalizations are composed of sequences containing 1 to 20 broad-band multi-harmonic syllables. Almost all of the communication calls were emitted during aggressive pairwise interactions.

Mann *et al.* (2011: 416) indicated that males do not form random associations with nearby conspecifics, but that they establish stable groups, in which some form of dominance hierarchy exists. They also found that *R. aegyptiacus* can make a distinction between familiar and unfamiliar conspecifics, most likely by means of olfactory and/or visual cues (Mann *et al.*, 2011: 411).

Bachorec *et al.* (2020b: 11) found that Egyptian fruit bats choose to forage with more related individuals but only during periods with plentiful food sources, suggesting that the bats rely on foraging decisions of relatives when things are good and follow group decisions when conditions are harsh.

In urban areas in Israel, Egert-Berg *et al.* (2021: 2) found that the bats visited more sites per hour and switched foraging sites more often on consecutive nights than in rural areas. They also found that many bats choose to roost in the countryside but during the night (for about 45 % of the time), they travelled to more urban areas to forage, whereas bats roosting in urban environments foraged for 72 % of their time in urban areas. Toledo *et al.* (2020: 188) collected four years of movement data and found that the bats only seldom used random search patterns, but often forage in goal-directed, long, and straight flights that include frequent shortcuts.

Harten *et al.* (2019a: 157) distinguished five steps during assisted learning of foraging: (1) Pups are attached to their mothers 24/7; (2) Gradual-detachment: Mothers carry pups for shorter bouts, drop-off pups on a tree, forage alone, then pick-up pups on their way back to the cave; (3) Pups are left alone in the cave; (4) Pups fly independently to known sites, where their mothers previously dropped them off; (5) Pups expand foraging to new sites unique to them. Goldshtein *et al.* (2021: 2) more or less make the same distinction, but do not differentiate between steps 3 and 4.

ROOST:
Type - Caves (Albayrak *et al.*, 2008); abandoned factories (Albayrak *et al.*, 2008).
Microclimate - Unknown.

R. aegyptiacus prefers to roost in deep and dark caves and do not inhabit talus caves (Makenov *et al.*, 2023: 5), nor trees (Weinberg *et al.*, 2023: 779).

Orozco (2012: 379), referring to Braack (1989), indicates that no scarab beetles were found in over 40 South African caves inhabited by *R. aegyptiacus*. Braack (1989: 77), however, does mention the presence of reduviid bugs (*Platymeris guttatipennis* (Stal)) preying on cockroaches (*Gyna caffrorum* (Stal, 1856), *Gyna* spp., *Herbardina* spp., *Symploce incuriosa* (Saussure, 1899)), parasitic evaniid and chalcidoid wasps (*Hockeria* sp.), trogid beetles (*Trox zumpti* Haaf, 1957) utilizing dead bats, tenebrionid (*Tenebrio guineensis Imhoff, 1843*) and ptinid beetles, thysanurans, as well as numerous haematophagous argasid ticks (*Ornithodoros faini* Hoogstraal, 1960) and nycteribiid flies (*Eucampsipoda africana* Theodor, 1955) using the bats as food source. Other "visitors" of cave, inhabited by *R. aegyptiacus*, were ants (*Pheidole crassinoda* Emery, 1895), spiders (*Smeringopus* sp.), troglophilic crickets,

In South Africa, Herzig-Straschil and Robinson (1978: 104) found *R. aegyptiacus* roosting together with *Miniopterus natalensis* [as *M. schreibersi*], *Rhinolophus capensis*, a few *M. fraterculus* and possibly *R. clivosus*. Similar associations were also reported from Zambia (Leopard's Hill cave) by Grafitti *et al.* (2003: 70), who reported on a colony of approximately 10,000 *R. aegyptiacus*, together with three colonies of *M. schreibersi* of about 50 - 300 animals, and single specimens of *R. hildebrandtii, R. simulator* and *Nycteris* sp.

Happold and Happold (2023:73) mention that these bats have to live in colonies and huddle together to stay warm as they do not become torpid nor hibernate.

DIET:
In Turkey, Albayrak *et al.* (2008) found two wild fruits were important (*Ficus elastica* (Rubber Tree) and *Melia azadirachta* (Persian Lilac)). In South Africa, Barclay and Jacobs (2011: 467) report that the diet includes the fruit of multiple species of figs, but also those of Cape Ash (*Ekebergia capensis* Sparrm.), Saffronwood (*Cassine crocea* (Thunb.) Kuntze), Yellowwood (genus *Podocarpus* Persoon), *Diospyros* L., and *Syzygium* R. Br. Ex Gaertn. Herzig-Straschil and Robinson (1978: 101) also included Bushman's Poison (*Acokanthera oppositifolia* (Lam.) Codd) and Mistletoe (*Viscum obscurumi* Thunb.).

Lamb *et al.* (2010: 215) reported that Cypriotic *R. aegyptiacus* specimens fed on *Agave americana* (Century Plant) during mid-summer, but moved on to *Ficus carica* (Figs) when these became available. During late-winter, the most important food items were *Phoenix dactylifera* (Dates), *Melia azedarach* (Persian Lilac), and flowers of Eucalypt, *Myrtus communis* (Common Myrtle), Mandarines and Lemons. Del Vaglio *et al.* (2011: 283) identified 11 plant species in the droppings of Cypriotic specimens, including *Melia azedarach* (Perzian Lilac or Chinaberry Tree), *Morus* spp. (Plum Tree), *Ceratonia siliqua* (Carob Tree or St John's-bread), *Eryobotria japonica* (Loquat, Japanese Medlar or Japanese Plum), *Ficus carica* / *F. microcarpa* (Common Fig / Laurel Fig), *Arbutus andrachne* (Eastern or Greek Strawberry Tree), *Washingtonia filifera* (Washingtonia), *Crataegus azarolus* (Mediterranean Hawthorn), *Citrus sinensis* (Orange Tree), and *Styrax officinalis* (Stirax). All of these plant species had limited economic importance.

In Israel, Egert-Berg *et al.* (2021: Suppl.) reported the following fruit species to be visited by *R. aegyptiacus*: Anacardiaceae: *Mangifera indica* (Mango), *Pistacia atlantica* (Mt. Atlas Mastic Tree), *Schinus molle* (Peruvian Pepper Tree); Araliaceae: *Schefflera actinophylla* (Australia Umbrella Tree); Arecaceae: *Dypsis decaryi* (Triangle Palm), *Phoenix canariensis* (Canary Island Date Palm), *Phoenix dactylifera* (Date Palm), *Sabal palmetto*, *Syagrus romanzoffiana* (Queen Palm), *Trachycarpus fortunei* (Chinese Windmill Palm), *Washingtonia filifera* (California Fan Palm), *Washingtonia robusta* (Mexican Washingtonia); Bignoniaceae: *Jacaranda mimosifolia* (Jacaranda); Caricaceae: *Carica papaya* (Papaya); Cycadaceae: *Cycas revoluta* (Sago Palm); Ebenaceae: *Diospyros kaki*, *Diospyros nigra* (Black Sapote); Fabaceae: *Albizia lebbeck*, *Ceratonia siliqua* (Carob), *Cercis siliquastrum*, *Dalbergia sissoo* (Agara), *Tipuana tipu* (Tipa); Juglandaceae: *Carya illinoinensis* (Pecan); Lauraceae: *Persea americana* (Avocado); Lythraceae: *Punica granatum*; Malvaceae: *Bombax ceiba* (Cotton Tree), *Brachychiton acerifolius*; Meliaceae: *Melia azedarach*; Moraceae: *Ficus benghalensis* (Indian Banyan), *Ficus benjamina*, *Ficus carica* (Edible Fig), *Ficus elastica* (Rubber Plant), *Ficus lyrata* (Fiddle-leaved Fig), *Ficus microcarpa* (Chinese Banyan), *Ficus neriifolia*, *Ficus religiosa* (Peepul Tree), *Ficus rubiginosa* (Port Jackson Fig), *Ficus sycomorus* (Sycamore Fig), *Morus nigra* (Black Mulberry); Muntingiaceae: *Muntingia calabura* (Calabur Tree); Myrtaceae: *Callistemon phoeniceus* (Bottlebrush), *Eucalyptus camaldulensis* (River Red Gum), *Psidium cattleyanum* (Cattley Guava); Oxalidaceae: *Averrhoa carambola* (Starfruit); Rhamnaceae: *Hovenia dulcis* (Japanese Raisin Tree), *Ziziphus spina-christi* (Christ's Thorn Jujube); Rosaceae: *Eriobotrya japonica* (Loquat), *Malus domestica* (Apple), *Prunus amygdalus n.p.a.*, *Prunus armeniaca* (Apricot), *Prunus persica* (Peach), *Pyrus* (Pears); Rutaceae: *Citrus* × *sinensis* (Sweet Orange); Salicaceae: *Populus euphratica* (Euphrates Poplar); Sapindaceae: *Alectryon tomentosus* (Hairy Birds Eye), *Dimocarpus longan* (Longan), *Litchi chinensis* (Lychee); Solanaceae: *Physalis peruviana* (Cape Gooseberry); Tamaricaceae: *Tamarix aphylla*; Ulmaceae: *Celtis sinensis*; Verbenaceae: *Citharexylum spinosum*; Vitaceae: *Vitis vinifera* (Wine Grape).

Ganitskiy and Tikhomirova (2021: 67, 68) observed *R. aegyptiacus* specimens in Turkey chewing leaves of the palm tree *Syagrus romanzoffiana* and sucking out all the juices. As this tree is a recent introduction, its use as a food resource is a very recent adaptation. Ganitskiy and Tikhomirova (2021: 68) also refer to Korine *et al.* (1999), who reported that, in Israel, leaves of *Ficus religiosa* make up to 6 % of the bat's diet.

Baum (1995: 339) mentioned that *R. aegyptiacus* is a frequent visitor of *Adansonia digitata* (Baobab), especially in the first two hours after dusk, where they licked nectar from the petal bases. Jacobsen and Du Plessis (1976: 271) found that in South Africa this bat fed mainly on *Ficus* spp. [*F. capensis, F. petersii, F. sansibarica*], although other fruits (e.g., *Litchis chinensis* - Litchis, *Syzgium gerrardii* - Water Pear, *Syzgium jamba* - Jamba, *Syzygium cordatum* - Waterberry, *Harpephyllum caffrum* - Kaffll Plum, *Ekebergia capensis* - Cape Ash, *Prunus africana* - Bitter Almond/Red Stinkwood, and possibly *Olea capensis* and *O. africana*) were eaten in other seasons. Nader and Kock (1983c: 271) also reported that captive bats ate 8 to 9

litchis per night or 97 g of fruit (Bananas). The bats were probably also feeding on the nectar of *Aloe dolomitica* as they found a number of animals covered in pollen and their faeces contained pollen too.

Seltzer *et al.* (2013: table S2) provided an overview of the plant species found beneath bat feeding roosts. For *R. aegyptiacus* these include *Ficus mucuso* Welw. ex Ficalho (Ipoh's Terrible Tree - Moraceae), *Ficus sur* Forssk. (Broom Cluster Fig - Moraceae) and *Eriobotrya japonica* (Thunb.) Lindl. (Loquat - Rosaceae).

Amitai *et al.* (2010: 2693) used stable carbon isotope ratio in exhaled CO_2 to assess the origin of metabolized substrates in 16 *R. aegyptiacus*, which were maintained on a diet of C3 plants. Amitai *et al.* (2010: 2693) found that both resting and flying individuals directly fueled their metabolism with freshly ingested exogenous substrates.

In Cape Town, Barclay *et al.* (2006: 549) observed *R. aegyptiacus* deliberately feeding on Scarabid Garden Fruit Chaffer Beetles (*Pachnoda sinuata*). Del Vaglio *et al.* (2011: 285) also reported the presence of coleopterans, lepidopterans (caterpillars), dipterans (fruit flies) and ticks in the bat's droppings, but these were most probably ingested by accident. Clare and Oelbaum (2024: 242) indicate that records of insectivory from other areas in this species' range are very scarse, but it might nevertheless be widespread, potentially during times of food scarcity.

In his study on *R. aegyptiacus* from the Kruger Park, Braack (1989: 79) found that they were feeding on the fruits of *Ficus sycomorus* (Sycamore Fig or Fig-mulberry), *Diospyros mespiliformis* (Jackalberry, African Ebony, Jakkalsbessie), and *Xanthocercis zambesiaca* (Mashatu Tree or Nyala Tree).

In the Kisangani area (DRC), Gembu Tungaluna (2012: 106 - 108) followed the fruit intake by *R. aegyptiacus* during the different seasons and came up with the following list: First heavy rain season (September - November): *Carica papaya* L. (papaya) (28%), *Musanga cecropioides* R. Br. & Tedlie (African Corkwood Tree, Umbrella Tree) (14%), *Dacryoides edulis* H.J. Lam (Safou, African Pear, Bush Pear, Nsafu, Bush Butter Tree, Butterfruit) (11%), *Persea americana* Mill., 1786 (Avocado) (8%), *Oncoba welwitschii* Oliv. (8%), *Myrianthus arboreus* P. Beauvois, 1805 (Giant Yellow Mulberry, Bush Pineapple, Corkwoord) (8%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, Otaheite Apple, Great Hog Plum) (6%), *Annonidium mannii* (Oliv.) Engl. & Diels (Junglesop) (6%), *Ficus wildemanniana* Warb. (5%), *Ficus leprieuri* Miq., 1867 (3%), *Ficus vallis-choudae* Delile (3%).
First mild rain season (December - February): *Musanga cecropioides* (36%), *Myrianthus arboreus* (22%), *Ficus vallis-choudae* (10%), *Annonidium mannii* (6%), *Spondias cytherea* (6%), *Carica papaya* (6%), *Uapaca guineensis* Müll. Arg., 1864 (Sugar Plum, Red Cedar, False Mahogany, Rikio) (6%), *Elaeis guineensis* Jacq. (African Oil Palm, Macaw-fat) (2%), *Ficus wildemanniana* (2%), *Pseudospondias microcarpa* (A. Rich.) Engl. (2%), Musa sp. (2%).
Second heavy rain season (March - May): *Persea americana* (19%), *Annonidium mannii* (16%), *Carica papaya* (16%), *Dacryoides edulis* (11%), *Spondias cytherea* (10%), *Musanga cecropioides* (7%), *Oncoba welwitschii* (7%), Myrianthus cecropioides (7%), *Uapaca guineensis* (3%), *Ficus vallis-choudae* (3%), Musa sp. (3%), *Parinari excelsa* Sabine (Guinea Plum) (1%), Ficus sp. (1%).
"Dry" season (June - August): *Oncoba welwitschii* (29%), *Ficus vallis-choudae* (15%), *Parinari excelsa* (14%), *Carica papaya* (14%), *Myrianthus arboreus* (14%), *Musanga cecropioides* (14%).

Izhaki *et al.* (1995: 340) report, that in Israel, *R. aegyptiacus* ingested only 2 % of the small seeds (< 4 mg), all other seeds were spat out between 25 and 400 m from the parent tree. Korine *et al.* (1998: 151) indicate that *R. aegyptiacus* feeds on two types of fruit ("syndromes"). The first one is similar to that eaten by most fruit bats: variable size (range 0.53 - 32.3 g), relatively high water content (57 - 87 %), relatively low fat content (1.3 - 4.1 %), low protein content (1.1 - 6.75 %), and relatively high sugar content (69 - 86 %). The second type is only found in eastern Mediterranean habitats and is characterized by the extremely low water content: 13 - 24 %. This type of food is generally eaten during winter, when other food sources are scarce.

A case of hemochromatosis or ISD (iron storage disease or excessive burden of iron) was reported by Clauss and Paglia (2012: S8) as the result of an accidental excessive dietary iron supplementation. Stasiak *et al.* (2014: 111) investigated whether mutations in the hepcidin gene might be the reason for the increased susceptibility to ISD, but they were unable to identify any differences in the sequence of the portion of the hepcidin gene that encodes the mature peptide. In their ISD study, Leone *et al.* (2016: 45) provided evidence of a positive correlation between hemochromatosis and HCC in any species other than humans.

In a study of *R. aegyptiacus* this was not evident as its blood plasma glucose concentrations were observed to be greater than 40 mmol/l after glucose uptake (Keegan, 1977; Michelmore *et al.*, 1998), this was not after natural feeding but during an oral glucose tolerance test (Mqokeli and Downs, 2012a: 351).

Herrera M. *et al.* (2015: 409) investigated the relationship between food and energy intakes, salt content and sugar types.

On São Tomé, Heleno *et al.* (2021: 6, Suppl.) found that *Rousettus aegyptiacus* dispersed seeds of up to 34.4 mm in size (mean size: 9.21 mm and mean weight: 7.65 g). These seeds belonged to *Annona muricata*, *Anthocleista* cf. *scandens*, *Artocarpus altilis, Artocarpus heterophylla, Averrhoa carambola, Carica papaya, Cecropia peltata, Dacryodes edulis, Discoglypremna caloneura, Eriobotrya japónica, Ficus* sp., *Mangifera indica, Milicia excelsa, Musa* sp., *Musanga cecropioides, Psidium guajava, Santiria trimera, Sterculia tragacantha*.

Pawęska *et al.* (2021: 4) found *Ficus sycomorus* L. to form the basic food for this bat in the Matlapitsi Valley (RSA), although *Ficus petersii* Warb., 1894 and *Ficus sansibarica* Warb., 1894 and other fruits are also eaten when available.

Dubrovina (2022: 494) [referring to Vilk et al., 2022] mentioned that during the summer, the bats were foraging at fewere locations than during the winter, probably because the abundance of fruit lowered the motivation for risky journeys to search for new fruit trees.

In their review paper Sivault *et al.* (2023: Suppl.) reported the following fruits and seeds were eaten by *Rousettus aegyptiacus*: *Ekebergia capensis* Sparrm., 1779, *Ficus capensis* Thunb., 1786, *Ficus sansibarica* Warb., 1894, *Ficus sur* Forssk. 1775, *Ficus thonningii* Blume, 1839, *Parkia bicolor* A. Chev., 1908, *Prunus africana* (Hook.fil.) Kalkman, 1965, *Syzygium cordatum* Hochst., 1844.

PREDATORS:
Jacobsen and Du Plessis (1976: 273) indicate that *R. aegyptiacus* has relatively few natural enemies in South Africa, but that genets (*Genetta* sp.) and Lanner falcon (*Falco biarmicus* Temminck, 1825) took them as prey.

Mikula *et al.* (2016: Supplemental data) mention the following avian predators: Black sparrowhawk (*Accipiter melanoleucus* A. Smith, 1830), Lanner falcon (*Falco biarmicus* Temminck, 1825), Peregrine falcon (*Falco peregrinus* Tunstall, 1771), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850); Black-and-white-casqued hornbill (*Bycanistes subcylindricus* (P.L. Sclater, 1871)).

Mikkola (2018: 4) shows a photo of a dead bat (with sucking pup) brought to the nest by an Eagle owl (*Bubo bubo* (Linnaeus, 1758)).

Mikula *et al.* (2024: 159) also show a photo, but of a bat captured by an African Rock Python (*Python sebae* (Gmelin, 1789)).

Chen *et al.* (2025: 1) name black rats (*Rattus rattus*) as potential predators.

POPULATION:
Structure and Density
Common in parts of Africa; generally uncommon in SW Asia although locally abundant in Israel and Jordan (Z. Amr *pers. comm.,* 2005 in Benda *et al.*, 2008a in IUCN, 2009 and Korine (2016)). In Africa it occurs in large colonies of up to 40,000 to 50,000 individuals. In SW Asia colonies generally number 50 to 500 individuals, although up to 3,000 individuals were recorded in a cave in Jordan. The population in Turkey is estimated at 5,000 to 10,000 individuals; the population there may be decreasing due to control measures in caves (A. Karatas *pers. comm.,* 2007 in Benda *et al.*, 2008a in IUCN, 2009 and Korine (2016)). In Syria only a single locality is known of 1,000 to 2,000 animals (A. Karatas *pers. comm.,* 2007 in Benda *et al.*, 2008a in IUCN, 2009 and Korine (2016)). Also see Albayrak *et al.* (2008).
Horáček *et al.* (2010: 175) indicate that there is a clear decline in the Cypriote population, whereas the situation in other Mediterranean countries (Lebanon, Jordan, Egypt) is more or less stable. They estimate the total Mediterranean population to include at most 75,000 specimens. Lučan *et al.* (2014c: 111) report a population decline of 90 % on Cyprus between 2005 and 2013 (from 8,000 to 800 animals).

Trend
2016: Stable (Korine, 2016). 2008: Stable (Benda *et al.*, 2008a; IUCN, 2009). *R. aegyptiacus* populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

LIFESPAN:
Mitchell (1911: 444) mentions for 13 captive specimens (as *Cynonycteris collaris*) an average lifespan of 18 months and a maximum lifespan of 108 months (= 25 yrs). Cushing *et al.* (2013: 794) reported on a captive female of over 11 years of

age that needed to be euthanised following a deterioration of its health due to a metastatic pancreatic carcinoma. Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 22.9 years.

Olds *et al.* (2015: 325) found the following tumour types in a captive population of male *R. aegyptiacus*: fibrosarcoma, cutaneous lymphoma, benign focal bronchioloalveolar neoplasm, anaplastic sarcoma, and sebaceous epithelioma.

ACTIVITY AND BEHAVIOUR:
Carpenter (1986: 93) mentions that the heartbeat for this species is as high as 728 beats per minute (bpm) during a flight with airspeeds of 5 m/s. Currie *et al.* (2019: 187) reported that over a 24 hour period the heartbeat can vary from 200 to 800 bpm.

During displacement experiments, Tsoar *et al.* (2011: E722) found that *R. aegyptiacus* primarily uses self-triangulation based on multiple distal visual landmarks to return to their roost cave. Ulanovsky *et al.* (2010: 302) provide evidence that the bats used a large-scale navigational map to return to their roosts after having been displaced over 44 km.

From flight corridor tests, Riskin *et al.* (2012: 2946) determined the average flight speed to be 4.41 ± 0.54 m/s.

In another flight corridor test, Sánchez *et al.* (2010: 555) found that bats fed with alcohol-rich fruits flew significantly slower than when fed with alcohol-free fruits. Additionally, the bats echolocation calls and behaviour changed too. (This research was awarded the 2025 IgNobel price for Aviation.)

In captive groups, Carter and Leffer (2015: 3) found that a group consisting of nine females and two castrated males spent 0.26 % of their awake time on social grooming. In a group of five males, no social grooming was observed at all.

Moreno *et al.* (2021: 1) studied the behaviour of "sick" bats and found them to perch alone and they appeared to voluntarily isolate themselves from the group. They also leave their roost for two or more nights, thereby reducing the risk of infecting bats from neighbouring roosts.

In Israel, Eitan *et al.* (2024: 1) found a shift in activity toward to a diurnal timeframe, especially in an urban environment and in females. They suggest that the shift in females is possibly linked with their reproductive metabolic demands

REPRODUCTION AND ONTOGENY:
Korine and Arad (1999) [in Andrianaivoarivelo *et al.* (2011a: 77)] mention that the new-borns of *R. aegyptiacus* are completely dependent on their mothers for the first 6 weeks of life. At birth, the pup weights about 18.0 % of the mother's body mass (22.7 versus 126.0 g) (Kurta and Kunz, 1987: 82). Barclay and Jacobs (2011: 467) indicate that the lactation period lasts from 9 to 12 weeks in South Africa. Davis (2007: 4) indicates that young are dependent until three months after birth in the UAE. At that time, they can fly, but do not leave the family colony.

In Uganda, Mutere (1968) observed a bimodal breeding pattern (pregnancies from December to March and from July to October and births in March and October), which was correlated to two rainfall peaks (April-May and October-November). Bartonička *et al.* (2013: 17) report that in both the Levant (Turkey, Cyprus, Lebanon and Jordan) and in the Dakhla Oasis in Egypt, births take place during most of the year, except for the winter months. The births peak in April-May and in August-September.

For Malawi, Happold and Happold (1990b: 564) reported births in mid-October, but they had no data for other months.

In Sierra Leone, Weber *et al.* (2019: 20) captured one lactating female on 7 April.

Lučan *et al.* (2014a: 110; 2014b: 1036) investigated the reproductive cycle in populations from the Mediterranean region and the Egyptian desert and found that both had a bimodality in birth timing regardless of climatic differences. The differences in birth times between the two populations were linked with differences in fruiting phenology of their major dietary plants. They also hypothesize that food abundance is an important trigger of male sexual activity.

In the Giza Governorate (Egypt), Taha and Soliman (2024: 281) distinguished four phases in the reproductive cycle of males: an active phase in autumn and the early winter (October to January), a regressing phase in late winter and early spring (February to April), a regressed phase in late spring and summer (May to August), and a recrudescence phase in early autumn (September). Males were considered sexually inactive between June and August as no active sperms were found in the cauda epididymis. Reproductively active females (pregnant, lactating) were found year-round with peaks in June-July and November-January.

Spitzenberger and Bauer (1979: 440, 448) also found a bimodal reproduction cycle for *R. aegyptiacus* on Cyprus, but remarked that the succession of the two phases is so quick that females only take part in one cycle.

Kozhurina and Ilchenko (2016: 13) found a bimodal reproduction cycle in captive *R. aegyptiacus* with a "tropical" polyoestrous continuous reproductive pattern, but found their cycle to take 11 months rather than 12. They also found that females usually began to produce offspring at the age of 14 - 15 months up to 2 years. The gestation period was very variable and lasted from 95 to 129 days. However, Tal and Shilo-Benjamini (2023: 1) mention that, in captivity, these bats reproduce year round, with births in every month.

Dietz and Kiefer (2016: 208) mention that occasionally females can carry two embryos of different size indicating that they can become pregant in both reproduction periods.

Mahmoud *et al.* (2018: 293) tested 3-monochloropropane-1, 2-diol (3-MCPD) to sterilize male rousettes to assess its use as pest management tool.

Stanley and Goodman (2011: 40) reported on three adult males with scrotal testes collected in the first half of August 1992 in Tanzania. Two females collected in the first half of August 1992 and 1993 were pregnant with a single embryo. Trentin and Rovero (2011: 49) report a lactating female captured in December 2005 in the Uzungwa Scarp Forest Reserve, Tanzania. For West Africa, Krutzsch (2000: 110) indicates that the male reproductive cycle is apparently in synchrony with the female, since they undergo biseasonal testicular hypertrophy.

In the southern Cape province of South Africa, Herzig-Straschil and Robinson (1978: 108) calculated that births took place from October to June. At Matlapitsi (RSA), Dietrich *et al.* (2018b: 4) found that 64 % of the females they sampled in September 2015 were pregnant, indicating that there were also non-pregnant females and both scrotal and non-scrotal males. In January 2016, they found large amounts of juveniles and lactating females, whereas in April 2016, most of the bats (83 %) were flying juveniles.

Weinberg *et al.* (2025) investigated the births in rural and urban bat populations and found that urban bats in spring gave birth some 2.5 weeks earlier than in rural environments. They also found that the reproductive success was not lower in urban populations.

In the United Arab Emirates, Davis (2007: 4) indicated that mating takes place from June to September, and that a single young (exceptionally twins) are born in October-December after a gestation period of 115 to 120 days. Szekely *et al.* (2015: Suppl.) report a gestation period of 116 days and they mention that weaning occurs after 122 days. During that period, the weight of the young has increased from 21.06 g to 73.8 g (adult: 125 g).

Laboratory tests performed by Taub *et al.* (2014: S122) provided strong evidence for vocal learning in this species.

Khannoon *et al.* (2020: 309, 313) described 13 developmental stages from middle pharyngula through immediately before birth, indicating that the wings are formed during stages 19 to 20. The nasal pits appear at stages 14 to 15, and at stage 17, the face starts to look 'fox-like' to attain its final shape at stage 19. Until stage 22, the crown-rump length of the embryo is very similar to that of embryos of other bat species, but then it starts to grow very rapidly.

Usui *et al.* (2022: 1) investigated the development of the facial muscles.

MATING:

Webber *et al.* (2017: Suppl.) indicated that *R. aegyptiacus* has a polygynandrous mating system.

Jacobsen and Du Plessis (1976: 272) and Barclay and Jacobs (2011: 467) mention that in South Africa, *R. aegyptiacus* mates in spring (July to September) and, after a gestation of approximately 4 months, a single pup is born in summer (end October to December). Occasionally, Start (1969: 272) recorded the birth of twins.

In a colony in the Prague zoo, Jahelková *et al.* (2013: 76) found courtship behaviour and matings taking place throughout the year, but parturitions were strongly synchronized in a one-week period in September/October and March/April.

In a captive colony in Israel, Harten *et al.* (2019b: 1895) determined the paternity of pups and found that females gave birth to young of males from which they used to scrounge food [=obtaining food from the mouth of the male], supporting the food-for-sex hypothesis in this species.

POSTNATAL DEVELOPMENT:

Prat *et al.* (2013: 123) studied *R. aegyptiacus* pups raised in small colonies and in acoustic

isolation and found that the latter displayed delayed vocal development and that their calls differed from young of the same age raised in colonies. The first sounds produced by young in both groups were isolation calls (Prat *et al.*, 2015: 1). These calls are innate and appear at postnatal day 1. Prat *et al.* (2017a) investigated vocal learning in pups that were exposed to playback calls, and found that their calls demonstrated distinct dialects, which were related to the playback calls they were accustomed to rather than to the calls produced by their mothers.

Noll (1979b: 89) was able to proof that starting from day 7, thermoregulation by means of control variations in body temperature occurs, and that metabolic response to cold reaches adult levels during the pups third week. He also found that - at birth - the young weighs 22.7 ± 2.5 g and have a forearm length of 38.2 ± 0.2 mm. Around day 36, the weight has doubled, but adult weight was not yet reached at day 200.

Smarsh *et al.* (2019: 136) found that pups can hear from day 0 onwards and are sensitive to all sounds, including calls and noise, suggesting that bats may not learn prenatally.

Genzel *et al.* (2019: 1) studied the vocal plasticity in adult bats and found that adult bats are able to modify distinct parameters of their vocalizations when exposed to broad-band, acoustic perturbation. The changes can persist months after the noise has ceased.

Harten *et al.* (2021: 1) found that urban pups displayed higher risk-taking levels, were faster learners, but less exploratory than rural pups and that these traits were acquired via post-birth non-genetic maternal effects, possibly through hormonal transfer from their mothers.

Nkoana *et al.* (2023: 169) distinguished five growth development stages based on the cranial suture fusion and the degree of second molar tooth eruption. The smaller stages (1, 2, 3) showed little overlap with the larger stages (4 and 5). Stages 1, 3 and 5 could be predicted based on linear morphometrics.

Soliman and Taha (2024: 149) used dried eye lens weight as an indicator for age (10 relative age groups) in this bat. They found that the average forearm length and the mean lenght of the fifth digit on the one hand and the eye lens weight on the other hand both increased upto group four in males (30 - 40 mg) and group six (50 - 60 mg) in females. For the mean third digit length, the increase was similar upto group three in males and group five in females.

Dudorova *et al.* (2024: 251) studied the affiliative relationships between adult males and juvenile bats left at the roost while their mothers were out foraging. The adult males did not show any sign of avoidance or aggression toward the infants, and the latter could stay in physical contact with the adult for up to 50 % of the time their mothers were away. This behaviour lasted until the youngsters became 100 - 120 days of age and started to fly. At that time, the adult males began to react aggressively towards the juvenile males and started exhibiting mating behaviour towards the females.

PARASITES:

BACTERIA

Federici *et al.* (2022: 5) [referring to Dietrich and Markotter (2019)] mention Proteobacteria of the genus *Actinobaccillus* and the Actinobacteria *Alkalibacterium* and *Nesterenkonia*.

Hughes *et al.* (2018: 867) and Farina and Lankton (2018: 619) reported the presence of *Yersinia pseudotuberculosis* in bats from a zoo colony.

Gram-positive bacterium

Three out of 55 tested *R. aegyptiacus* bats from Gabon tested positive for *Staphylococcus aureus* and two for *S. schweitzeri* (Held *et al.*, 2016: 119). The positive bats were captured at the fringe of the forest, in the vicinity of humans. None of the bats that were captured in the forest were infected by this bacterium.

Gram-negative bacteria

Pinus and Müller (1980) and Sara (2002: 41) reported *Citrobacter freudii*, *Enterobacter cloacae*, *Escherichia coli*, *Klebsiella pneumonia*, *Proteus morganii*, and *Proteus rettgeri*. Han *et al.* (2010) isolated a pure sample of *Kluyvera ascorbata* from blood of an individual found dead at a zoo in Seoul, Korea, which had originally been imported (possibly illegally) from Egypt. Childs-Sanford *et al.* (2009: 8) reported *Yersinia pseudotuberculosis* from a colony of bats kept in a zoo in Syracuse, New York.

Two of three bats from the Republic of Congo, tested by Nowak *et al.* (2017: 6) were positive for *E. coli*.

Bartonellae - Bacteria

Bartonella - Kosoy *et al.* (2010: 1878) found 15 *Bartonella* spp. *gltA* sequences in *R. aegyptiacus*, and also found six unique *gltA* varients of *Bartonella* which clustered in a monophyletic genogroup. Kosoy *et al.* (2010: 1877) and Bai and Kosoy (2012: 58) reported a prevalence of *Bartonella* spp. in *R. aegyptiacus* from Kenya of

22/105 (21.0%) cultured from blood samples. See also Kosoy (2010: 719) for further information. Dietrich *et al.* (2016b: 3) found one positive testing bat (out of 7) in Mahune (RSA).
Bai *et al.* (2018: 2319) identified a new *Bartonella* species (*B. rousetti*) from bats collected in the Idanre Hills area in Nigeria, which can infect humans as they also found antibodies against this bacteria in people living in surrounding communities.
Candidatus Bartonella rousetti was reported from Zambian bats by Qiu *et al.* (2020: 1).

Lei and Olival (2014: Suppl.) mention *R. aegyptiacus* as host for *Leptospira* bacteria. These were further identified as *L. interrogans* and a second species as having sequences closely related to *L. borgpetersenii*.

Nakamura *et al.* (2012: 410) report on an outbreak of yersiniosis (caused by *Yersinia pseudotuberculosis*) in a colony of captive *R. aegyptiacus* in a zoological park in the Kanto region in Japan.

Kolodny *et al.* (2018: 116) examined the microbial composition of fur and gut samples of a captive and free-living colony of Egyptian fruit bats and found that the fur samples of different animals from the same colony taken at the same time were more similar than samples taken from the same animal at different time. The gut samples, however, were more individualized and sex related. The gut microbiome was also investigated by Berman *et al.* (2023) in relation to infections. They found that the antigen challenge caused a shift in the composition of the microbiome (specifically for *Weissella, Escherichia* and *Streptococcus*).

Dietrich and Markotter (2019: 1733, Suppl.) investigated the differences between direct and indirect sampling of urine and feces in South African *R. aegyptiacus*. During this study, they found the following bacteria in the urine (in descending LDA [Linear discriminant analysis] order): direct: *Streptococcus, Bacillus, Rhizobium, Brevudimonas*, Rhizobiales, *Corynebacterium, Achromobacter, Acinetobacter, Phenylobacterium, Deinococcus, Methylobacterium, Paenibacillus, Lyninibacillus, Cellulomonas, Cellulosimicrobium*, Planococcaceae, *Nocardiodes, Serratia, Devosia, Solirubracacter, Providencia, Brucella*, Sphingomonadacea, *Stenotrophomonas*, Oxalobacteraceae, *Gp4, Terribacillus, Gemmatimonas, Ochrobactrum, Gp6, Blastococcus*, Comamonadaceae, *Microvirga*, Sphingobacteriaceae, Microbacteriaceae, *Gp3*, Solirubrobacterales, *Massilia, Arthrobacter*, Geodermatophilaceae, *Microbacterium, Leucobacter*, Beijerickiaceae, Planococcaceae, Burkholderiales, *Shinella, Rubellimicrobium, Gp16, Novosphingobium*, Alcaligenaceae, *Rubrobacter*, Betaproteobacteria, *Dyadobacter, Actinomyces, Agromyces*, Ruminococcaceae, Polyangiaceae, *Lysobacter*, Bradyrhizobiaceae, *Moraxella, Aurantimonas*, Acetobacteraceae, *Flavobacterium, Ramlibacter, Caenispirillum, Bordetella, Leifsonia*, Paenibacillaceae_1, Bacillaceae_1, Xanthobacteraceae; indirect: Planctomycetes, *Lentibacillus, Actinocatenispora*, Xanthomonadales, *Marinomonas, Ignavibacterium*, Jiangellaceae, *Methylohalomonas, Fodinicurvata, Salinicoccus, Nocardiopsis*, Deinococcales, Ectothiorhodospiraceae, *Nitrosospira, Nocardia, Saccharopolyspora*, Nocardiopsaceae, Nakamurellaceae, *Ureoplasma, Pntibaca, Phycisphaera, Nitrococcus, Actinophytocola, Nesterenkonia, Luteibacter*, Enterobacteriaceae, *Jiangella, Brevibacteriu*, Bacteroidetes, Gammaproteobacteria, *Salinisphaera*, Actinomycetales, *Gracillimonas*. In the faeces, the following bacteria were found: direct: *Actinobacillus*, Pasteurellaceae, Flavobacteriaceae, *Salinisphaera, Gp1*, Gammaproteobacteria, *Kytococcus, Mycobacterium, Gracilimonas, Chryseobacterium, Mycoplasma*, Geodermatophilaceae, Chloroflexi, *Rhizobium*, unclassified Bacteria, *Helicobacter, Rhodococcus, Blastococcus, Deinococcus*, Chitinophagaceae, *Acinetobacter, Brevundimonas*, Sphingobacteriales, Comamonadaceae, *Sphingomonas, Mosesorhizobium, Comamonas, Gemmatimonas*, Proteobacteria, *Achromobacter, Agrmyces, Nitrosococcus, Devosia, Gp10, Gp3, Flavobacterium, Roseomonas, Marmoricola, Gp6*, Ectothiorhodospiraceae, *Campylobacter*, Solirubrobacterales, *Isoptericola*, Nocardioidaceae, Deltaproteobacteria, *Gordonia*, Sphingomonadaceae, Neisseriaceae, *Luteibacter, Actinomadura*, Erythrobacteraceae, Acidimicrobiales, "3_genus_incertae_sedis", *Nocardioides, Spirosoma, Truepera*, Sphingomonadales, *Moraxella, Solirubrobacter, Tessaracoccus*, Alphaproteobacterai, Myxococcales, *Paenibacillus*, Bacteroidetes, Oxalobacteraceae, *Stenotrophomonas, Phenyobacterium*, Caulobacteraceae, *Gp7, Arthrobacter*, Polyangiaceae, *Geminicoccus, Rubellimicrobium, Gp4, Azospirillum*, Sphingobacteriaceae, Rhodospirillaceae, *Dermacoccus, Nitrospira*, Pseudomonadaceae, Acetobacteraceae, *Cellulosimicrobium, Lysobacter, Dyadobacter, Sphingopyxis*, Betaproteobacteria, *Ornithobacterium*; indirect: *Granulicatella*, Carnobacteriaceae,

Streptococcaceae, *Alkalibacterium, Nesterenkonia*.

Modesto *et al.* (2019: 8, 9) described two new species of *Bifidobacterium* from the feaces of a captive colony of *R. aegyptiacus*: *B. vespertilionis* and *B. rousetti*.

In their review, Ramanantsalama *et al.* (2022b: 5) mention the following bacterial infections for *R. aegyptiacus*: *Bartonella rousetti*, *Bartonella* sp., *Borrelia* sp., *Escherichia* sp., *Mycoplasma* sp., *Leptospira interrogans*, *Leptospira borgpetersenii* or (-like), *Yersinia pseudotuberculosis*. They also mention the following Protozoa: *Eimeria rousetti*, *Heptocystis* sp., *Plasmodium rousetti*, *Plasmodium voltaicum*, *Trypanosoma* sp.

PROTOZOA

Perkins and Schaer (2016: Suppl.) mentioned the presence of *Plasmodium roussetti* van Riel, l'Hoest et l'Hoest, 1951 in bats from the DRC.

Adam (1973: 8) mention on an infection by *Trypanosoma megadermae* Wenyon, 1909. Barbosa *et al.* (2016: 215) and Espinosa-Álvarez *et al.* (2018: Suppl.) reported a specimen from Gabon being infected by "*Trypanosoma* sp. bat". Babyesiza *et al.* (2025: 4) mentioned *Trypanosoma livingstonei* and *T.* 'flying-fox' from Ugandan bats.

Atama *et al.* (2019: 1550) reported the first case of a *Hepatocystis* parasite present in *R. aegyptiacus* (in one of 32 bats from the Amurum forest reserve, Nigeria).

ACARI

Macronyssidae

Weinberg *et al.* (2023: 778) mention *Liponyssus glutinosus* [=*Macronyssus granulosus* (Kolenati, 1856)] and *Liponyssus longimanus* [=*Macronyssus longimanus* (Kolenati, 1856)] from Egyptian *R. aegyptiacus*.

Myobiidae

Bochkov and Fain (2003: 13) mentioned that *R. aegyptiacus* is the type host for *Binuncus (Binuncus) jamesoni* (Hiregaudar and Bal, 1956)

Spinturnicidae

Hirst (1923: 979) indicates that Kolenati stated that either *R. microphyllum* or *Pteropus ægyptiacus* [=*Rousettus aegyptiacus*] is the host for *Ancystropus zelebori* Kolenati, 1856 (Acari). Another mite, he reported (p. 987) from *R. aegyptiacus* is *Ancystropus* (*Meristaspis*) *lateralis* [=*Meristaspis lateralis* (Kolenati, 1856)]. Taufflieb (1962: 112) also reported *Ancystropus leleupi* Benoit, 1959.

Trombiculidae

Stekolnikov (2018a: 50) reported this species as host for *Whartonia novemsetosa* Goff, 1982 in Tanzania. Zajkowska *et al.* (2018: 140) mentioned *Trombigastia hirsuta* Vercammen-Grandjean and Fain, 1958 foud on a Congolese bat.

From the Lanner Gorge cave [22°27'S 31°09'E], in the Kruger National Park, Braack (1989: 81) reported argasid ticks (*Ornithodoros faini* Hoogstraal, 1960), nycteribiid flies *Eucampsipoda africana* Theodor, 1955), spinturnicid mites (*Ancystropus zeleborii*, Kolenati, 1857), and the flea *Thaumapsylla breviceps* Rothschild, 1907 (Ischnopsyllidae).

In Jordan, Benda *et al.* (2010b: 201) found the following ectoparasites: Argasidae: *Argas vespertilionis* (Latreille, 1802), *Ornithodoros* (*Reticulinasus*) *salahi* (Hoogstraal, 1953).

Sándor *et al.* (2021a: 4) reported the following argasid mites: *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933), *Reticulinasus salahi* (Hoogstraal, 1953), and *Carios vespertilionis* Latreille, 1802.

Nycteridocoptes pteropodi Rodhain and Gedoelst, 1923 (Acari: Sarcoptidae) was reported by Fain (1958: 236) from "*Rousettus leachi*" specimens from Kivu, DRC. Fain (1958: 244, 245) also described *Nycteridocoptes lavoipierrei*, *Nycteridocoptes macrophallus* and *Nycteridocoptes rousetti* from the same bat species collected at Mahuysa cave, Katana-Kivu, DRC. Another species (*Nycteridocoptes rousetti* Fain,1958) was mentioned by Fain (1959b: 345) from *R. aegyptiacus* from Thysville (=Mbanza-Ngungu), DRC. Fain (1960: 83) described *Stomatodex rousetti* (Acari: Demodecidae) from "*R. leachi*" from Mahyusha cave, near Katana, DRC. Fain (1967: 367) furthermore reported on the presence of *Teinocoptes rousetti* Fain, 1959 on *R. aegyptiacus leachi* from Mahyusha cave, Kivu, DRC.

Reinhardt *et al.* (2008: 173) report that the cimicid bug *Afrocimex constrictus* Ferris and Usinger, 1957 infested *R. aegyptiacus* colonies at Makingeny and Ngwarisha (Mount Elgon region, Kenya) and that these bats were bitten between 0.5 and 1.5 times a day, and that to up to 28 µl of blood was removed each time.

Afrocimex leleupi Schouteden, 1951 was reported by Kock and Aellen (1987: 877) the Kakontwe cave (DRC).

In Iran, Benda *et al.* (2012a: 185) report the presence of *Meristaspis lateralis* (Kolenati, 1856) (Spinturnicidae). This mite was already reported by Delfinado (1963: 913) to be widely distributed on *R. aegyptiacus* in Egypt and Palestine.

Bianco *et al.* (2019: 552) indicate that demodicosis, caused by *Demodex* mites (Demodicidae, Prostigmata) was reported from zoo-kept Egyptian fruit bats.

Schuh *et al.* (2020: 2944) reported on *Ornithodoros (Reticulinasus) faini* [=*Carios faini*] (Argasidae) having been observed living within rock crevices and feeding on *R. aegyptiacus*.

DIPTERA

Nycteribiidae

Eucampsipoda africana (Theodor, 1955), widely distributed over the Ethiopian region and recorded from localities in Senegal to the Sudan and southwards to the Cape (Haeselbarth *et al.*, 1966: 115; Duron *et al.*, 2014: 2108; Obame-Nkoghe *et al.*, 2016: 5; Júnior *et al.*, 2020: Suppl.). This bat fly might be a carrier of *Bartonella* (Zhu *et al.*, 2014: 2160; Szentiványi *et al.*, 2019a: Suppl.) and *Arsenophonus* bacteria (Szentiványi *et al.*, 2019a: Suppl.), and the fungus *Anthrorhynchus eucampsipodae* Thaxter, 1901 (see Balazuc, 1971: 214; Haelewaters *et al.*, 2017: Suppl. for a record from Gabon; Haelewaters *et al.*, 2018: 794; Szentiványi *et al.*, 2019a: Suppl., de Groot *et al.*, 2020: Suppl.), as well as the blood parasite *Polychromophilus melanipherus* and Mahlapitsi and Wolkberg viruses [Szentiványi *et al.*, 2019a: Suppl.). *Eucampsipoda hyrtlii* (Kolenati, 1856) has been identified with certainty only from the Middle East (Arabia, Egypt, Palestine and Syria), but probably also occurs in East Africa (Haeselbarth *et al.*, 1966: 115). Balazuc (1971: 214) reported this bat fly from a "Chiroptera" from Egypt, which was infected by the fungus *Anthrorhynchus eucampsipodae* Thaxter, 1901. However, as pointed out by Blackwell (1980: 151), *E. hyrtlii* is only known as parasiting on *R. aegyptiacus* (see also Haelewaters *et al.*, 2018: 794). *Dipseliopoda biannulate* (Oldroyd 1953) distributed over the tropical parts of Africa and recorded from localities in Nigeria, Cameroon, the Congo and the Sudan and Kenya (Haeselbarth *et al.*, 1966: 116). Morse *et al.* (2013: Suppl. 1) refer to *Eucampsipoda africana* (Diptera: Hippoboscoidea: Nycteribiidae: Cyclopodiinae) collected from a Kenyan *R. aegyptiacus*. This bat fly was also reported from Sierra Leone by Blackwell (1980: 146), where it was found to be infected by the fungus *Arthrorhynchus eucampsipodae* Thaxter, 1901. In Jordan, Benda *et al.* (2010b: 201) found *Eucampsipoda aegyptia* (Macquart, 1851). They also mention that two other Nycteribiidae were previously found in Palestine: *Nycteribia pedicularia* Latreille, 1805 and *N. schmidlii* Schiner, 1853. The latter species (as *Nycteribia schmidlii scotti* Falcoz, 1923) was also reported from Gabon by Obame-Nkoghe *et al.* (2016: 5).

Jansen van Vuren *et al.* (2016: 1) described a new orthoreovirus, which was collected from a bat fly (*Eucampsipoda africana* (Theodor, 1955)), which in turn was captured from a *R. aegyptiacus* bat from South Africa.

Lutz *et al.* (2021: Suppl.) reported a *Dipseliopoda setosa* Theodor, 1955 from a bat captured in Uganda. One bat from Kenya was parasitized by *Nycteribia schmidlii* Schiner, 1853. Most other *R. aegyptiacus* they reported on were hosts for *Eucampsipoda africana* Theodor, 1955.

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Rousettus aegyptiacus*: *Cyclopodia greeffi greeffi* Karsch, 1884, *Dipseliopoda biannulata* (Oldroyd, 1953), *Dipseliopoda setosa* Theodor, 1955 and *Eucampsipoda africana* Theodor, 1955.

Streblidae

Brachytarsina africana (Walker, 1849) recorded in Katanga, but Haeselbarth *et al.* (1966: 100) suggests that this may be accidental and *R. aegyptiacus* is not its true host. *Brachytarsina alluaudi* (Falcoz, 1923) recorded in Katanga (Haeselbarth *et al.*, 1966: 101), Gabon (Obame-Nkoghe *et al.*, 2016: 5). *Brachytarsina bequaerti* (Jobling, 1936) collected in Tanzania and Kenya (Haeselbarth *et al.*, 1966: 101).

HEMIPTERA

Cimicidae

Kock *et al.* (1998b: 236) reported *Cacodmus villosus* (Stål, 1855) from *Rousettus aegyptiacus leachii*.

SIPHONAPTERA

Ischnopsyllidae

Thaumapsylla breviceps Rothschild 1907, where the nominate subspecies *T. b. breviceps* Hopkins and Rothschild, 1956, was found in the Cape, Natal and Transvaal provinces of South Africa, Kenya and DRC (Haeselbarth *et al.*, 1966: 186).

Pulicidae

Korine *et al.* (2012: 1435) experimentally infected *R. aegyptiacus* specimens with the flea *Xenopsylla ramesis*, whose natural host is Sundevall's jird (*Meriones crassus*). They found that female fleas engorged the same amount of

blood from these bats as from the jirds. Male fleas, however, sucked much less blood.

Besides the above mentioned bacteria and protozoa, Ramanantsalama *et al.* (2022b: 10 - 11) also reported the following ectoparasites from *R. aegyptiacus*: *Acarus* sp., *Argas vespertilionis, Ornithodoros camicasi, Ornithodors faini, Ornithodoros salahi, Carpoglyphus* sp., *Alabidocarpus roustti, Ixodes* sp., *Steatonyssus longipes, Binuncus rousetti, Pyemotis* sp., *Meristaspis kenyaensis, Meristaspis lateralis, Ancystropus aequatorialis, Ancystropus leleupi, Ancystropus taprobanius, Spinturnix americana, Spinturnix delacruzi, Periglischrus paracutisternus, Periglischrus ojastii, Odontopsyllus* sp., *Afrocimes constrictus, Cyclopodia greefi, Eucampsipoda africana, Eucampsipoda aegyptia, Eucampsipoda hyrtlii, Nycteribia alternana, Nycteribia schmidlii, Nycteribia pedicularia, Brachytarsina allaudi* and *Megastrebla bequaerti*.

Farina and Lankton (2018: 626.e3) mentioned a case of disseminated microsporidiosis caused by *Encephalitozoon hellem* in a captive female adult *Rousettus aegyptiacus*.

VIRUSES:

In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Rousettus aegyptiacus*: Adenoviruses, Astroviruses, Caliciviruses, Coronaviruses, and Rotaviruses.

Willoughby *et al.* (2017: Suppl.) mention the following viruses: Chikungunya virus, European bat 1 lyssavirus, Israel turkey meningoencephalomyelitis virus, Kasokero orthonairovirus, Lagos bat lyssavirus, Marburg marburgvirus, Rousettus bat coronavirus HKU9, Shamonda orthobunyavirus, West Nile virus, Yogue virus, Zaire ebolavirus.

Nieto-Rabiela *et al.* (2019: Suppl.) mention the following viruses: Bat coronavirus, Bat flavivirus, Bat paramyxovirus, Bat pegivirus, Betacoronavirus, Betaherpesvirus, Chikungunya virus, Cytomegalovirus, European bat lyssavirus, Gammaherpesvirus, Kasokero virus, Lagos bat virus, Marburg virus, Polyomavirus, *Rousettus aegyptiacus* papillomavirus, Sosuga virus, Yogue virus.

In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against Yellow fever virus (YFV), non-specific Flaviviruses, Babanki virus (BBKV), non-specific Alphaviruses, and Rift Valley fever virus (RVFV).

Raulino *et al.* (2022: 256) reported antibodies against Chikungunya, Dengue, O'nyong nyong, West Nile and Zika viruses found in *R. aegyptiacus* from Guinea.

In their review, Ramanantsalama *et al.* (2022b: 4 - 5) list the following virus infections for *R. aegyptiacus*: Bat mastadenovirus, Betacoronavirus sp., Zairi ebolavirus, Ravn virus, Marburg virus, Uganda S virus, Entebee bat virus, Ntaya virus, Usutu virus, West Nile virus, Yellow fever virus, Zika virus, Herpesviridae spp., Kasokero virus, Yogue virus, Crimean-Congo hemorrahgic fever orthinairovirus, Bunyamwera orthobunyavirus, Wolkberg orthobunyavirus, Rift valley fever phlebovirus, Influenza A virus, Hendra(-like) henipavirus, Nipa henipavirus, Cedar henipavirus, Sosuga pararubulavirus, Rubulavirus spp., Sosuga pararubula(-like) virus, Betapolyomavirus sp., Polyomaviridae sp., Poxviridae sp., Lagos bat virus, European bat Lyssavirus, Shimoni bat virus, Mikola virus, Chikungunya virus, Semliki Forest virus, Alphavirus sp. and O'nyong'nyong virus.

Amman *et al.* (2025: 1016) studied virus infections in Uganda and Sierra Leone and found that 1.5 % (23/1,511) of the Rousettus aegyptiacus bats were co-infected with different combinations of Marburg, Sosuga, Kasokero, or Yogue viruses.

Elbert *et al.* (2025: 1) mention that *Rousettus aegyptiacus* is a natural reservoir host for Marburg virus (MARV) and Ravn virus (RAVV), as well as a vertebrate reservoir for Kasokero virus (KASV) and a putative reservoir for Sosuga virus (SOSV).

Adenoviridae

Mastadenovirus

Jansen van Vuren *et al.* (2018: 1) isolated a new virus (RaegAdV-3085) from an apparently healthy wild-caught Egyptian fruit bat in South Africa. Shchelkanov *et al.* (2020a: 14) assigned this virus to Bat Mastadenovirus I.

Astroviridae

El Taweel *et al.* (2020: 8) found a number of viruses belonging to the genus Mamastrovirus in bats from Egypt, but also one Avastrovirus (which is usually found in birds).

Coronaviridae - Coronaviruses

SARS

Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in 29 individuals from Limpopo Province, South Africa, 11 were tested positive (11/29, 37.9 %) and 142 individuals from Oriental Province, DRC, 17

tested positive (17/142, 12 %) (28/171, 16.4 %). In Nigeria during June 2008, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs, none tested positive. Twelve of the 120 Guinean animals tested by Lacroix *et al.* (2020: 5) was positive for CoV.

Van Doremalen *et al.* (2018: 3, 10) inoculated 12 adult bats from a captive colony with WIV1-CoV (SARS-like WIV1-coronavirus) and were unable to detect efficient replication of the virus and only modest seroconversion in two of the bats.

Tong *et al.* (2009) found several alpha- and betacoronaviruses in *Rousettus aegyptiacus* collected in Kenya in 2006 based on detection of coronavirus RNA in fecal swabs. Some of the coronaviruses were highly divergent, whereas others showed similarity to *Rousettus* sp. coronaviruses identified in China.

Shehata *et al.* (2016) tested 265 Egyptian bats and found 12 infected with HKU9-like viruses.

Anthony *et al.* (2017b: Suppl.) mention beta-coronaviruses Bat_CoV_HKU9 and Kenya_CoV_BtKY56.

19 out of 397 (4.8 %) of the Kenyan bats tested by Tao *et al.* (2017: Suppl.) were positive for CoV.

Nziza *et al.* (2019: 156) found Bat coronavirus HKU9 and Kenya bat coronavirus/BtKY56/BtKY55 in rectal swaps from Rwandan bats. The viruses in the Rwandan bats were assigned to the subgenus *Nobecovirus* by Motayo *et al.* (2020: 4).

The coronaviruses found in the Kenyan bats were identified as Beta-D coronavirus by Joffrin *et al.* (2020: 7).

Montecino-Latorre *et al.* (2022: 5) mention Eidolon bat coronavirus/Kenya/KY24/2006.

Saeed *et al.* (2021a: 59) tested 800 samples (liver, spleen, intestine and lung) from 200 bats from Egypt on the presence of SARS_CoV_2 and found no positive bats, suggesting that - at least during the duration of the test - *R. aegyptiacus* was not a reservoir species for this virus.

In their longitudinal surveillance study, Geldenhuys *et al.* (2023: 10) found that factors related to coronavirus maintenance may not be universal among these virus species within bat populations.

Filoviridae - Filo viruses

For Zambia and the RSA, Niu and McKee (2025: 235) reported seriological evidence of filoviruses that presented a clear seasonal pattern, with a peak from October to January and a subsequent decrease between February and April. The peak period aligned with the birth pulses of the bats.

Becker *et al.* (2025: 4) mention that *Rousettus aegyptiacus* is susceptible to MARV but resistant to EBOV, which is illustrated by the below volume of study results:

Ebolavirus

Muyembe-Tamfum *et al.* (2012: 9) refers to Pourrut *et al.* (2005) who found ZEBOV-specific antibodies in this species.

Paweska *et al.* (2016: 1) experimentally inoculated *R. aegyptiacus* bats and were unable to find any viral RNA in oral, nasal, ocular, vaginal, penile and rectal swabs from any of the experimental groups. They concluded (p. 9) that these bats are unlikely to maintain and perpetuate EBOV in nature (see also Mandl *et al.*, 2018: 7), which would qualify them as 'dead-end' hosts (Schuh *et al.*, 2018: 1716).

One to four of the five bats examined by Lacroix *et al.* (2021: 7) in the DRC tested positive for Ebola antibodies.

Marburgvirus

Towner *et al.* (2007) tested 283 individuals from Gabon for Marburg virus [MARV] RNA by conventional and real-time RT-PCR and 242 individuals for anti-Marburg virus IgG antibodies by ELISA; 4 individuals (1.5 %) were PCR positive and 29 (12 %) were IgG positive. Peterson and Holder (2012: 1831) indicate that the Gabonese clade represents a virus form that has not been reported from human infections. Kuzmin *et al.* (2010b) detected RNA in a female *R. aegyptiacus* bat collected at Kitum cave in July 2007. Adjemian *et al.* (2011: S796 - S798) report on four cases of MHR [Marburg haemorrhagic fever] in miners, which they contracted while working in a mine tunnel at Kitaka mine in Ibanda District, Uganda, where thousands of *R. aegyptiacus* bats lived. These cases resulted in the destruction of the residing bat population. Van Paassen *et al.* (2012: 635) report on the death of a Dutch woman, who probably contracted the virus after visiting a cave in Uganda, where *R. aegyptiacus* bats were living. Amman *et al.* (2013: 6) indicate that a long-term study at this site showed that 2 to 5 % of the bat population was actively infected by the MARV virus. Amman *et al.* (2014: 1762) estimated that both the cave and the mine contained about

40,000 to 100,000 *R. aegyptiacus* bats at the time the miners and the tourist were infected. The bats were exterminated by November 2008, but in November 2012 a small colony was (1 - 5 % of the original numbers) was found in the re-opened Kitaka Mine.

Maganga *et al.* (2011: S800) indicate that MARV is enzootic in Gabon due to the fact that MARV-positive bats were captured in between 2005 and 2009.

Kuzmin *et al.* (2011a: 4) report that MARV RNA was found in bats from Gabon, Uganda, and Kenya.

Paweska *et al.* (2012: 1) inoculated captive *R. aegyptiacus* specimens - captured in northeastern South Africa - and were able to confirm the susceptibility of this species to infections with MARV irrespective of sex and age. In a subsequent study, Paweska *et al.* (2015) recovered the virus from 15 different tissues and plasma, but only sporadically in mucal swab, urine and fecal samples. Amman *et al.* (2015b) also experimentally infected bats and found viruses in liver, spleen, blood, kidneys, salivary glands, bladder, large intestine as well as in oral and rectal swaps. The infected bats did not show any significant changes in daily food consumption, body weight, or daily body temperature, and no signs of overt morbidity or behavioural changes such as waning appetite, overly aggressive behaviour, separation from cage mates, lethargy, or reduced or abandoned grooming (p. 121). Schuh *et al.* (2017c) found prove for horizontal transmission of MARV as virus RNA was found in contact bats that were kept together with MARV-inoculated bats. Schuh *et al.* (2017b), furthermore, reported that following infection of ERBs with MARV, virus-specific IgG antibodies are induced, but after 3 months the bats are seronegative again.

Amman *et al.* (2012: 1) and Albariño *et al.* (2013a: 99) link an outbreak of MARV in October 2012 in Uganda with the second annual virus pulse in *R. aegyptiacus* populations, more specifically in older juvenile bats of about six months of age. The viral genome sequences collected from infected humans were approximately 99.3 % to two MARV isolates captured in 2008 and 2009 in the Python Cave in the Queen Elisabeth National Park. Amman *et al.* (2013: 6) indicate that at the time of these pulses, the juvenile bats are about 6 months old and are 5 to 6 times more likely to be infected by the virus than the adults (see also Olival and Hayman, 2014). Storm *et al.* (2018: 1) found that maternal immunity against MARV was lost in juvenile bats by 5 months of age, and that antibodies to MARV remained present in 84 % of naturally exposed bats at least 11 months after capture.

Butera *et al.* (2024: 422) and Nsanzimana *et al.* (2025: 983) traced the index case of an outbreak of Marburg disease in Rwanda to a mining cave inhabited by *Rousettus aegyptiacus*.

Amman *et al.* (2023: 2238) linked 8 of the 17 known Marburg virus disease outbreaks to human encroaching into the bat's habitat. For the nine remaining outbreaks, they point to the bats feeding on cultivated fruit trees near homes.

Peterson and Holder (2012: 1832) state that *R. aegyptiacus* is now seen as central in the picture of Marburg virus maintenance, but they also are somewhat confused about the fact that two lineages of Marburg virus are maintained in the same cave or mine in Uganda.

Carroll *et al.* (2012: 2613) indicate that *Rousettus aegyptiacus* has been identified as a potential natural reservoir for Marburg and Ravn viruses (*Marburg marburgvirus*).

Jones (2015: 3420) experimentally inoculated *R. aegyptiacus* specimens with Marburg and five Ebola viruses (Sudan, Ebola, Bundibugyo, Taï Forest, and Reston). In the Ebola virus groups, viral RNA tissue distribution was limited, whereas in the Marburg virus group, the virus was widely dissimated. They concluded that this bat species is very unlikely to be a source for Ebola viruses in nature and that there is support for a single filovirus - single reservoir host relationship (here with Marburg virus).

Pawęska *et al.* (2018: 1135) tested 1,431 South African bats and found 53.04 % (759) to be positive for antibodies against MARV. These percentages varied between 17.75 % in April 2013 and 82.1 % in October 2013. In adults, these numbers varied between 39.6 % in August 2013 and 100 % in February 2013 (overall 71.56 %), whereas in young bats, they varied between 1.3 % in June 2013 and 77.3 % in January 2014 (overall 30.6 %).

An extensive test by Changula *et al.* (2018: S313-S315) showed 158 out of 290 Zambian *R. aegyptiacus* bats was positive for anti-filovirus antibodies, but no viral RNA genomes were detected. They also found that the seroprevalence peaked in November-December and decreased in January-February. The seroprevalence was also lowest in animals weighing 51 - 60 g, and increased when the bats grew, suggesting that maternal antibodies might

have disappeared. Kajihara *et al.* (2019b: 1578), however, were able to extract viral RNA from two Zambian bats, which showed close relationship to the virus found in Uganda.

In Sierra Leone, Amman *et al.* (2020a: 2) tested 435 *R. aegyptiacus* bats of which 11 (2.5 %) were positive for active Marburg virus infection. The positive bats were all juveniles.

Jones *et al.* (2019: 1) inoculated Egyptian fruit bats with MARV to investigate the clinical and pathologic effects. They found a mild elevation in alanine aminotransferase (ALT) at 3, 6 and 7 days after inoculation. Nine days after inoculation, Lymphocyte and monocyte counts were slightly elevated and the liver histology revealed small foci of inflammatory infiltrate, similar to lesions previously described in wild, naturally infected bats.

Prescott *et al.* (2019: 3) suggest that a coevolved strategy exists between the virus and the antiviral responses in *R. aegyptiacus*.

The role of the argasi tick *Ornithodoros faini* as transmission vector between *R. aegyptiacus* specimens in Uganda was rejected by Schuh *et al.* (2016: 1) as none of the 3,125 ticks examined tested positive for the Marburg virus.

A similar study on the role of Nycteribiid flies (*Eucampsipoda africana* Theodor, 1955 in South Africa by Pawęska *et al.* (2021: 1) showed that these flies do not play a significant role in the transmission and enzootic maintenance of MARV as only one out of 1693 flies (0.06 %) tested positive for MARV RNA.

Amman *et al.* (2021: 9) found that infected *R. aegyptiacus* bats can shed the virus onto discarded fruit (e.g., mangoes and bananas), which can then be eaten by other animals and/or humans.

Pavlovich *et al.* (2020: 1) investigated the antiviral activity of type I interferons (IFN-ω) in *Rousettus aegyptiacus.*

Pawęska *et al.* (2020: 3051) found Marburg virus RNA in rectal swaps of bats from the RSA, which suggests that fecal contamination of natural bat habitats might be a potential source of infection for humans. They also found that the lowest seropositivity in juveniles occurred in April-May.

Data obtained by Guito *et al.* (2024: 1) suggest that natural immunomodulatory stressors such as food scarcity and habitat disruption may increase viral shedding, transmission and therefore outbreak risk.

Brüssow (2025b: 1) mentions that MARV transmission among adult bats is inefficient and primarily occurs between older juvenile bats.

Flaviviridae

Flavivirus

Uganda S virus

Reported in 1947 from Uganda by Butenko (1996). This virus was mentioned by Luis *et al.* (2013: suppl.). Maganga *et al.* (2014a: 5) tested 305 animals from Gabon, of which only one tested positive for a *Flavivirus*.

Malmlov *et al.* (2019: 3) referred to Simpson *et al.* (1968) who experimentally inoculated three Egyptian fruit bats with Zika virus, of which one became viraemic and two seroconverted.

Pegivirus (BPgV)

Quan *et al.* (2013: Table S5) found 3 out of 26 Kenyan and 9 out of 91 Nigerian bats examined to be infected with clade K type *Pegivirus* (overall 10.3 % infection).

Zikavirus (ZIKV)

Fagre *et al.* (2021: 1) found ZIKV sfRNA, but not NS5, in one bat from Uganda.

Hantaviridae

In Zambia, Sarii *et al.* (2024: 14) found *Rousettus aegyptiacus* to be seropositive for Brno virus, Dakrong virus, Quezon virus, Robina virus and Xuan Son virus.

Herpesviridae

Jánoska *et al.* (2011: 118) reported two viruses, from captive specimens from the Budapest Zoo, belonging to the *Betaherpesvirinae* and *Gammaherpesvirinae*. Viruses belonging to these two subfamilies were also reported from Zambia by Harima *et al.* (2023: 7).

Nairoviridae

Orthonairovirus

de Jong *et al.* (2011: 12) and Luis *et al.* (2013: suppl.) mention the presence of an unassigned Kasokero virus (KASV), as well as an unassigned Yogue virus. The latter was also reported by Kemp (1975: 617) from Senegal in June 1968.
Following an experimental inocculation, Schuh *et al.* (2022: 1) suggest that *E. rousettus* are competent, natural vertebrate reservoir hosts for KASV.

Of the 1979 specimens from Gabon tested by Müller *et al.* (2016: 3), 48 were positive for

Crimean Congo haemorrhagic fever virus (CCHFV).

Jansen van Vuren *et al.* (2017: 935) discovered an orthobynyavirus (Wolkberg virus - WBV) in a bat fly (*Eucampsipoda africana*) collected on a *R. aegyptiacus* from South Africa. WBV was detected in one serum pool from bats, and at relatively low concentration.

Kirejczyk *et al.* (2023: 1) investigated tissues of bats previously experimentally infected with Kasokero orthonairovirus (KASV) and concluded that these bats have effective mechanisms to respond to this virus, clearing it without evidence of clinical disease. Kirejczyk *et al.* (2025: 2) mention that KASV is maintained in a complex enzootic cycle involving *R. rousettus* and the argasid tick *Ornithodoros (Reticulinaus) faini* (Hoogstraal, 1960).

Orthomyxoviridae

Kandeil *et al.* (2019: 1) reported a new influenza A virus (IAV) from bats collected in the Nile delta.

Experimental inoculation with avian influenza A virus (H9N2) by Halwe *et al.* (2021) showed that *R. aegyptiacus* was resistant against this virus, but when inoculated with a bat-borne virus of the same subtype, the bats were susceptible (see also El-Shesheny *et al.*, 2024). Rademan *et al.* (2023: 1) found a virus closely related to H9N2 to be circulating in Southern African bat populations.

Orthoreoviridae

Harima *et al.* (2019: 165) found a new *Orthoreovirus* in a colon swap from a Zambian *R. aegyptiacus*.

Papillomaviridae

McKnight *et al.* (2006: 193) reported some carcinomas near the eye and on wing membranes of a *R. aegyptiacus* kept in captivity in the USA. These were caused by a putative novel close-to-root papillomavirus, belonging to a new genus. Tse *et al.* (2012: 7) refer to a *Rousettus aegyptiacus* papillomavirus type 1 (RaPV1), belonging to the genus *Psipapillomavirus* (GenBank: DQ366842).

Paramyxoviridae

Drexler *et al.* (2012a: Suppl. Table S1) reported that three of the 213 specimens (1.4 %) they examined from Gabon and Congo tested positive for *Henipavirus*. 15 of these bats (7.0 %) were positive for *Rubulavirus*. Conrardy *et al.* (2014: 259) found one out of 10 tested animals from the Kitum cave (Kenya) and one of six from the Watamu cave to test positive for *Paramyxovirus*.

Two out of 84 Kenyan *R. aegyptiacus* specimens tested by Mortlock *et al.* (2015: 1481) were found to test positive for *Paramyxovirus* sequences.

Amman *et al.* (2020b: 2) reported on Ugandan bats that tested positive for Sosuga virus (SOSV) RNA. They experimentally infected 12 *R. aegyptiacus* bats and found all of them to be seropositive after 21 days, without showing any overt clinical illness. Amman *et al.* (2024: 1, 10) detected this virus also in bats from Sierra Leone, where they found that there was an age bias, as the virus was found more frequently in adults (43.79 %) than in juveniles (30.47 %), as well as a sex related bias (45.86 % in females and 30.41 % in males), possibly because juvenile females showed more antibody activity than juvenile males.
Kemenesi and Kurucz (2025: 2) indicate that Sosuga viruses were also found in *R. aegyptiacus* specimens from Sierra Leone, which represents a significant range extension for this virus.

Mortlock *et al.* (2021: 5) investigated the temporal shedding of *Henipavirus* in the Matlapitsi cave (Limpopo Province, RSA) and found peaks occurring around June/July (Austral winter) and lower levels from September to November, and no viruses between February and May. The peaks were apparently in line with the weaning of maternal antibodies and nutritional stress (Sánchez *et al.*, 2024: 5). Niu and McKee (2025: 235), however, found no direct link with weaning and parturition, but attributed this to the cold temparatures and limited availability of food.

Mohl *et al.* (2024b) intranasaly inoculated eight bats with Cedar henipavirus (CedV) and found only trace levels of viral RNA in the upper respiratory tract, kidneys, oral and anal swaps after two days.

Orthorubulavirus

In South Africa, Mortlock *et al.* (2019b: 13) found a number of putative *Rubula-* and related virus RNA in spleen (9.54 %) and urine samples. In October, the virus observations peaked, which coincides with females aggregating in the cave during late stages of gestation. Additionally, high values were also found during December-January, when the bats were lactating. A second excretion peak was found in June-July, probably linked with the juveniles being no longer protected by maternal antibodies.

Pararubulavirus

Amman *et al.* (2015a: 776) tested 1331 Ugandan *R. aegyptiacus* specimens of which 62 (4.6 %)

tested positive for Sosuga [pararubula] virus (SOSV) (see also Markotter *et al.*, 2020: 6).

Phenuiviridae
Phlebovirus
Balkema-Buschmann *et al.* (2018: 3) infected three bats from a captive colony with Rift Valley fever phlebovirus (RVFV) and found that viruses could be isolated from the spleens of all three animals and from the liver of one of them, proving that the virus can replicate in the bats.

Polyomaviridae
Polyomavirus
Initially, two polyomaviruses were detected from Kenya in 2006 by Tao *et al.* (2012). Further surveillance identified four more from Kenyan caves (including Watamu cave) where three of the 11 individuals tested positive (Conrardy *et al.*, 2014: 259).

Poxviridae
David *et al.* (2020: 1) discovered a new pox virus in a captive colony at Tel Aviv Zoo: Israel Rousettus aegyptiacus pox virus (IsrRAPXV). David *et al.* (2021: 7) indicate that this virus might caused the death of juvenile *R. aegyptiacus*.

Reoviridae
Orbivirus
Fagre *et al.* (2019: 1) described Bukakata orbivirus (BUKV) from a bat from Uganda.

Rotavirus
Sasaki *et al.* (2018: 106) isolated Group A Rotavirus (RVA) from *R. aegyptiacus* in Zambia, which was very similar to the strain they collected from *Eidolon helvum* specimens from that country, suggesting interspecies transmission and genetic reassortment between these bat species.

Nelson Bay orthoreovirus
Harima *et al.* (2021: 1) isolated a PRV (Pteropine reovirus strain) tentatively named Nachunsulwe-57 from a *Rousettus aegyptiacus* bat from Zambia.

Rhabdoviridae
Lyssavirus - Rabies related viruses
In Nigeria during June 2008, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluroescent antibody testing.

European bat lyssavirus
1 is reported by Van der Poel *et al.* (2000: 1919), Wellenberg *et al.* (2002: 349), Omatsu *et al.* (2008:169), de Jong *et al.* (2011: 9), Luis *et al.* (2013: suppl.).

Lagos bat virus
Kuzmin *et al.* (2008a) found a 29 - 46% seroprevalence of Lagos bat virus neutralizing antibodies in Kenya. Kuzmin *et al.* (2011b: 1467) reported 37 seropositive Kenyan bats on a total of 79 examined (46.8 %). Picard-Meyer *et al.* (2004) isolated the virus from a *R. aegyptiacus* from an unknown location in Africa. Hayman *et al.* (2011a: 88) and Kuzmin *et al.* (2011a: 3) refer to a *R. aegyptiacus* specimen from France, which came originally from either Egypt or Togo.

Shimoni bat virus
Kuzmin *et al.* (2011b: 1467) found 26 bats to be seropositive for this virus on a total of 79 specimens examined in Kenya between 2009 and 2010.

Horton *et al.* (2014: Table S1) tested 54 Kenyan *R. aegyptiacus* specimens, but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Togaviridae
Alphavirus
de Jong *et al.* (2011: 10) and Luis *et al.* (2013: suppl.) reported Chikungunya virus occurring on *R. aegyptiacus*.

In their overview table, Maganga *et al.* (2014a: 8) report the following viruses were already found on *R. aegyptiacus*: Lagos Bat Virus (LBV), Bat Gammaherpesvirus (1, 2, 4, 5, 6, 7), Bat Gammaherpesvirus 3, Betaherpesvirus, Marburg virus (MBGV), Coronavirus, Zaire Ebola virus (ZEBOV), Yogue virus, Kasokero virus, Chiropteran Papillomavirus, Henipavirus, Rubulavirus, Flavivirus.

In their literature review, Fagre and Kading (2019) reported that serologic evidence was found for the following viruses: Crimean-Congo Haemorrhagic Fever Virus (CCHF), Rift Valley fever virus (RVFV) and Bunyamwera virus (BUNV). The latter virus was also isolated (or molecular evidence was found), which was also the case for Kasokero (KKOV) and Yogue (YOGV) viruses.

Goldberg *et al.* (2017: 2) and Feng *et al.* (2017: 99) mention that two viruses were identified from Nycteribiid bat flies (*Eucampsipoda africana*), which were retrieved from *R. aegyptiacus*: the putative orthoreovirus Mahlapitsi virus (from South Africa) and the putative orthobunyavirus Wolkberg virus.

UTILISATION:
Vora *et al.* (2014: 334) report on an annual bat festival in Idanre, Nigeria, where males of all ages enter caves inhabited by *R. aegyptiacus* to capture these bats. Many of these animals are prepared as food and some are transported to markets in other parts of the country to be sold as bushmeat.
During the Yam hunting festival in Buoyem, Ghana, fruit bats (possibly *R. aegyptiacus* were collected (Anti *et al.*, 2015: 1418).

ANTHROPOPHILOUS:
In Turkey, Albayrak *et al.* (2008) observed 11 of 15 roosts (73%) were destroyed by human efforts to exterminate the bats over a five-year period.

Centeno-Cuadros *et al.* (2017: 6234) found that, in the Mediterranean area, *R. aegyptiacus* benefits from human-mediated habitats for daily movements and foraging behaviour. On the other hand, they also found that dispersal (promotor of gene flow between colonies) is apparently not influenced by human-altered habitats.

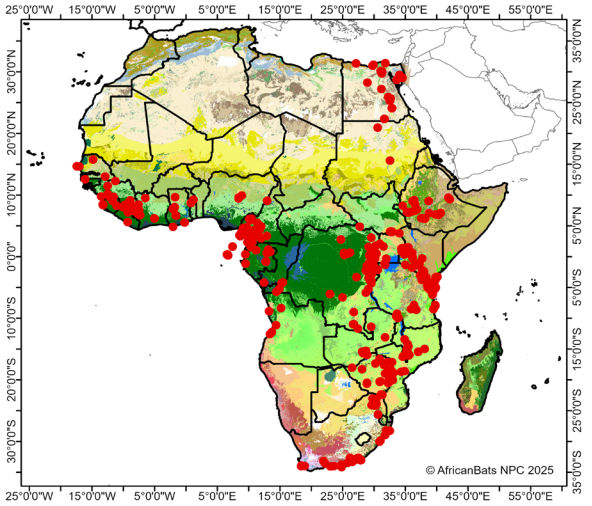

Figure 41. Distribution of *Rousettus aegyptiacus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Burundi, Cameroon, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mali, Mozambique, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Rousettus madagascariensis G. Grandidier, 1929

*1929. *Rousettus madagascariensis* G. Grandidier, Bull. Acad. Malgache, (NS) 11: 91, pl 4 text-figs (for 1928). Type locality: Madagascar: E Madagascar: Beforona: between Tananarive [=Antananrivo] and Andevoranto: Grand Forêt de l'Est. Holotype: MCZ 45432: ad ♂, skull and alcoholic. Collection date: 1917. Presented/Donated by: Guillaume Grandidier. Received from the "Académie Malgache" in 1917; see Bergmans (1994: 119); Peterson *et al.* (1995: 49); Helgen and McFadden (2001: 141). (Current Combination).
2016. *R[ousettus] madagascar:* Lengkong, Arisoesilaningsih, Hakim and Sudarto, Online J. Biol. Sci., 16 (2): 98. Publication date: 14 April 2016. (Lapsus).
? *Rousettus madagascariensis madagascariensis:* (Name Combination).
? *Rousettus sp. cf. R. madagascariensis*

TAXONOMY:
Considered a subspecies of *lanosus* by Hayman and Hill (1971: 12); but see Bergmans (1977a) and Simmons (2005: 348).
Bergmans (1994: 119) indicates that the year of publication is often cited as 1928, but Tome XI of the Bulletin de l'Academie Malgache, Nouvelle Série, for 1928, in which it appeared, was published in 1929. Helgen and McFadden (2001: 141) indicate that it might even be published in 1930.

COMMON NAMES:
Czech: kaloň Grandidierův. English: Madagascan Rousette, Madagascar Rousette. French: Roussette de Madagascar. German: Madagaskar-Höhlenflughund. Malagasy: Andrehy, Bemainty, Fanihy vato, Matavikely, Nanavirovana.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 57 - 58) found *Rousettus* sp. cf. *R. madagascariensis* within the deposits (NCC-1 locality) dating estimated as 69,600 to 86,800 years old within the Anjohibe cave. Samonds (2007: 60) found samples of *R. madagascariensis* in deposit (SS2) which was collected from the surface near the main cave entrance, the dating attemps revealed this sample was contaminated, therefore no date is known for Anjohibe cave, Madagascar.
Gunnell *et al.* (2014: 3) also refer to Goodman and Junkers (2013), who report on fossil material from the Andrahomana cave in Madagascar.

CONSERVATION STATUS:
Global Justification
This species is listed as Vulnerable as it is suspected to have undergone a decline in the region of more than 30% over the last three generations (15 years) as a result of chronic

hunting. Evidence has accumulated on the widespread hunting of this species for bushmeat throughout Madagascar (Andrianaivoarivelo *et al.*, 2012a; Cardiff *et al.*, 2009; Golden, 2005; Jenkins and Racey, 2008; Rakotonandrasana and Goodman, 2007).

Assessment History

Global

2018: VU A2d ver 3.1 (2001) (Andrianaivoarivelo *et al.*, 2019). 2008: NT ver 3.1 (2001) (Andriafidison *et al.*, 2008q; IUCN, 2009). 2000: LR/nt ver 2.3 (1994). 1996: VU ver 2.3 (1994).

Regional

In Madagascar, its legal status is "animaux gibiers (game)".

MAJOR THREATS:

Andriafidison *et al.* (2008q) [in IUCN (2009)] report that the extent to which the destruction and degradation of natural forest threatens this species is poorly understood, while Andrianaivoarivelo *et al.* (2011b: 81) indicate that this is an indirect threat. Although Goodman *et al.* (2005a) suggested that *R. madagascariensis* is not dependent on relatively intact forest there are insufficient data on its annual dietary requirements to decide this matter. It is clear, however, that some of the roosting colonies are located some distance from intact forest and additional study is therefore needed on the mobility of this species. The main threats to *R. madagascariensis* are to its roosts where it is subject to hunting pressure (Jenkins *et al.*, 2007a; Rakotonandrasana and Goodman, 2007; Jenkins and Racey, 2008; Andrianaivoarivelo *et al.*, 2011b: 78, 81) in virtually all sites that are not inside protected areas (Goodman *et al.*, 2005a) or considered sacred (Rakotoarivelo and Randrianandrianina, 2007). Jenkins *et al.* (2011: 1), however, indicate that the taboo on hunting in sacred areas is rapidly eroding. It appears to be hunted exclusively for subsistence and bats are harvested using locally made traps as well as being knocked down from the cave ceiling with wooden batons (Rakotonandrasana and Goodman, 2007). *R. madagascariensis* can legally be hunted between the first of May and the first of September (Anonymus, 2007b: 6). On Ile Sainte Marie the reported offtake was between 360 and 480 bats per year (Rakotonandrasana and Goodman, 2007).

Jenkins *et al.* (2007b: 213) point out that *R. madagascariensis* is very vulnerable to hunters because it roosts in caves, which can easily be covered by a trap system. They mention that one local farmer was able to capture 170 bats in a single night.

Andrianaivoarivelo *et al.* (2022: 1915) indicate that these bats are primarily hunted for domestic consumption and that they are not found alive on markets or served in restaurants.

Cardiff *et al.* (2012: 479) investigated the influence of tourist disturbance on roosting *R. madagascariensis*. They found that the bats were slightly less disturbed when ambient light was present. Directly illuminating the bats resulted in higher disturbance. Also in roosts which were previously visited by hunters, the bats were more easily disturbed. They suggest keeping a minimum visit distance of 12 m, not illuminating the bats directly, and not opening other roost sites for tourism to limit the disturbance of the bats.

CONSERVATION ACTIONS:

Andriafidison *et al.* (2008q) [in IUCN (2009)] report that, as a game species under Malagasy law (Durbin, 2007), *R. madagascariensis* is only protected when it occurs in nature reserves. In a survey of western Madagascar, it was found in six protected areas: Réserve Spéciale d'Ankarana, Réserve Spéciale d'Analamerana, Parc National d'Ankarafantsika, Parc National de Namoroka, Parc National du Tsingy de Bemaraha and Parc National d'Isalo (Goodman *et al.*, 2005a). Roosts within existing protected areas (only three of which are known - Cardiff and Jenkins, 2016: 99) need to receive close attention from park staff to discourage hunting. Other roosts need to be conserved and this might be best achieved through their inclusion within new protected areas and with the cooperation of local communities.

GENERAL DISTRIBUTION:

Rousettus madagascariensis is endemic to the island of Madagascar where it is widespread but rare or absent from the central highlands and the arid south-west (MacKinnon *et al.*, 2003; Goodman *et al.*, 2005a). It has also been recorded from the off-shore islands of Nosy Be, Nosy Komba, and Ile Sainte-Marie (Rakotonandrasana and Goodman, 2007: 6).

This bat has not been recorded above 1,150 m (Garbutt, 2022: 79).

Native: Madagascar (MacKinnon *et al.*, 2003; Goodman *et al.*, 2005a; Rakotonandrasana and Goodman, 2007: 6).

BIOGEOGRAPHY:

Goodman *et al.* (2010b: 600) did not find any clear phylogeographic structure for populations of *R. madagascariensis* on Madagascar. Across the 1,600 km length of Madagascar individuals of *R.*

madagascariensis from extreme ends of the island and across numerous biomes, and nearshore islands up to 13 km from the island, demonstrated complete genetic mixing.

GEOGRAPHIC VARIATION:
Andrianaivoarivelo *et al.* (2022: 1915) mention morphological differences according to geographic sites and elevation. Animals from the east and at localities higher than 500 m tend to be heavier with shorter forearms.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
R. madagascariensis is the smallest African *Rousettus* (Garbutt, 2022: 78), and the smallest fruit bat on Madagascar (Andrianaivoarivelo *et al.*, 2022: 1914).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 55) indicate that the baculum has a rounded distal tip and a distinctly narrower proximal base; length: 2.25 ± 0.228 (1.96 - 2.57) mm, width: 0.98 ± 0.179 (0.76 - 1.19) mm.

SEXUAL DIMORPHISM:
Goodman *et al.* (2017b: 72) measured 271 adult males and 289 adult females, and found males to be significantly larger in both forearm length and body mass, although with a considerable overlap: ♂♂: Fa: 75.3 ± 2.00 (70 - 80) mm, Weight: 64.6 ± 6.85 (48.0 - 81.5) g; ♀♀: Fa: 73.0 ± 2.04 (66 - 80) mm, Weight: 56.8 ± 6.54 (31.0 - 75.5) g.

ECHOLOCATION:
Goodman *et al.* (2022: 1900) [referring to Russ *et al.*, 2003] mention that *Rousettus madagascariensis* produces echolocation clicks in pairs that are about 30 ms apart and at about 115 ms intervals.

MOLECULAR BIOLOGY:
Karyotype
2n = 36 and FN = 66, containing 7 large metacentrics, 4 medium-sized submetacentrics, 5 small metacentrics and one acrocentric pair; X: large submetacentric; Y: smallest chromosome, largely heterochromatic (see Richards *et al.*, 2016d: 187, 189).

Genetics
Goodman *et al.* (2010b) examined Cyt-*b* from 131 individuals from 17 sites across Madagascar.

Andrianaivoarivelo *et al.* (2008: 1025) isolated 22 nuclear microsatellite loci, which will provide valuable information for population genetic studies.

Wang *et al.* (2025b: 7) report that the total length of the genome is 2.34 Gb.

HABITAT:
Due to its small size, Andrianaivoarivelo *et al.* (2011a: 70) suggest that it is potentially an important seed disperser and pollinator inside forests, since the two other Madagascan fruit bat species are rather large and unable to fly within dense foliage. It was also found to forage in relatively intact forest and highly modified habitats close to villages (see Andrianaivoarivelo *et al.*, 2011a: 76), although this contradicts observations by Randrianandriananina *et al.* (2006), who did not find any *R. madagascariensis* specimens in relatively intact humid forest.

Dammhahn and Goodman (2013: 108) indicate that mid- to upper-canopy in forest and trees growing in open areas form the foraging habitat of this species.

R. madagascariensis is widespread in various forest types and in agricultural areas, but missing in vast treeless areas (Crowley and Goodman, 2025: 4).

HABITS:
Using radio tracking and light-tagged individuals, Andrianaivoarivelo *et al.* (2011a: 69, 73) found that these bats travelled over 8 km (up to 14.2 km for females and 14.8 km for males) from their roost sites to their feeding grounds, and that round trips might be as far as 27 km. Goodman (1999: 253) and Andrianaivoarivelo *et al.* (2011a: 73) report that they only grasp a ripe fruit in their mouths and then fly off to consume it.

ROOST:
Rousettus madagascariensis roosts in caves and although it is widespread, relatively few roosts are known (MacKinnon *et al.*, 2003). Even though some roosts are protected from hunters because they occur in protected areas (Kofoky *et al.*, 2007) or sacred sites (Rakotoarivelo and Randrianandrianina, 2007), there are many reports of hunting in and around caves (Rakotonandrasana and Goodman, 2007; Jenkins *et al.*, 2007b).

Ramanantsalama *et al.* (2019: 115) examined the seasonal behavioural activity in a cave day roost and found that the behaviour changed according to season. During the dry season, bats formed 'tight' groups, and spent more time in 'rest' and 'consume ectoparasites' behaviours and limited 'move' (flight and crawl) and 'groom' activities. During the wet season, 'groom' behaviour frequency was higher, and individuals formed a more dispersed roosting group configuration.

The thresholds for the shift were the average temperature outside the cave, the mean temperature in the cave and the average relative humidity. If these were respectively ≤ 25.3°C, ≤ 24.0°C and ≤ 68.2%, 'tight' groups were formed. When the values were respectively ≥ 27.1°C, ≥ 25.0°C and ≥ 93.4%, the bats changed to a 'loose' group configuration.

Roosts can contain several thousands of bats (Andrianaivoarivelo *et al.*, 2022: 1915)

DIET:

Goodman (1999: 253), Andrianaivoarivelo *et al.* (2007: 3) and Andrianaivoarivelo *et al.* (2011a: 69) reported that this species extensively feeds on the fruits of banana (*Musa paradisiaca*, family Musaceae), litchi (*Litchi chinensis*, family Sapindaceae), and *Dimocarpus longan* (Sapindaceae). Jenkins *et al.* (2007b: 213) [referring to Rakotonirainy, 2001] mention these bats visiting *Ficus soroceoides, F. pyrifolia*, and *F. guatteriifolia*. However, Andrianaivoarivelo *et al.* (2012a: 19) indicate that in flight cage experiments, *R. madagascariensis* preferred native or introduced fruit of no commercial value (*Ficus polita, Syzygium jambos* and *S. malaccense* (Myrtaceae)) to commercially important fruits (*Litchi chinensis* and *Diospyros kaki*).

Faecal analysis performed by Nogales *et al.* (2006: 69) indicated that small amounts of seeds were present, which suggests that these bats either feed on nectar, flowers and leaves or on fruits with seeds too large to swallow. They did find *Ficus* seeds in the faeces during the months of March and April.

Jenkins (2007: 17) reported the following plant species being found in faecal samples: *Ficus soroceoides, Ficus botryoïdes, Ficus pyrifolia, Ficus brachyclada* and *Rubus mollucanus*. Seeds less than 2.5 mm in length were swallowed. The seeds that passed through the bat's gut germinated faster than non-ingested seeds.

Andrianaivoarivelo *et al.* (2011a: 75) also indicate that seeds of *Ficus rubra*, which have passed through the digestive tract of *R. madagascariensis* germinate faster than those not passing through it.

Andrianaivoarivelo *et al.* (2012a: 24) found that *R. madagascariensis* preferred natural (non-commercial) fruits over litchis as the former have higher lipid and calcium content. Andrianaivoarivelo *et al.* (2012b: 178) studied the food preference of this species for either *Ziziphus jujuba* (Jujube - Rhamnaceae) and *Ficus sakalavarum* (fig - Moraceae) during the dry season. They found that the figs were intensively eaten by juvenile bats, whereas the adults had a preference for the Jujube, but also ate figs.

Hending *et al.* (2021b: 2) observed these bats feeding on flowers of *Ceiba pentandra* (kapok).

Andrianaivoarivelo *et al.* (2022: 1915) mention that they consumed *Litchi chinensis* (Sapindaceae), *Diospyros kaki* (Ebenaceae); *Syzygium malaccense* (Myrtaceae), and *Ziziphus mauritiana* (Rhamnaceae), the latter providing continuous food, especially during the dry season. They also indicate that the consumption of marketable/commercial fruits is inversely related to the range size of natural feeding sites.

Ramanantsalama *et al.* (2022a: 1) reported that *R. madagascariensis* actively feeds on its nycteribiid and streblid bat fly ectoparasites which represent 4 to 10 % of its daily protein requirements. They also indicated that *Ficus politoria* (Lamarck, 1788), *Ficus reflexa* (Thunberg, 1786), *Ficus tiliifolia* Baker, 1885 and *Mangifera indica* (Linnaeus, 1753) are among the fruits eaten. The daily energy requirements for a bat of this size is 35 to 117 kJ, which is found in about 10 g of fruit, and a daily consumption of 37 bat flies would represent 0.25 to 2.11 % of the required energy (Ramanantsalama *et al.*, 2022a: 7).

Ramanantsalama *et al.* (2018: 6) reported that adult *R. madagascariensis* consumed 37 ± 16 (range 2 - 67) ectoparasites (Streblidae and Nycteribiidae) per day while grooming, whereas juveniles did not ingest any parasites. However, they do admit that this number is an overestimation as they refer to Rajemison *et al.* (2017b), who reported an average of 6.6 bat flies per adult.

Ramanantsalama *et al.* (2022b: 6) [referring to Barclay *et al.* (2006)] mention that these bats were observed ingesting its bat fly ectoparasites *Eucampsipoda madagascariensis* (Nycteribiidae) and *Megastrebla wenzeli* (Streblidae), and a colony of about 1,500 bats might consume over 57,000 hematophagous bat flies on a daily basis during the mating period (see Ramanantsalama *et al.*, 2018).

Rasoarimanana *et al.* (2023: 257) collected faeces of bats leaving and entering their roost caves and found higher proportions of ectoparasite fragments in faeces of bats leaving the roost than in the faeces of bats returning.

The amount of parasites was also linked with the age of the bats.

PREDATORS:
In one locality on Madagascar (near Antonibe), Goodman and Griffiths (2006: 555) found that 81.3% of the total biomass predated by the barn owl (*Tyto alba*) consisted of *R. madagascariensis*.

POPULATION:
Structure and Density
It roosts in aggregations of up over a thousand individuals (MacKinnon *et al.*, 2003; Rakotoarivelo and Randrianandrianina, 2007), but smaller colonies of a few hundred are also known (Jenkins *et al.*, 2007a; Kofoky *et al.*, 2007; Andrianaivoarivelo *et al.*, 2011b: 80; Andrianaivoarivelo *et al.*, 2011b). It can be locally abundant and is often the most commonly trapped species in mist-netting surveys in the west of Madagascar (Kofoky *et al.*, 2007; Rakotoarivelo and Randrianandrianina, 2007) and in the southeast.
For the "Grotte des Chauves-souris, Ankarana", Noroalintseheno Lalarivoniaina *et al.* (2017: 72) estimated the population size to be between 675 and 4000 (IC 95 %, between September 2014 and September 2015). For the same population, Noroalintseheno Lalarivoniaina *et al.* (2018: 26-27) found that in adults there was a male bias during the dry season and a female bias during the wet season, whereas this was the inverse for juvenile bats. Adults were also present in higher numbers during the dry season than during the wet season.

Trend
2018: Decreasing (Andrianaivoarivelo *et al.*, 2019). 2008: Decreasing (Andriafidison *et al.*, 2008q; IUCN, 2009; Andrianaivoarivelo *et al.*, 2011b: 80).

LIFESPAN:
Noroalintseheno Lalarivoniaina *et al.* (2017: 73) found that the survival rate of males tended to exceed that of females. This was confirmed for adults (♂♂: 0.50 / ♀♀: .047) by Noroalintseheno Lalarivoniaina *et al.* (2019: 103), who also found that the inverse was the case for subadults (♂♂: 0.55 / ♀♀: .070).

ACTIVITY AND BEHAVIOUR:
Ramanantsalama and Goodman (2020: 24, 27) studied the timing of emergence from and return to a northern Madagascar cave. During the dry season the bats started to emerge at 19:13 and returned around 05:05. Adult females remained outside for about 09:52 hours, whereas adult males returned after 09:10 hours (subadult males and females returned after 09:37 and 09:31 hours respectively). During the wet season (when there was more daylight), the exit on average started at 19:26 (1 hour 10 minutes after sunset) and they returned at 03:51. Adult females remained outside for 08:33 hours, sub-adult females for 08:00 hours and adult males for 07:52 hours. The longer outside time in the dry season might be due to the bats needing to travel further as food resources become limited, whereas in the wet season, heavy night showers might force the bats to return early (Ramanantsalama and Goodman, 2020: 31).

REPRODUCTION AND ONTOGENY:
Andrianaivoarivelo *et al.* (2011a: 69, 73) report that most juveniles were captured between March and July, and they suspect that young are weaned before 8 weeks of age. Pregnancy (October-December), lactation (December-January) and weaning occurs in the austral summer, when food is readily available.

Goodman *et al.* (2023b: 235) mentioned that of the 59 *Rousettus* bats collected in November 2019, 26 were adult females with embryos (3 to 45 mm), 1 had placental scars, two were subadults (presumably born late during the last reproductive cycle), and none of these were neonates. This period coincided with when females where close to the end of pregnancy and about to give birth. 18 of the males had scrotal testes and 12 non-scrotal. At Andatsakala (March and April 2022), 16 adult females had large mammae, four had embryos (crown-rump lengths 20 - 35 mm), eight were lactating, and 10 were subadults. 11 males had scrotal testes, 5 non-scrotal testes and two were subadults.

MATING:
Goodman *et al.* (2017b: 74) indicate that this species probably has a diffused polygamous mating system, with male-male competition for access to females.

Noroalintseheno Lalarivoniaina *et al.* (2017: 69) indicate that mating occurs in the dry season and births follow in the wet season. This was also confirmed by Noroalintseheno Lalarivoniaina *et al.* (2018: 26), who only found neonates during the wet season, with an unbiased sex ratio.

Ramanantsalama *et al.* (2023: 327) observed most matings occurring between July and September, and parturition occurred between December and February, when fruit abundance is at its highest.

POSTNATAL DEVELOPMENT:
Andrianaivoarivelo *et al.* (2011a: 69) were unable to distinguish juveniles from adults in December

and therefore assume that *R. madagascariensis* reaches somatic maturity within one year.

PARASITES:
Andrianiaina *et al.* (2025: 8) reported the following ectoparasites from 831 *Rousettus madagascariensis* bats: Fleas: Ischnopsyllidae spp.; Bat flies: *Eucampsipoda madagascariensis* Theodor, 1955, *Megastrebla wenzeli* (Jobling, 1952) and mites: *Meristaspis* Kolenati, 1857, *Ornithodoros* Koch, 1837, "other mites". The bats carried on average 2.11 different ectoparasite taxa, with *E. madagascariensis* being found much frequenter than *M. wenzeli* and in higher numbers. If the bat was parasitized by the latter, there was a 96.9 % chance that the other bat fly was present too. *E. madagascariensis* was abundant late February/early March in females and March in males.

BACTERIA
Gomard *et al.* (2016: 5) found 15 out of the 49 bats they tested to be positive for *Leptospira* bacteria.

In their review, Ramanantsalama *et al.* (2022b: 4 - 5) mention the following bacterial infections for *R. madagascariensis* and *Leptospira borgpetersenii* or (-like).

DIPTERA
Tortosa *et al.* (2013: 3), Wilkinson *et al.* (2016), Rajemison *et al.* (2017a; 2017c: 805) and Ramasindrazana *et al.* (2017: Suppl.) report the presence of the Nycteribiid bat fly *Eucampsipoda madagascarensis* Theodor, 1955. Rajemison *et al.* (2017b: 72; Rajemison *et al.* (2017c: 805) reported a second bat fly: *Megastrebla wenzeli* (Jobling, 1952), belonging to the Streblidae. They found that the number of *E. madagascarensis* flies per bat (up to 27) varied by season and was lowest during the rainy season, and that the sex ratio for this fly was biased towards males (especially during the dry season). As for the bats, adult males were more infected by *E. madagascarensis* than females, subadults and neonates. No such variation was observed for *M. wenzeli*.
Szentiványi *et al.* (2019a: Suppl.) indicated that the *E. madagascarensis* bat flies were found to carry Enterobacteriales and *Rickettsia* bacteria.

Pawęska *et al.* (2021: 20) mention that it was estimated that the mean number of nycteribiid flies consumed by an adult Madagascar fruit bat during auto- and allo-grooming was 37 daily.

Rajemison *et al.* (2018: 514) studied the reproductive biology of the bat fly *Eucampsipoda madagascarensis* in northern Madagascar, and found that during the bat mating period (dry season - September), pregnant bat flies did not show any preference for hosts of both sexes that were in reproductive or non-reproductive state, except that males with scrotal testes were more parasitized by gravid flies than non-scrotal males. During the lactation period (wet season - January), gravid flies were excessively present on lactating females.

SIPHONAPTERA
Hastriter (2016: 15) reported the collection of a male flea (*Araeopsylla martialis* (Rotschild, 1903)) from a *Rousettus madagascariensis*, but believes this to be an accidental association.

Ramanantsalama *et al.* (2022b: 10 - 11) also reported the following ectoparasites from *R. madagascariensis*: *Carios salahi, Chirobia* sp., *Teinocoptes* sp., *Meristaspis* sp., *Eucampsipoda madagascariensis* and *Megastrebla wenzeli*.

VIRUSES:
Astroviridae
Two out of 41 by Lebarbenchon *et al.* (2017: Suppl.) tested bats were positive for Astroviruses.

Horigan *et al.* (2024: 9) reported that three astroviruses found in *Rousettus madagascariensis* resolved to very different places on the phylogeny tree: one within the Yinpterochiroptera clade and most closely related to a Rhinonycterid virus, one within the Miniopterid clade, and a novel virus within the Molossid clade.

Coronaviridae
Joffrin *et al.* (2020: 7) reported Beta-D coronavirus from these bats.

Filoviridae
Ebola virus
Brook *et al.* (2019b: 1004) reported the presence of reliable reactive antibodies to tested antigens in serum from *R. madagascariensis*. However, they also mention (p. 1010) that some of the seropositives recovered in their study result from cross-reactivity of Malagasy bat antibodies to related, but distinct, antigens from those assayed by them.

Paramyxoviridae
Henipavirus
Cedar (CedPV)
Brook *et al.* (2019b: 1004) reported the presence of reliable reactive antibodies against CedPV in the serum.

Hendra (HeV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) were unable to detect the virus. Brook *et al.* (2019b: 1004), however, were able to find antibodies against this virus in the serum.

Nipah (NiV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) could not detect the virus. Kuzmin *et al.* (2011a: 5) suggest that their exposure to NiV might be the result of contact with infected *Pteropus rufus* specimens.

Pararubulavirus
Tioman (TiV)
In Madagascar during 2003 - 2004, Iehlé *et al.* (2007) found an overall contamination of 20.0 %.

Rhabdoviridae
Lyssavirus
Lagos bat virus (LBV)
A sero reaction was found by Mélade *et al.* (2016a: 6) in seven out of 35 bats tested.

Duvenhage lyssavirus (DUVV)
Four out of 33 bats tested positive in the same study.

In their review, Ramanantsalama *et al.* (2022b: 4 - 5) mention the following virus infections for *R. madagascariensis*: Mamastrovirus sp., Betacoronavirus sp., Ebolavirus sp., Hendra(-like) henipavirus, Cedar henipavirus, Tioman(-like) virus, Lagos bat virus and Duvenhage lyssavirus.

UTILISATION:
Golden (2005) reported large annual harvests in the Makira forest and Maroantsetra were unsustainable.
See Jenkins *et al.* (2007b) and Goodman *et al.* (2008d).

Golden and Comaroff (2015: 5) indicate that flying foxes and other fruit bats (including *R. madagascariensis*) are frequently the subject of food taboos, which they link to the fact that these bats are carriers of virulent zoonotic diseases.

It appears to be hunted exclusively for subsistence and bats are harvested using locally made traps as well as being knocked down from the cave ceiling with wooden batons (Rakotonandrasana and Goodman, 2007; Andrianaivoarivelo *et al.*, 2011b).

ANTHROPOPHILOUS:
Cardiff *et al.* (2012) suggests that a minimum visit distance of 12 m should be maintained and not illuminating the bats directly at tourist caves, as well as not opening other roost sites to tourism, is likely to help to limit disturbance of *R. madagascariensis* by tourists at Ankarana.

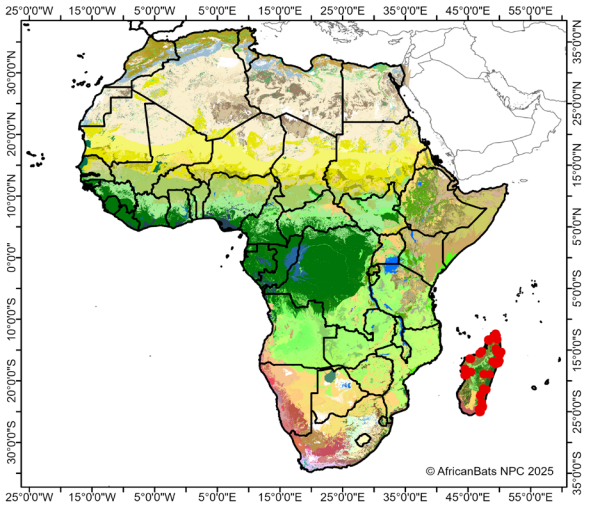

Figure 42. Distribution of *Rousettus madagascariensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Rousettus obliviosus Kock, 1978

*1978. *Rousettus (Rousettus) obliviosus* Kock, in: Olembo, Castelino, and Mutere, Proceedings of the 4th International Bat Research Conference Nairobi, 208. Type locality: Comoros: Grand Comoro: Boboni, cave near [ca. 11 35 S 43 20 E, 640 m]. [Goto Description]. Holotype: ZFMK MAM-1958.0207. Holotype: ZMB 58207: ad ♂. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 3 August 1903; original number: 60. See Turni and Kock (2008: 21). Paratype: SMF 47973: ad ♂, skull and alcoholic. Formerly ZMB 58201; see Turni and Kock (2008: 21). Paratype: ZMA MAM.20903: imm ♀, skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903; original number: 94. From Anjouan [= Nzwani, Comoro Ids.]. Formerly ZMB 58196, exchanged in 1979, see Turni and Kock (2008: 21), Bergmans (2011: 842). Paratype: ZMA MAM.20906: imm ♀, skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 11 October 1903. Paratype: ZMB 4908: skull only. Collected by: Dr. Johann Maria Hildebrandt; collection date: 3 August 1903. From Anjouan [Nzwami, Comoro Isls.]; see Turni and Kock (2008: 21). Paratype: ZMB 58189: skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903; original number: 91. From Cercle de Bambao, Anjouan [= Nzwani, Comoro Ids.]; see Turni and Kock (2008: 21). Paratype: ZMB 58197: sad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903; original number: 88 ?. From Anjouan [= Nzwani, Comoro Ids.]; see Turni and Kock (2008: 21). Paratype: ZMB 58198: ad ♀, skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903. From Cercle de Bambao, Anjouan [= Nzwani, Comoro Ids.]; see Turni and Kock (2008: 21). Paratype: ZMB 58199: sad ♀. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903; original number: 88 ?. From Anjouan [= Nzwani, Comoro Ids.]; see Turni and Kock (2008: 21). Paratype: ZMB 58200: juv ♀, skull and

alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 10-11 October 1903; original number: 97. From Cercle de Bambao, Anjouan [= Nzwani, Comoro Ids.]; see Turni and Kock (2008: 21). Paratype: ZMB 58202: ad ♀, skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow. From Boboni cave, Grand Comoro; see Turni and Kock (2008: 21). Paratype: ZMB 58203: skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 21 December 1903. From Grand Comoro; see Turni and Kock (2008: 21). Paratype: ZMB 58204: skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 21 December 1903. From Grand Comoro; see Turni and Kock (2008: 21). Paratype: ZMB 58205: skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 21 December 1903. From Grand Comoro; see Turni and Kock (2008: 21). Paratype: ZMB 58206: skull and alcoholic. Collected by: Prof. Dr. Alfred Voeltzkow; collection date: 21 December 1903. From Grand Comoro; see Turni and Kock (2008: 21). - Etymology: In allusion to the history leading to the rediscovery of this species, from Latin "*oblivisosus*" = forgotten (Kock, 1978b: 209).

? *Rousettus oblivisosus:* (Name Combination, Current Combination).

TAXONOMY:
Considered a valid species by Meirte (1987), Koopman (1993a: 153), Bergmans (1994: 79), Wilson and Cole (2000: 40), and Simmons (2005: 348), but as a subspecies of *madagascariensis* by Peterson *et al.* (1995: 48).

Goodman *et al.*, 2010b: 599) shows that *R. obliviosus* is a sister taxon of *R. madagascariensis* with a 6.2-8.7 % sequence divergence, and clearly form a reciprocally monophyletic clade. Both are closer related to the Asian *R. leschenaultii* than to *R. aegyptiacus* (Ramanantsalama *et al.*, 2022b: 3).

COMMON NAMES:
Czech: kaloň Kockův. English: Comoro Rousette. French: Roussette des Comores, la petite roussette des Comores. German: Komoren-Höhlenflughund.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (VU B1ab(iii)+2ab(iii) ver 3.1 (2001)) in view of the species has a limited range; both its extent of occurrence and area of occupancy are less than thresholds of 20,000 km^2 and 2,000 km^2, respectively (the minimum convex polygon including all three islands it inhabits is 9,085 km^2, and the total area of all three islands it inhabits is 1,783 km^2). It is also known to exist at no more than ten locations (seven consistently-used roosting caves are known), and it is experiencing a continuing decline in the extent and quality of its habitat (due to increasing human pressures leading to substantial loss of native forests; ongoing loss of trees from plantations, orchards, and agroforestry areas; and increasing human disturbance at roost sites) (Sewall, 2016; Sewall, 2020).

Assessment History
Global
2016: VU B1ab(iii)+2ab(iii) ver 3.1 (2001) (Sewall, 2016; Sewall, 2020). 2008: VU B1ab(iii)+2ab(iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2008v; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004cr; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Sewall (2016) and Sewall (2020) reported that *Rousettus obliviosus* has a limited range; its area of occupancy is less than the total area of the three islands (Sewall *et al.*, 2003), which is 1,783 km^2 (Louette, 2004), and its extent of occurrence (including unsuitable ocean areas between the islands) is less than 9,085 km^2. It is therefore susceptible to single threatening processes, like cyclones, that could simultaneously or rapidly affect its entire range.

The major threat to the species within this range appears to be disturbance at roost sites. The bats appear highly susceptible to human disturbance, and infrequent hunting and rock falls in unstable lava tubes have been recorded at roost sites (Middleton, 1998b; 1999; Sewall *et al.*, 2003). Additionally, cave surveys between 2000-2005 revealed the bats were absent from three caves where they apparently formerly occurred (Sewall *et al.*, 2003, W. Masefield, *pers. comm.* in Sewall (2016; Sewall, 2020)), though it is unclear whether this suggests intermittent use of some roost sites or abandonment after disturbance.

Over the last few decades, the Comoros have undergone a sustained, rapid deforestation, resulting in the loss of nearly all its native forests. During the past 20 years alone, the country has lost 75% of its remaining forests, the fastest rate of any country in the world (UNDP 2013). Human pressures on native forests are expected to continue, as the growth rate of the human population remains high at 2.5% (UNDP 2013). Because *R. obliviosus* is regularly recorded in human-modified landscapes, loss of foraging habitat via deforestation is possibly not a major threat (Bergmans, 1994). However, even human-modified landscapes containing non-native and remnant native trees are disappearing in the Comoros to make room for ground crops (FAO

2010); thus food resources for this species have probably been declining in recent years. Further, the loss of natural and underplanted forests may reduce its ability to cope with droughts and cyclones, and may limit its access to food resources when fruit from horticultural species is unavailable (Sewall *et al.*, 2003). In addition, the replacement of native forests with agricultural land on Anjouan and Mohéli may render formerly inaccessible roost sites on Anjouan and Mohéli more easily reached, possibly exposing roosts to increased levels of human disturbance. Finally, the loss of native forests has resulted in impermanence or complete drying of nearly all rivers on Anjouan and most on Mohéli (Louette, 2004). *R. obliviosus* roosts on those islands are typically near waterfalls, and it is unclear whether that is simply where suitable caves and rock shelters occur or if the bats benefit from the adjacent water source. The species could benefit from an adjacent water source if, for instance, local humidity reduces evaporative water loss in the normally hot climate of the Comoros. If so, then it is possible the seasonal or year-round loss of water flow could affect this species on Anjouan and Mohéli as well.

CONSERVATION ACTIONS:
Sewall (2016) and Sewall (2020) reports that *Rousettus obliviosus* receives the highest level of legal protection available in the Union of the Comoros. It is listed as an 'integrally-protected species' (list 1 of RFIC 2001), which prohibits the capture or detention of *R. obliviosus* individuals without a permit. This law also expressly prohibits the killing of members of the Family Pteropodidae (flying foxes); transport, purchase, sale, export or re-export of living or dead individuals or their body parts; all disruption during the period of reproduction and raising of young; and the destruction of roosts (RFIC 2001). The Union of the Comoros also ratified the Convention on Biological Diversity in 1994, and in response has developed a National Biodiversity Conservation Strategy (Roby and Dossar, 2000). This strategy highlights the importance of, threats to, and conservation recommendations for fruit bats of the Union of the Comoros (Sewall and Granek, 2000). In practice, however, there are currently no direct conservation actions in place for *R. obliviosus*, and no formal terrestrial protected areas in the country.

The national Conservation Action Plan for *Pteropus livingstonii* (Sewall *et al.*, 2007), another threatened pteropodid from the Comoros, includes an appendix for the conservation of *Rousettus obliviosus*. This appendix addresses current and potential emerging threats to *R. obliviosus* and recommends five targeted conservation actions for *R. obliviosus*. Specifically, it recommends (1) protection of roost caves, especially the caves with the largest known colony on each island (these are now thought to be Panga Chilamouinani near Fassi on Grande Comore, Bakomdrundru near Ndrondroni on Mohéli, and Mangua Mitsano near Limbi on Anjouan); (2) discouraging, through environmental education, the hunting of all fruit bats; (3) conducting a comprehensive field search for more roost sites; (4) providing incentives to individuals owning land near roost sites to conserve caves and bats; and (5) devising a suitable population monitoring protocol and conducting regular visits to all known roost sites to track population changes (Sewall *et al.*, 2007). Other key actions for this species include efforts to prevent further native forest habitat loss and additional studies designed to track the species' population and inform its management (Sewall *et al.*, 2003).

GENERAL DISTRIBUTION:
Rousettus obliviosus is restricted to the lower elevations of the islands of Grande Comores, Moheli and Ajouan in the Comoros, western Indian Ocean. The species has not been reported on Mayotte Island (Louette, 1999; Sewall *et al.*, 2003; Goodman *et al.*, 2010c: 124); Goodman *et al.* (2010c: 125) suggest that the reason for the absence from Mayotte island is that it is geologically the oldest (Emerick and Duncan, 1982) and the former lava tubes - important day roost sites for this species elsewhere in the archipelago - have collapsed (Goodman *et al.*, 2010c: 125). On Grande Comore it has an elevational range from near 30 to 1,750 m, on Anjouan from 200 to 1,350 m, and on Moheli from 10 to 700 m (Sewall *et al.*, 2003; Goodman *et al.*, 2010c: 125).

ZMB 3891 refers to "Caffaria", which has been interpreted as South Africa, or southern Africa. This specimen needs to be examined to confirm if it is really *E. obliviosus* and not a mainland *Epomophorus*.

Native: Comoros (Mickleburgh *et al.*, 1992; Carroll and Feistner, 1996; Sewall *et al.*, 2003; Goodman *et al.*, 2010c: 124).

BIOGEOGRAPHY:
Goodman *et al.* (2010b: 600) did not find any clear phylogeographic structure for populations of *R. obliviosus* on Grand Comore, Anjouan and Moheli, with open-water distances separating these islands between 40 and 80 km.

ECHOLOCATION:
Although Reason *et al.* (1994: 402) did not see flying *R. obliviosus* before dusk, it is unknown whether this species is able to echolocate.

MOLECULAR BIOLOGY:
Genetics
Goodman *et al.* (2010b) examined Cyt-*b* from 44 individuals from three islands in the Comoro island (Grande Comore, Anjouan, and Moheli).

HABITAT:
R. obliviosus has been found roosting in forest caves near waterfalls (Anonymus, 2000: 30) and it feeds in the Comoron rain forests. Forages in agricultural zones, degraded or largely intact-forested areas, and understory plantations (Goodman *et al.*, 2010c: 125). Several cave roost sites are at considerable distances from native forests (Goodman *et al.*, 2010c: 125).

HABITS:
R. obliviosus is strictly nocturnal, as Goodman *et al.* (2010c: 125) recorded exit times commenced on the 16 November 2006 at 18h45, after complete darkness at a cave roost at Nyamaoui Panga (Grand Comore).

ROOST:
Roosts in lava tube caves or difficult to access rock crevices (Goodman *et al.*, 2010c: 125). Reason *et al.* (1994) suggested that it uses tree hollows for day roost sites. However, there is no evidence for this (Goodman *et al.*, 2010c: 125). Wilkinson *et al.* (2012: 160) indicate that caves are typical roosting sites for this species on the Comoros.

Middleton and Hume (2010: 137) found a colony of a few thousand animals in a large overhang 12.4 m high, 15 m deep and about 35 m long, beside a waterfall on Anjouan Island.

DIET:
Young *et al.* (1993) [in Carroll and Feistner (1996: 330)] indicate that *R. obliviosus* and *P. livingstonii* were captured at the same kapok and fig feeding sites on Anjouan, which would suggest that their feeding niches might overlap. However, they also indicate that there might be a vertical separation between the two species.

Based on direct observations and food plants recovered from ejecta, *R. obliviosus* commonly feeds on several species of introduced fruiting plants (Mickleburgh *et al.*, 1992; Sewall *et al.*, 2003). Goodman *et al.* (2010c: 125) list *Ceiba pentandra* [= Kapok tree] (Malvaceae), *Musa* spp. [= Banana] (Musaceae), *Artocarpus integrifolia* [= Jackfruit] (Moraceae), and *Carica papaya* [= Papaya] (Caricaceae). Most of these are introduced plants which are abundant in agricultural areas with degraded forest. Ratrimomanarivo (2007) characterized *R. obliviosus* as a forest dependent species, which is not supported by Goodman *et al.* (2010c: 125).

POPULATION:
Structure and Density
Sewall (2016) and Sewall (2020) reports that *Rousettus obliviosus* is rarely observed outside of research studies due to its nocturnal foraging and cryptic roosting habits. It has nonetheless been captured frequently by bat researchers (Reason *et al.*, 1994, Clark *et al.*, 1997, Sewall *et al.*, 2003, Goodman *et al.*, 2010c), and thus the species is considered fairly common (Reason *et al.*, 1994, Louette, 2004, Goodman *et al.*, 2010c). The true population size is unknown. The only abundance estimates available are from roost counts, and very few roost sites are known. Sewall *et al.* (2003) searched Grande Comore, Anjouan, and Mohéli and found or confirmed five permanent roosts plus a sixth that was intermittently used. They estimated that colony size at roosts ranges from around 100 to several thousand animals, and that the total population of these six sites was between 7,100 and 17,100 bats (Sewall *et al.*, 2003). Since then, two additional roosts have been discovered, one small (~100 bats) and one mid-sized (~2,000 bats) (Hume and Middleton, 2011, I. Saïd and W. Masefield *pers. comm.* in Sewall (2016)). Thus, the current population at known roosts is estimated to number about 10,000 to 20,000 bats. Estimates of demographic parameters from genetic analyses suggest recent population stability in this species (Goodman *et al.*, 2010b). Further, no genetic population structure is evident among the three islands, despite separation of at least 40 km of open water between adjacent islands; this indicates inter-island dispersal (Goodman *et al.*, 2010b).

Reason *et al.* (1994: 399) reported a female sex ratio bias on Anjouan, which was not statistically significant.

Trend
2016: Unknown (Sewall, 2016; Sewall, 2020).
2008: Decreasing (Mickleburgh *et al.*, 2008v; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Reason *et al.* (1994: 125) noted that during the months of July and August 1992 on Anjouan, non-reproductive subadults were captured, estimated to be between 3 and 12 months old. Similarly, Carroll and Thorpe (1991) on Anjouan late July 1990 captured four parous adult females and two non-parous adult females; not one

showed signs of reproductive activity. On the 16 November, Goodman *et al.* (2010c: 125) visited Nyamaoui Panga on Grande Comore, where among the 14 free-flying adults captured, seven were male, one of which had scrotal testes measuring 8 x 4 mm with partially convoluted epididymes, and the remaining six were not in reproductive condition. Amongst the seven females, two were pregnant, with single embryos measuring 2 - 31 mm in crown rump length, four lactating, and one non-reproductive. Goodman *et al.* (2010c: 125) revisited the site on the 6 December 2006 and amongst the six individuals caught, one male had abdominal testes, one was a female that had previously reproduced and showed no sign of active reproduction, and the balance were lactating females with single placental scars. This indicates that individuals at different reproductive stages during the same period, and there also appears to be notable inter-island synchronization in the reproductive season (Goodman *et al.*, 2010c: 125). The birthing period would seem to coincide with the wet season, October to April.

Reason *et al.* (1994: 401) suggest that females can reach sexual maturity in their first year (earlier than males).

PARASITES:
R. obliviosus from the Comoros tested positive for *Leptospira* bacteria (Lagadec *et al.*, 2012: 1696). Dietrich *et al.* (2018a: 3) identified these further as *L. interrogans* and *L. borgpetersenii*. Lei and Olival (2014: Suppl.) mention that the species is also a host for *Bartonella* bacteria.

Tortosa *et al.* (2013: 3) and Wilkinson *et al.* (2016) report the presence of the Nycteribiid bat fly *Eucampsipoda theodori*. These bat files were found to carry Enterobacteriales and *Bartonella* bacteria (Szentiványi *et al.*, 2019a: Suppl.).

Reason *et al.* (1994: 399) collected *Brachytarsia* sp. (possibly *B. wenzeli* [=?*Megastrebla wenzeli*]).

In their review, Ramanantsalama *et al.* (2022b: 5) mention the following bacterial infections for *R. obliviosus*: *Leptospira interrogans* and *Leptospira borgpetersenii* or (-like). They also reported (p. 11) the bay fly *Eucampsipoda theodori* (see also Attaullah *et al.*, 2023: 4; Atobatele *et al.*, 2023: Suppl.).

VIRUSES:
Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 26 individuals from the Comoros using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

UTILISATION:
Infrequent hunting has been recorded (Sewall, 2016).

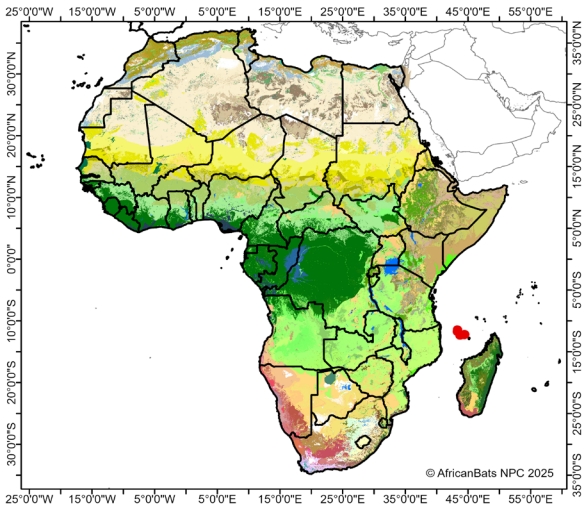

Figure 43. Distribution of *Rousettus obliviosus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros, South Africa.

†***Rousettus pattersoni*** Gunnell and Manthi, 2018

*2018. *R[ousettus] pattersoni* Gunnell and Manthi, J. Hum. Evol., p "2", "3", fig 1C-D. Publication date: 6 April 2018. Type locality: Kenya: Kanapoi Bat Site. Holotype: NMK KP-68719. Holotype is a P_4. - Etymology: Named in honour of Brian Patterson, who, in 1966-1967, initiated the early field work in Kanapoi (Gunnell and Manthi, 2018: "3").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Timeframe: Early Pliocene (Gunnell and Manthi, 2018: "3").

TRIBE Scotonycterini Bergmans, 1997

*1997. *Scotonycterini* Bergmans, Beaufortia, 47 (2): 11, 69. Publication date: 20June 1997.

TAXONOMY:
Includes the genera ***Casinycteris*** Thomas, 1910 and ***Scotonycteris*** Matschi, 1894 (Almeida *et al.*, 2020: 11).

Genus ***Casinycteris*** Thomas, 1910

*1910. *Casinycteris* Thomas, Ann. Mag. nat. Hist., ser 8, 6 (31): 111. Publication date: 1 July 1910 [Goto Description]. - Comments: Type species: *Casinycteris argynnis* Thomas, 1910.

TAXONOMY:
Revised by Bergmans (1991).

Included in the Scotonycterini tribe by Bergmans (1997: 69), Almeida *et al.* (2016: 83) and Hassanin *et al.* (2020: 5), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter two.

Currently (Simmons and Cirranello, 2024a) recognized species of *Casinycteris*: ***argynnis*** Thomas, 1910; ***campomaanensis*** Hassanin, 2014; ***ophiodon*** (Pohle, 1943).

COMMON NAMES:
Czech: krátkonebí kaloni. English: Short-palate Fruit-bats, Short-palated Fruit-bats. French: Casinyctère. German: Kurzgaumen-Flughunde.

Casinycteris argynnis Thomas, 1910

*1910. *Casinycteris argynnis* Thomas, Ann. Mag. nat. Hist., ser 8, 6 (31): 111. Publication date: 1 July 1910. Type locality: Cameroon: Ja River: Bitye [03 13 N 12 22 E, 2 000 ft]. [Goto Description]. Holotype: NHMUK 1911.5.5.1: ad ♀, skin and skull. Collected by: George Latimer Bates Esq. Collection date: 19 November 1909; original number: 502. (Current Combination).
1943. *[Scotonycteris] argynnis:* Pohle, Sber. Ges. naturf. Freunde Berlin, 86 (for 1942). (Name Combination).
2021. *Casinycteris argynis:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 6. Publication date: 14 May 2021. (Lapsus).
2022. *Casinycteris arginnis:* Raulino, Thaurignac, Keita, Esteban, Goumou, Diallo, Ndimbo-Kumugo, Ndong Bass, Mbala Kingebeni, Toure, Delaporte, Ahuka-Mundeke, Muyembe Tamfum, Mpoudi-Ngole, Peeters and Ayouba, Vector-Borne Zoon. Dis., 22 (4): 255. Publication date: 19 April 2022. (Lapsus).

TAXONOMY:
See Bergmans (1991) and Simmons (2005: 315 - 316).

COMMON NAMES:
Czech: kaloň krátkonebý. English: Golden Short-palate Fruit-bat, Yellow-winged Short-palate Fruit-bat, Thomas's Short-palate Fruit-bat, Short-palated Fruit Bat, Golden Short-palated Fruit Bat. French: Casinyctère dorée, Roussette à petit palais, Chauve-souris frugivore à palais court, Casinyctère. German: Goldener Kurzgaumen-Flughund.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008c; IUCN, 2009, Webala *et al.*, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Webala *et al.*, 2016). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008c; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004k; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Mickleburgh *et al.* (1992) indicate that there is little information on the threats to this species, but that it may be threatened by deforestation. It is possible that this species eats cultivated fruits, and consequently might be persecuted as a crop pest (Mickleburgh *et al.*, 2008c; IUCN, 2009).

CONSERVATION ACTIONS:
Current conservation efforts
There appear to be no direct conservation measures in place (Mickleburgh *et al.*, 2008c, in IUCN (2009), although in the Democratic Republic of Congo the species is present in some protected areas such as Mbiye island sanctuary, Yangambi Man and Biosphere Reserve, Yoko Forest Reserve and Masako Forest Reserve (Webala *et al.*, 2016).

Conservation needs/priorities
Webala *et al.* (2016):- Studies are needed on the species' population sizes, distribution, and extent of occurrence throughout its range. Monitoring of population sizes and locations over time are also important to establish whether these are stable or experiencing trends of decline.

The threats to these bats are poorly understood. Studies are needed on the species' habitat requirements and on the effects of forest loss and degradation on the species' population sizes/distribution. Research is also needed on the amount of hunting and the level of bushmeat trade, and the effects of that hunting on population sizes and persistence.
Effective roost site protection efforts are needed to minimize hunting mortality and disturbance to nontarget individuals. Like most threatened flying foxes, local capacity building for conservation managers and education and awareness within local communities are greatly needed to support conservation efforts.

Past suggestions
Mickleburgh *et al.* (2008c) [in IUCN (2009)] and Mickleburgh *et al.* (1992) recommend that surveys are needed to assess the conservation status of this species, to determine if it is present in protected areas, and to learn more about the food plants and general natural history of this species.

GENERAL DISTRIBUTION:
This lowland species is distributed in Central Africa. It has been recorded from southern Cameroon, the Central African Republic and the Democratic Republic of the Congo.

Native: Cameroon; Central African Republic; Congo (The Democratic Republic of the) (Bergmans, 1991; Lunde *et al.*, 2001: 537; Monadjem *et al.*, 2010d: 550); Equatorial Guinea; Gabon (Drexler *et al.*, 2012a: Suppl. Table S1).

Presence uncertain: Congo.

DETAILED MORPHOLOGY:
Brain
Chawana *et al.* (2013: 160) report an average brain mass of 0.83 g (n = 2). Tambusso and Fariña (2015: Suppl.) mention a brain mass of 0.92 g for an average body mass of 40.5 g. Bhagwandin *et al.* (2020: 3027) found that the bat's brain contained 138,458 white matter interstitial cells (WMICs) for a brain mass of 0.75 g..

FUNCTIONAL MORPHOLOGY:
The eye of this bat contains about 130,000 retinal ganglion cells (Coimbra *et al.*, 2016: 191). The minimum angle of resolution was about 0.227° (ca. 8 mm at 1 m distance).

HABITAT:
This species is generally associated with lowland tropical moist forest, swamp forest, a mosaic of these two forest habitats, and a mosaic of swamp forest and secondary grassland (Bergmans, 1991).

ROOST:
It is a solitary rooster, with one specimen collected in the dense foliage of a bush Nowak (1999).

DIET:
Gembu Tungaluna (2012: 91 - 93) followed the consumption of fruits by this species year-round in the DRC and reported the following: First heavy rain season (September - November): *Uapaca guineensis* Müll.Arg., 1864 (Sugar plum, red cedar, false mahogany, rikio) (31%), *Ficus leprieuri* Miq., 1867 (19%), *Ficus wildemanniana* Warb. (14%), *Pseudospondia microcarpa* Engl. (10%), *Musanga cecropioides* R. Br. & Tedlie (African corkwood tree, umbrella tree) (8%), *Myrianthus arboreus* P. Beauvois, 1805 (giant yellow mulberry, bush pineapple, corkwoord) (8%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, otaheite apple, great hog plum) (2%), *Dacryoides edulis* H.J. Lam (safou, African pear, bush pear, Nsafu, bush butter tree, butterfruit) (2%), *Carica papaya* L. (papaya) (2%).
First mild rain season (December - February): *Ficus leprieuri* (42%), *Musanga cecropioides* (27%), *Myrianthus arboreus* (11%), *Spondias cytherea* (5%), *Uapaca guineensis* (5%), *Ficus vallis-choudae* Delile (5%), *Ficus wildemanniana* (5%).

Second heavy rain season (March - May): *Ficus wildemanniana* (62%), *Ficus leprieuri* (25%), *Pseudospondias microcarpa* (A. Rich.) Engl. (13%).
"Dry" season (June - August): *Ficus leprieuri* (100%).

PREDATORS:
Blanding's Tree Snake (*Toxicodryas blandingii* (Hallowell, 1844)) was found in a mist net eating a traped *C. argynnis* in the Democratic Republic of the Congo (Nagy *et al.*, 2011).

POPULATION:
Structure and Density
It is locally not uncommon, with many specimens (~20) caught in mist nets from a locality in the

eastern Democratic Republic of the Congo (Mickleburgh *et al.*, 2008c; IUCN, 2009).

Trend
2008: Unknown (Mickleburgh *et al.*, 2008c; IUCN, 2009). 2004: Unknown (Mickleburgh *et al.*, 2004k; IUCN, 2004).

REPRODUCTION AND ONTOGENY:
The female gives birth to a single young (Hayssen *et al.*, 1993).

VIRUSES:
Circoviridiae
Human associated cyclovirus 9
Vidovszky *et al.* (2023: Suppl.) reported this virus from a bat from the DRC.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, three individuals for antibody to SARS-CoV in sera from Bandundu Province, DRC, none were found to be positive (0/3).

Filoviridae - Filo viruses
Marburgvirus
Towner *et al.* (2007) tested 2 individuals from Gabon using real-time RT-PCR and conventional and nested RT-PCR; neither were found to be positive for Marburg virus specific RNA.

Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 21 specimens they examined from Gabon tested positive for *Respirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

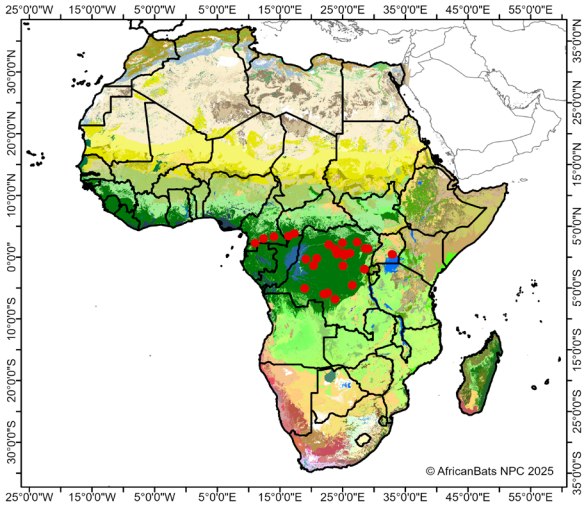

Figure 44. Distribution of *Casinycteris argynnis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Central African Republic, Congo (Democratic Republic of the), Uganda.

Casinycteris campomaanensis Hassanin, 2014

*2014. *Casinycteris campomaanensis* Hassanin, C. R. Biologies, 337 (2): 134, 137, figs 1B, 3, 4. Publication date: 5 February 2014. Type locality: Cameroon: South Region: Campo-Ma'an area: Nkoélon-Mvini [02 23.831 N 10 02.691 E, 117 m]. Holotype: MNHN ZM-2011-637: ad ♀, skull and alcoholic. Collected by: Alexandre Hassanin; collection date: 21 November 2007; original number: C07-41. - Etymology: The specific epithet refers to the Campo-Ma'an area, where the holotype was collected (see Hassanin, 2014: 137). (Current Combination).

COMMON NAMES:
English: Campo-Ma'an fruit bat. French: Casinyctère de Campo-Ma'an. German: Campomaan-Flughund.

CONSERVATION STATUS:
Global Justification
This species is listed as Data Deficient (DD ver 3.1 (2001)) because it is only known from three specimens and no other information is available regarding its demographic trend, threats and ecology (Hassanin, 2017).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2016: DD ver 3.1 (2001) (Hassanin, 2017).

Reginal
None known.

MAJOR THREATS:
Threats to this species are currently unknown (Hassanin, 2017).

CONSERVATION ACTIONS:
Hassanin (2017) report that this species is undoubtedly present in the Campo Ma'an National Park, a protected area located near the type locality. Further studies are however needed to better understand the distribution, natural history and threats of this species.

GENERAL DISTRIBUTION:
Native: Cameroon, Nigeria (Tanshi *et al.*, 2019: 14788).

POPULATION:
Structure and Density
Nothing is known about population trend and size for the species (Hassanin, 2017).

Trend
2016: Unknown (Hassanin, 2017).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon.

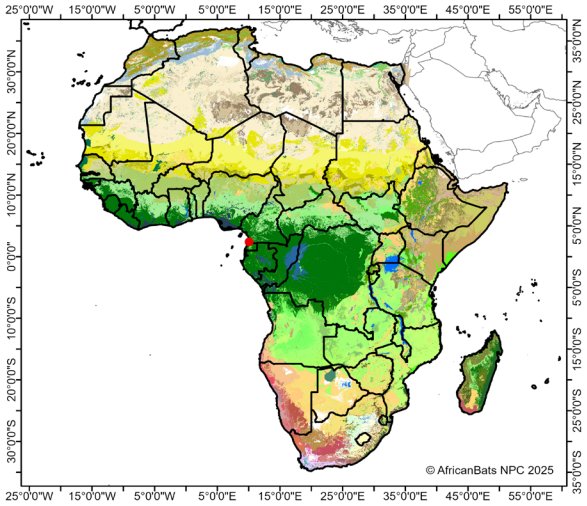

Figure 45. Distribution of *Casinycteris campomaanensis*.

Casinycteris ophiodon (Pohle, 1943)

*1943. *Scotonycteris ophiodon* Pohle, Sber. Ges. naturf. Freunde Berlin, 78, figs 1 -2 (for 1942). Type locality: Cameroon: Kribi, Bez: Bipindi [03 06 N 10 30 E]. [Goto Description]. Holotype: ZMB 50001: sad ♀, skull and alcoholic. Collected by: Georg August Zenker; collection date: May 1899. See Turni and Kock (2008: 21). Pohle (1943: 78) mentioned that the skull was removed from the alcoholic specimen. Taku Bisong *et al.* (2023: 506) furthermore mentioned that the specimen was already 44 years in alcohol prior to the description, so its original colour could not be assessed by then. They also mentioned that the specimen was originally reported with number 50051. - Etymology: From "*ophiodon*" meaning snake-toothed.

1946. *Scotonycteris ophiodon cansdalei* Hayman, Ann. Mag. nat. Hist., ser 11, 12 (95): 766 (for 1945). Publication date: 19 September 1946. Type locality: Ghana: Central province: Oda district: Oda [05 55 N 00 56 W]. [Goto Description]. Holotype: NHMUK 1946.229: ad ♀, skin and skull. Collected by: George Soper Cansdale; collection date: 24 December 1945; original number: 420. - Etymology: In honour of Mr. George Soper Cansdale, the collector of the type specimen (see Hayman, 1946: 770). (Name Combination).

2014. *Casinycteris ophiodon:* Hassanin, C. R. Biologies, 337 (2): 141. Publication date: 5 February 2014. (Current Combination).

TAXONOMY:
See Simmons (2005: 349).

COMMON NAMES:
Czech: kaloň hadozubý. English: Snake-toothed Harlequin Fruit-bat, Pohle's Harlequin Fruit-bat, Snake-toothed Tear-drop Fruit-bat, Pohle's Tear-drop Fruit-bat, Pohle's Fruit Bat. French: Scotonyctère à dents de serpent, Roussette de Pohle. German: Schlangenzähniger Harlekin-Flughund, Pohles Harlekin-Flughund, Poehle's Traenenflughund.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (VU A2c ver 3.1 (2001)) because it is suspected that a population decline, estimated to be more than 30% would be met over the next 10 years or three generations, inferred from the susceptibility of the specialist species to habitat degradation (Mickleburgh *et al.*, 2008db; IUCN, 2009).

Assessment History
Global
2008: VU A2c ver 3.1 (2001) (Mickleburgh *et al.*, 2008db; IUCN, 2009). 2004: EN A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004co; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is highly impacted by deforestation, and through forest fragmentation and degradation. Threats presumably include logging and mining activities, and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008db; IUCN, 2009).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008db) [in IUCN (2009)] report that this species has been recorded from the Mount Nimba World Heritage Site (Guinea, Liberia and Côte d'Ivoire) and from Tai National Park (Côte d'Ivoire). There is a need to maintain areas of suitable primary forest throughout much of West Africa, especially in areas where this seemingly rare bat has been recorded. Further field surveys are needed to locate any additional populations of this species.

GENERAL DISTRIBUTION:
Scotonycteris ophiodon is known only from a relatively few scattered records in West Africa and Central Africa. It has been recorded from Liberia, Côte d'Ivoire, Ghana, Cameroon and Congo. It seems to be known from 16 localities only and has not been recorded from a number of areas where intensive netting has taken place. The species has been recorded at elevations from 120 m (Oda, Ghana) to 1,200 m asl (Mount Nimba).

Native: Cameroon; Congo; Côte d'Ivoire (Henry *et al.*, 2004: 24); Ghana; Liberia.

MOLECULAR BIOLOGY:
Karyotype
Haiduk *et al.*, 1980; 1981: 226) reported 2*n* = 34, FN = 62, BA = 32, a subtelocentric X chromosome and an acrocentric Y chromosome for specimens from Cameroon.

POPULATION:
Structure and Density
This appears to be a naturally rare species (Mickleburgh *et al.*, 2008db; IUCN, 2009).

Trend
Decreasing (Mickleburgh *et al.*, 2008db; IUCN, 2009).

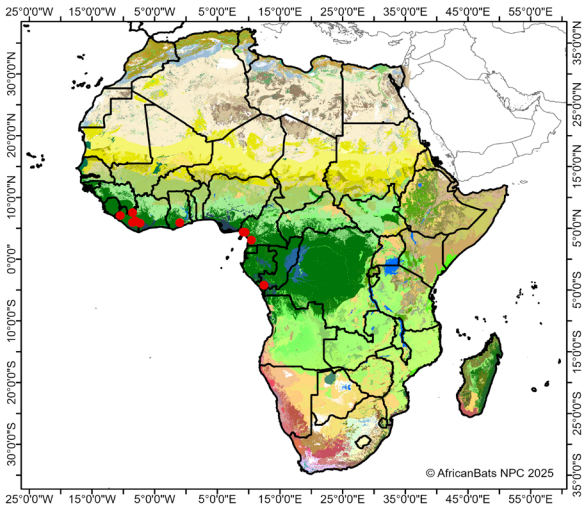

Figure 46. Distribution of *Casinycteris ophiodon*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo, Côte d'Ivoire, Ghana, Liberia.

Genus ***Scotonycteris*** Matschie, 1894

*1894. *Scotonycteris* Matschie, Sber. Ges. naturf. Freunde Berlin, 200. - Comments: Type species: *Scotonycteris zenkeri* Matschie, 1894. - Etymology: From the Greek "*σκόοτος*", meaning darkness and "*νυκτερίς*", meaning bat (see Palmer, 1904: 627). (Current Combination).

TAXONOMY:
Reviewed by Bergmans (1991). See also Simmons (2005: 349), Hassanin *et al.* (2015).

Based on cyt *b* analyses, Hassanin (2014: 141) transferred *ophiodon* Pohle, 1943 from *Scotonycteris* to *Casinycteris*. Further analyses on cyt *b* and nuclear DNA data led Hassanin *et al.* (2015: 206) to split up *S. zenkeri* in four clades of which they recognized three as full species.

Included in the Scotonycterini tribe by Bergmans (1997: 69), Almeida *et al.* (2016: 83) and Hassanin *et al.* (2020: 5), which was considered part of the Epomophorinae by the former and of the Rousettinae by the latter two.

Currently (Simmons and Cirranello, 2024a) recognized species of *Scotonycteris*: ***bergmansi*** Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné, and Bonillo, 2015, ***occidentalis*** Hayman, 1947, ***zenkeri*** Matschie, 1894.

COMMON NAMES:
Czech: hadozubí kaloni. English: Harlequin Fruit-bats, Tear-drop Fruit-bats, West African fruit bats. French: Scotonyctères. German: Harlekin-Flughunde.

GENERAL DISTRIBUTION:
Tanshi *et al.* (2022a: 326) indicate that the specific assignment of *Scotonycteris* specimens from Nigeria remains unresolved as both *zenkeri* and *occidentalis* occur in that country and the latter has only been recently recognized as a separate species.

MOLECULAR BIOLOGY:
Genetics
Based on analyses of mitochondrial cyt *b* and nuclear DNA sequences, Hassanin *et al.* (2015: 205) found support for four clades: Upper Guinea (Liberia and Côte d'Ivoire), Cameroon, western Equatorial Africa (EG, Gabon, RC, and southwestern CAR), and eastern DRC. The mtDNA distances calculated between these four geographic clades are slightly higher than those found between the three species of the genus *Casinycteris*, which suggest that *S. zenkeri* might contain four cryptic species. These results are confirmed nuclear DNA data, except for the eastern DRC clade. Hassanin *et al.* (2015) suggest that females from eastern DRC and

western Equatorial Africa have remained isolated since the end of the Pliocene (2.7 Mya), whereas males were able to disperse, at least occasionally during interglacial periods, resulting in male-mediated nuclear gene flow between these distant populations, apparently from western Equatorial Africa to eastern DRC.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Equatorial Guinea.

Scotonycteris bergmansi Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, 2015

*2015. *Scotonycteris bergmansi* Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, C. R. Biologies, 338 (3): 206. Publication date: 27 January 2015. Type locality: Central African Republic: Mabaéré-Bodingué National Park: Case of Kpoka [3.90 N 17.16 E, 430 m]. Holotype: MNHN ZM-2011-713: ad ♀, alcoholic (skull not removed). Collected by: Alexandre Hassanin, Emmanuel Nakouné, Nicolas Nesi and Carine Ngoagouni; collection date: 16 November 2008; original number: R08-119. - Etymology: In honour of Dr. Wim Bergmans, a Dutch zoologist, for his outstanding contributions in the fields of taxonomy and biogeography of African fruit bats (see Hassanin *et al.* (2015: 206).

COMMON NAMES:
English: Bergmans's fruit bat. French: Scotonyctère de Bergmans. German: Bergmans Harlekin-Flughund.

CONSERVATION STATUS:
Global Justification
Assessed as Least Concern (LC ver. 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in some protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Hassanin, 2020).

Assessment History
Global
2016: LC ver 3.1 (2001) (Hassanin, 2020).

Regional
None known.

MAJOR THREATS:
Threats to this species are currently unknown (Hassanin, 2020).

CONSERVATION ACTIONS:
This species is undoubtedly present in the Campo Ma'an National Park, a protected area located near the type locality. Further studies are needed to better understand the distribution, natural history and threats of this species (Hassanin, 2020).

GENERAL DISTRIBUTION:
Scotonycteris bergmansi occurs in Equatorial Africa, where it is known from the rainforests of Gabon, Equatorial Guinea, Republic of Congo, southern Central African Republic, and eastern Democratic Republic of the Congo Hassanin *et al.* (2015: 207).

Native: Gabon, Equatorial Guinea, Congo, Central African Republic, Democratic Republic of the Congo.

POPULATION:
Structure and Density
Hassanin (2020) this species is a rarely recorded in western Equatorial Africa, but it seems to be more common (at least locally) in eastern Democratic Republic of the Congo.

Trend
2016: Unknown (Hassanin, 2020).

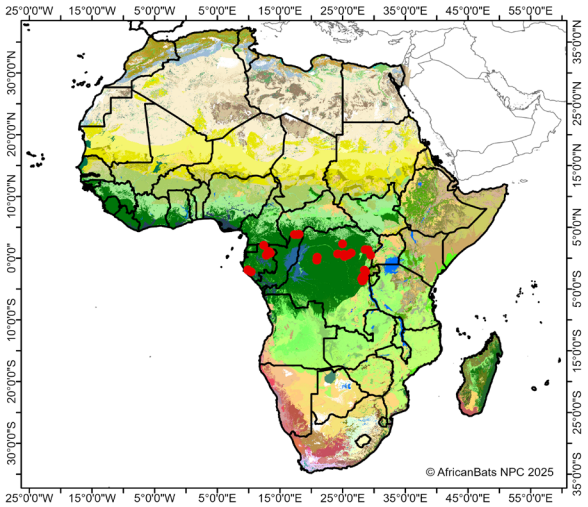

Figure 47. Distribution of *Scotonycteris bergmansi*.

Scotonycteris bergmansi bergmansi Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, 2015

*2015. *Scotonycteris bergmansi bergmansi* Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, C. R. Biologies, 338 (3): 206. Publication date: 27 January 2015. Type locality: Central African

Republic: Mabaéré-Bodingué National Park: Case of Kpoka [3.90 N 17.16 E, 430 m]. - Etymology: In honour of Dr. Wim Bergmans, a Dutch zoologist, for his outstanding contributions in the fields of taxonomy and biogeography of African fruit bats (see Hassanin *et al.* (2015: 206).

GENERAL DISTRIBUTION:
Scotonycteris bergmansi bergmansi is found in the rainforests of western Equatorial Africa in the following countries: Central African Republic (South), Republic of Congo, Gabon, and Equatorial Guinea.

MOLECULAR BIOLOGY:
Karyotype
Primus *et al.* (2006) reported a male "*S. zenkeri*" from Gabon with a 2*n* = 32.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Central African Republic, Equatorial Guinea, Gabon.

Scotonycteris bergmansi congoensis Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, 2015

*2015. *Scotonycteris bergmansi congoensis* Hassanin, Khouider, Gembu, Goodman, Kadjo, Nesi, Pourrut, Nakouné and Bonillo, C. R. Biologies, 338 (3): 207. Publication date: 27 January 2015. Type locality: Congo (Democratic Republic of the): Sukisa [2.31 N 24.98 E, 470 m]. Holotype: MNHN ZM-2014-564: ad ♀, alcoholic (skull not removed). Original number: K13-48.

GENERAL DISTRIBUTION:
Scotonycteris bergmansi congoensis is found in the rainforests of eastern DRC.

Native: Congo (Democratic Republic of the).

DIET:
Gembu Tungaluna (2012: 110 - 112) reported the following fruits being eaten by "*Scotonycteris zenkeri*" in the Kisangani area (DRC) during the various seasons: First heavy rain season (September - November): *Ficus leprieuri* Miq., 1867 (29%), *Ficus wildemanniana* Warb. (22%), *Uapaca guineensis* Müll.Arg., 1864 (Sugar plum, red cedar, false mahogany, rikio) (14%), *Musanga cecropioides* R.Br. & Tedlie (African corkwood tree, umbrella tree) (14%), *Spondias cytherea* Sonnerat, 1782 (Ambarella, otaheite apple, great hog plum) (7%), *Annonidium mannii* (Oliv.) Engl. & Diels (Junglesop) (7%), *Pseudospondias microcarpa* (A. Rich.) Engl. (7%).
First mild rain season (December - February): *Ficus wildemanniana* (33%), *Ficus leprieuri* (27%), *Myrianthus arboreus* P. Beauvois, 1805 (giant yellow mulberry, bush pineapple, corkwood) (20%), *Musanga cecropioides* (20%).
Second heavy rain season (March - May): *Annonidium mannii* (17%), *Musanga cecropioides* (17%), *Oncoba welwitschii* Oliv. (11%), *Ficus leprieuri* (11%), *Ficus vallis-choudae* Delile (11%), *Ficus* sp1 (11%), *Parinari excelsa* Sabine (Guinea plum) (6%), *Carica papaya* L. (papaya) (6%), *Uapaca guineensis* (5%), *Spondias cytherea* (5%).
"Dry" season (June - August): *Parinari excelsa* (50%), *Ficus leprieuri* (25%), *Musanga cecropioides* (25%).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

Scotonycteris occidentalis Hayman, 1947

1947. *Scotonycteris zenkeri occidentalis* Hayman, Ann. Mag. nat. Hist., ser 11, 13 (104): 547 (for 1946). Publication date: 25 June 1947. Type locality: Ghana: Central province: Oda [05 55 N 00 56 W]. [Goto Description]. Holotype: NHMUK 1946.898: ad ♀, skin and skull. Collected by: George Soper Cansdale; collection date: 1946. - Etymology: *occidentalis* refers to the western Africa.
? *Scotonycteris occidentalis:* (Current Combination).

COMMON NAMES:
English: Hayman's tear-drop fruit bat. French: Scotonyctère de Hayman. German: Haymans Harlekin-Flughund.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bm) [in IUCN (2009)] report that although there appear to be no direct conservation measures in place [for "*S. zenkeri*"], it has been recorded from a number of protected areas (e.g., Tai National Park, Côte d'Ivoire). There is a need to investigate whether this species can adapt to secondary forest habitats. Further studies are needed to fully determine if the species is present in forested areas between known localities.

GENERAL DISTRIBUTION:
Scotonycteris occidentalis is distributed in West Africa, where it ranges from Liberia and Guinea, into Côte d'Ivoire, Ghana and possibly Nigeria.

Native: Côte d'Ivoire (Heim de Balsac, 1934b: 24 - as "*S. zenkeri*); Ghana; Guinea; Liberia; Nigeria [Hassanin *et al.* (2015: 206) indicate that some Nigerian populations might belong to *S. zenkeri*, leaving the possibility that some others might belong to *S. occidentalis*].

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

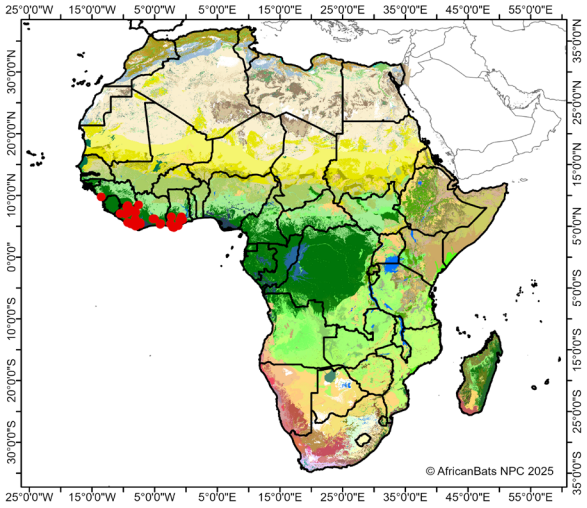

Figure 48. Distribution of *Scotonycteris occidentalis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea, Liberia.

Scotonycteris zenkeri Matschie, 1894

*1894. *Scotonycteris zenkeri* Matschie, Sber. Ges. naturf. Freunde Berlin, 202. Type locality: Cameroon: Yaunde [03 52 N 11 31 E]. Holotype: ZMB 66533: ad ♀, skull and alcoholic. Collected by: Georg August Zenker. See Turni and Kock (2008: 21).
Taku Bisong *et al.* (2023: 507) indicate that this specimen was considered a lectotype, but is actually the holotype. (Current Combination).

1904. *Scotonycteris bedfordi* Thomas, Abstr. Proc. Zool. Soc. Lond., 4: 14. Publication date: 8 March 1904. Type locality: Equatorial Guinea: Bioko: Fish Town. [Goto Description]. Holotype: NHMUK 1904.7.1.28: ad ♀, skin and skull. Collected by: E. Seimund; collection date: 2 January 1904; original number: 31. Presented by Fernando Poo Committee: see Andersen (1912b: 568).

? *Scotonycteris zenkeri zenkeri:* (Name Combination).

TAXONOMY:
See Simmons (2005: 349).

See also Hassanin *et al.* (2015: 206), who split-off *occidentalis* and *bergmansi*.

COMMON NAMES:
Castilian (Spain): Zorra Voladora de Zenker. Czech: kaloň Zenkerův. English: Zenker's Harlequin Fruit-bat, Zenker's Tear-drop Fruit-bat, Zenker's Fruit Bat. French: Scontonyctère de Zenker, Roussette de Zenker. German: Zenkers Harlekin-Flughund, Zenker's Traenenflughund.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in some protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bm; IUCN, 2009; Bergmans *et al.*, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Bergmans *et al.*, 2017a). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bm; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bk; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

This status is for *S. zenkeri* as perceived prior to the publication of Hassanin *et al.* (2015) and will need to be re-evaluated in view of the split-up of this species.

Regional
None known.

MAJOR THREATS:
The species is threatened by habitat loss, presumably largely through logging and mining operations and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008bm; IUCN, 2009; Bergmans *et al.*, 2017a).

CONSERVATION ACTIONS:
Bergmans *et al.* (2017a) report that although there appear to be no direct conservation measures in place, it has been recorded from a number of protected areas (e.g., Tai National Park, Côte d'Ivoire). There is a need to investigate whether this species can adapt to secondary forest habitats. Further studies are needed to fully determine if the species is present in forested areas between known localities.

GENERAL DISTRIBUTION:
Hassanin *et al.* (2015: 206) restricted the distribution of *S. zenkeri* to Cameroon, with the remark that additional data are needed to assess the taxonomic status of some populations from Nigeria. Tentatively, we assigned the Nigerian specimens to this species.

Native: Cameroon; Nigeria(?).

DETAILED MORPHOLOGY:
Brain
Chawana *et al.* (2013: 160) mention that the average brain mass for 2 specimens was 0.64 g.

FUNCTIONAL MORPHOLOGY:
Sagot and Chaverri (2015: 191) indicated that the retinal area in the eye of *S. zenkeri* covers about 40 - 50 mm^2 and contains about 90,000 retinal ganglion cells. The minimum angle of resolution was about 0.227° (ca. 8 mm at 1 m distance).

MOLECULAR BIOLOGY:
Karyotype
Primus *et al.* (2006) reported a male from Gabon with a $2n = 32$, but the specimen on which this is based, would currently be assigned to *S. bergmansi*, so the karyotype for *S. zenkeri* is still to be confirmed.

HABITAT:
Juste B. and Perez del Val (1995: 144) reported that *S. zenkeri* was only netted below 400 m, and was found more frequently in cultivated clearings than in rainforests. However, in Cameroon, Bakwo Fils *et al.* (2021b: 6) reported its occurrence in undisturbed Afromontane forest only.

POPULATION:
Structure and Density
It appears to be a rare, or at least rarely recorded, species (Mickleburgh *et al.*, 2008bm; IUCN, 2009; Bergmans *et al.*, 2017a).

Trend
2016: Decreasing (Bergmans *et al.*, 2017a).
2008: Decreasing (Mickleburgh *et al.*, 2008bm; IUCN, 2009).

The above statements pertain to *S. zenkeri* s.l. and need to be re-evaluated in view of the split-up proposed by Hassanin *et al.* (2015: 206).

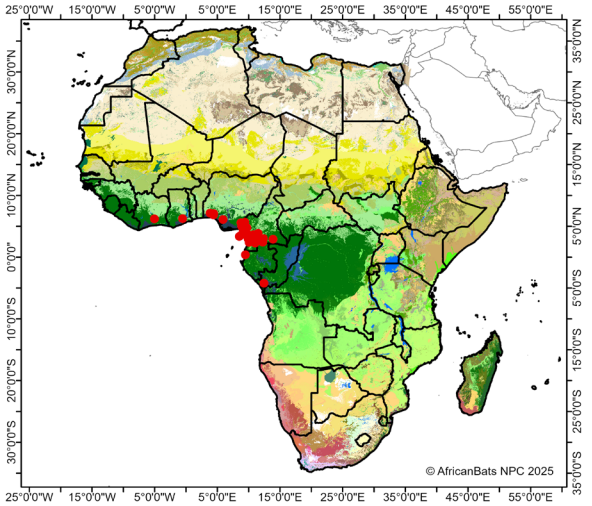

Figure 49. Distribution of *Scotonycteris zenkeri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo, Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Nigeria.

TRIBE Stenonycterini Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, 2012

*2012. *Stenonycterini* Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylog. Evol., 66 (1):. Publication date: 10 October 2012.

TAXONOMY:
Includes only the genus ***Stenonycteris*** K. Andersen, 1912 (Almeida *et al.*, 2020: 11).

Genus ***Stenonycteris*** K. Andersen, 1912

1912. *Stenonycteris* K. Andersen, Catalogue of the Chiroptera in the British Museum, 2nd Edition, xiv, 23. Publication date: 23 March 1912. - Comments: Considered a valid genus by Giannini and Simmons (2003: 504), Lavrenchenko *et al.* (2004b: 130), but only a synonym according to Bergmans (1994: 79). Sometimes considered a subgenus or *Rousettus* containing *lanosa*. - Etymology: From the Greek *stenos* meaning narrow and *nycteris* meaning bat (see Andersen, 1912b: 23).

TAXONOMY:
Included in the Stenonycterini tribe (Almeida *et al.*, 2016: 83), and in the Epomophorini tribe and Stenonycterina subtribe by Hassanin *et al.* (2020: 5).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Stenonycteris*: ***lanosus*** (Thomas, 1906).

Stenonycteris lanosa (Thomas, 1906)

*1906. *Rousettus lanosus* Thomas, Ann. Mag. nat. Hist., ser 7, 18 (104): 137. Publication date: 1 August 1906. Type locality: Uganda: Ruwenzori East: Mubuku Valley [00 15 N 30 10 E, 13 000 ft]. [Goto Description]. Holotype: NHMUK 1906.7.1.2: ad ♂, skull and alcoholic. Collected by: Mr. Richard Bowen Woosnam. Presented by Ruwenzori Exploration Committee: see Andersen (1912b). - Comments: Type locality originally "Ruwenzori East at 13,000 ft", but restricted to Mubuku Valley by Hayman *et al.* (1966: 30) (see Bergmans, 1994: 109). - Etymology: From the Greek/Latin? "*lanosus*" for woolly.

1909. *Rousettus kempi* Thomas, Ann. Mag. nat. Hist., ser 8, 4 (24): 543. Publication date: 1 December 1909. Type locality: Kenya: Southern slopes Mount Elgon, Kirui's: Twere [ca. 00 46 N 34 37 E, 6 000 ft]. [Goto Description]. Holotype: NHMUK 1910.4.1.6: sad ♂, skin and skull. Collected by: Robert ("Robin") Kemp Jr. Collection date: 16 September 1909; original number: 269. Presented/Donated by: C.D. Rudd Esq. Formerly in Rudd collection.

2012. *Stenonycteris lanosus:* Nesi, Kadjo, Pourrut, Leroy, Pongombo Shongo, Cruaud and Hassanin, Mol. Phylog. Evol., 66 (1): 135 (for 2013). Publication date: 10 October 2012. (Name Combination, Current Combination).

2013. *Rousettus (Stenonycteris) lanosa:* M. Happold, in: Happold, M; Happold, D., Mammals of Africa. Volume IV. Hedgehogs, shrews and bats, 227. (Alternate Spelling).

2023. *Stenonycteris lanosa:* Simmons and Ciranello, Bats of the World. Publication date: 11 July 2023. (Current Combination, Current Spelling).

? *Rousettus (Stenonycteris) lanosus:* (Name Combination).

? *Rousettus lanosus kempi:* (Name Combination).

? *Rousettus lanosus lanosus:* (Name Combination).

TAXONOMY:
Revised by Bergmans (1994), but see Simmons (2005: 348).

Included in the genus *Stenonycteris* by Almeida *et al.* (2011a: 5, 7, 9, 10) and Patterson and Webala (2012: 10) since it consistently recovered in another clade allied to *Myonycteris, Lissonycteris*, and *Megaloglossus*.

Nesi *et al.* (2012: 126) confirm that *Stenonycteris* should be considered a separate genus and should even be placed in its own tribe (Stenonycterini), within the subfamily Epomophorinae.

COMMON NAMES:
Chinese: 狭齿果蝠. Czech: kaloň vlnatý. English: Mountain Rousette, Long-haired Rousette, Woolly Rousette, Ruwenzori Long-haired Rousette. French: Roussette du Ruwenzori, Roussette à longs poils. German: Gebirgs-Höhlenflughund. Kinande (DRC): Karakonube. Malawian: Lichinji, Mleme.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) [as *Rousettus lanosus*] in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because the global population is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dg; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008dg; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cx; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The major threats to this species include ongoing deforestation in montane regions, likely disturbance of cave roosting sites (possibly from tourists in parts of its range), and possible overhunting of bats at roost sites for subsistence

food by local people (Mickleburgh *et al.*, 2008dg; IUCN, 2009).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dg) [in IUCN (2009)] report that although there appear to be no direct conservation measures in place, it has been recorded from a number of protected areas (e.g., Mount Elgon National Park, Kenya). There is a need to maintain remaining areas of suitable montane forest and to protect major roosting colonies from disturbance. In areas where this species is identified as being overhunted, there is a need to encourage the sustainable use of susceptible populations.

GENERAL DISTRIBUTION:
Stenonycteris lanosa is distributed in East Africa and marginally in Central Africa. It ranges from Ethiopia and southern Sudan in the north of its range, into Kenya, Uganda, eastern Democratic Republic of the Congo and Rwanda, to Tanzania and northern Malawi. It is largely, but not strictly, a montane species being found between 500 and 4,000 m asl (with most records above 1,000 m, e.g., at 13,000 ft in the Mubuku Valley, E. Ruwenzori [Thomas and Wroughton, 1910: 486]).

Native: Congo (The Democratic Republic of the); Ethiopia (Bergmans, 1994: 79); Kenya; Malawi (Bergmans, 1994; Bergmans, 1994: 79; Monadjem *et al.*, 2010d: 555); Rwanda (Bergmans, 1994: 79); Sudan; Tanzania (Stanley and Goodman, 2011: 41); Uganda (Kityo and Kerbis, 1996: 60).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data: Fa: 94.5 mm, mass: 121 g, wing loading: 21.8 N/m^2, aspect ratio: 5.6.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Monadjem *et al.* (2011)] mention a wing loading value of 21.8 Pa, aspect ratio 5.6 for a wingspan of 55 cm and a wing area of 540 cm^2 and a body mass of 121 g.

POPULATION:
Structure and Density
This appears to be a little recorded, but locally abundant species (Mickleburgh *et al.*, 1992). It forms colonies of up to a few hundred bats (Mickleburgh *et al.*, 2008dg; IUCN, 2009).

Trend
2008: Decreasing (Mickleburgh *et al.*, 2008dg; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) report a maximum longevity of 18.7 years.

REPRODUCTION AND ONTOGENY:
Stanley and Goodman (2011: 40) reported on five pregnant females collected between 19 and 24 July 1993 in the South Pare Mountains (Tanzania).

Kingdon (1974) [in Krutzsch (2000: 111)] showed that *S. lanosa* is one of the species in which pregnant or lactating females are present in the population in all months of the year, and where most adult males have enlarged spermatogenic testes and hypertrophied, secretion-filled accessory glands. This would indicate that while males are fecund population-wide, they enter periods of inactivity individually.

PARASITES:
BACTERIA
Stockinger and Doster (2017: 1260) found *Staphylococcus aureus* bacteria in pulmonary tissue of a captive bred "*Rousettus lanosus*". From the same bat, they also reported an achlorophyllic, aerobic, unicellular alga (*Prototheca zopfii* W. Krüger, 1894).

HAEMATOSPORIDA
The two South Sudanese "*Rousettus lanosus*" specimens tested by Schaer *et al.* (2017: 2) were infected by *Hepatocystis* parasites.

DIPTERA
Nycteribiidae
Dipseliopoda setosa Theodor, 1955 from Kenya and Tanzania (Haeselbarth *et al.*, 1966: 116; Dick *et al.*, 2023: 72). Lutz *et al.* (2021: Suppl.) reported this fly also from Ugandan bats.
The fly *Stylidia scissa* Speiser, 1901 was collected on a bat from South Sudan (the same bat where also *T. dina* was collected from, see below), although Bergmans (1982: 161) indicates that this fly is generally found on Microchiropterans and its find might "be due to straggling between spirit specimens".

Streblidae
Two of the 37 Ugandan bats examined by Lutz *et al.* (2021: Suppl.) were hosts of *Megastrebla bequaerti* (Jobling, 1936).

SIPHONAPTERA
Ischnopsyllidae
Thaumapsylla breviceps Rothschild 1907, where the nominate subspecies *T. b. breviceps* Hopkins and Rothschild, 1956 is occurring in Kenya and the DRC (Haeselbarth *et al.*, 1966: 186). *Thaumapsylla dina* Jordan, 1937 in the

mountains of the Ruwenzori, Congo and Kenya (Haeselbarth *et al.*, 1966: 186). (Bergmans (1982: 161) reported that this flea was also collected from a "*Rousettus lanosus*" from South Sudan.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Burundi, Congo (Democratic Republic of the), Egypt, Ethiopia, Kenya, Malawi, Rwanda, South Sudan, Tanzania, Uganda.

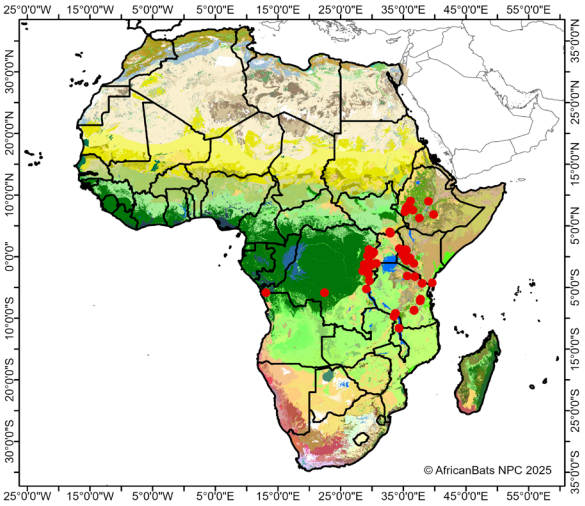

Figure 50. Distribution of *Stenonycteris lanosa*.

†Genus ***Turkanycteris*** Gunnell and Manthi, 2018

*2018. *Turkanycteris* Gunnell and Manthi, J. Hum. Evol., p "2", "4". Publication date: 6 April 2018. - Etymology: Referring to the Turkana Basin, where Kanapoi (the type locality of the species) is located (Gunnell and Manthi, 2018: "4").

†***Turkanycteris harrisi*** Gunnell and Manthi, 2018

*2018. *Turkanycteris harrisi* Gunnell and Manthi, J. Hum. Evol., p "2", "4", fig 1A. Publication date: 6 April 2018. Type locality: Kenya: Nzube's Mandible Site. Holotype: NMK KP-68723. The holotype is a M_1. - Etymology: In honour of John M. Harris for his many contributions to the understanding of African Neogene vertebrates (Gunnell and Manthi, 2018: "4").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Timeframe: Early Pliocene (Gunnell and Manthi, 2018: "4".).

INFRAORDER RHINOLOPHIFORMACEI Van Cakenberghe, Kearney and Seamark, 2007

1866. *Histiorrhina* Haeckel, Generelle Morphologie der Organismen, 2: clx. - Comments: Proposed as family, including the genera *Rhinolophus* Lacépède, 1799; *Megaderma* É. Geoffroy, 1810; and *Phyllostoma* G. Cuvier, 1800 [= *Phyllostomus* Lacépède, 1799] (see Jackson and Groves, 2015: 229).

1998. *Megachiropteramorpha* Simmons and Geisler, Bull. Am. Mus. Nat. Hist., 235: 135, 136. - Comments: Originally included the fossil *Archaeopteropus* Meschinelli, 1903 and the suborder Megachiroptera (Dobson, 1875) (see Jackson and Groves (2015: 229).

*2007. *RHINOLOPHIFORMACEI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Infraorder is based on *Rhinolophus* Lacépède, 1799 (type of RHINOLOPHIDAE Gray, 1825). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Guan *et al.* (2025: 7) estimate that the split between the Rhinolophidae and the Hipposideridae occurred some 37.27 mya.

DETAILED MORPHOLOGY: Smith (1990: 14) studied the hyoid morphology of a selection of species belonging to this infraorder.to assess the inter-familial relationships. This resulted in two possible cladigrams depending on whether the shift of the sternothyroid origin onto the manubrium of the sternum is the shared-derived character uniting Rhinolphidae with Megadermatidae ([[Rhinolophidae - Megadermatidae] - [Rhinopomatidae - [Nycteridae - Emballonuridae]]]) or whether it was the shift of the omohyoid origin ([Rhinolophidae - [Megadermatidae - [Rhinopomatidae - [Nycteridae - Emballonuridae]]]]).

Superfamily RHINOLOPHOIDEA J. E. Gray, 1825

1825. *Rhinolophina* J. E. Gray, Ann. Philos., 10 (5): 338. - Comments: Proposed as tribe and originally containing the genera *Megaderma* É. Geoffroy, 1810; *Rhinolophus* Lacépède, 1799; *Nycteris* É. Geoffroy & G. Cuvier, 1795; *Mormoops* Leach, 1821 and *Nyctophilus* Leach, 1821. Jackson and Groves (2015: 241, 242) placed this name in the synonymy of both Rhinolophoidea and Rhinolophidae.

*1825. *Rhinolophoidea* J. E. Gray. - Comments: The name of the Superfamily is based on *Rhinolophus* Lacépède, 1799 (type of RHINOLOPHIDAE Gray, 1825).

Some publications assigned the name to Bell (1836). (Current Combination).

COMMON NAMES:
Czech: vrápencovci, vrápenci.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Shi and Rabosky (2015: 1532) [based on Teeling *et al.* (2005)] mention 55 million years ago as approximate fossil date for the Rhinolophoidea, and Patterson and Webala (2012: 12) indicate that the separation between the Rhinolophidae and the Hipposideridae took place some 28.7 mya, although Shi and Rabosky (2015: 1532) set this about 8 million years earlier (at 37 mya). Foley *et al.* (2014: 320) provide another estimate for the African divergence between the Rhinolophidae and the Hipposideridae from their common ancestor: 42 mya. Based on transcriptome RNA-seq data, Lei and Dong (2016: 2) placed the split in the Middle Miocene at about 40 mya.

Ravel *et al.* (2016: 358) indicate that the oldest occurrence of the Hipposideridae in northern Africa and the oldest occurrence of the Rhinolophidae in eastern Asia suggest that a common ancestor for these two families might have occurred in Central Asia. Unfortunately, there are no fossil records to substantiate this.

Chornelia and Hughes (2022: 1) suggest that the Rhinolophidae most probably have an Oriental origin, and colonized Africa at the time of Tethys Ocean closure around the Oligocene to Miocene (around 27 Mya). The Hipposideridae, on the other hand, originated in the Oriental and African regions. The diversification of the latter family occurred over Eurasia and the Afro-Arabian region since the Middle Eocene. The Rhinonycteridae originated in the African region, where they split off from a common ancestor with the Hipposideridae.

BIOGEOGRAPHY:
Foley *et al.* (2014: 320) indicate that the Rhinolophoidea and Pteropodidae diverged approximately 59 Mya. While within the Rhinolophoidae, the families Rhinolophidae and Hipposideridae diverged in Africa from their common ancestor approximately 42 May during the Eocene. The family Rhinonycteridae separated from the other Hipposideridae approximately 39 Mya, also in Africa (Foley *et al.*, 2014: 320).

HABITS:
Rainho *et al.* (2023: 7) assigned the *Rhinolohus, Hipposideros* and *Triaenops* bats in Meru county (Kenya) to a low-flying guild flying at altitudes less than 1.5 m.

Family HIPPOSIDERIDAE Lydekker, 1891

1860. *Phyllorrhina* Koch, Ber. Oberhess. Ges. Nat. Heilkde, 8 (4): 26. - Comments: Pavlinov *et al.* (1995: 75) mention *Phyllorrhina* with a question mark as synonym of Hipposideridae. Lanza *et al.* (2015: 121) mention "*Phyllorhina*" Koch as a synonym of the genus *Asellia*. Type genus: *Phyllorrhina* Bonaparte, 1837 [1832–1841] [= *Hipposideros* J. Gray, 1831]. Jackson and Groves (2015: 245) indicate the name is unavailable.

1863. *Phyllorhina* Koch, Bericht der Oberhessischen Gesellschaft für Natur- und Heilkunde, 309.

*1891. *Hipposideridae* Lydekker, in: Flower and Lydekker, Mammals Living and Extinct, 657.

1891. *Hipposiderinae* Lydekker, in: Flower and Lydekker, Mammals Living and Extinct, 657. - Comments: Type genus: *Hipposideros* Gray, 1831. Originally included the genera *Hipposiderus* [sic] J. Gray, 1834 [= *Hipposideros* J. Gray, 1831]; *Anthops* Thomas, 1888; *Rhinonicteris* J. Gray, 1847; *Triaenops* Dobson, 1871; and *Coelops* Blyth, 1848 (see Jackson and Groves, 2015: 244).

1907. *Hipposideridae* Miller, Bull. U.S. natl. Mus., 57: viii, 109. Publication date: 29 June 1907. - Comments: Type genus: *Hipposideros* J. Gray, 1831. Originally included the genera *Hipposideros* J. Gray, 1831; *Asellia* J. Gray, 1838; *Anthops* Thomas, 1888; *Coelops* Blyth, 1848; *Cloeotis* Thomas, 1901; *Rhinonicteris* J. Gray, 1847; and *Triaenops* Dobson, 1871 (see Jackson and Groves, 2015: 245).

1941. *Coelopinae* Tate, Am. Mus. Novit., 1140: 11. Publication date: 20 August 1941. - Comments: Type genus: *Coelops* Blyth, 1848.

1970. *Hipposiderini* Koopman and J.K. Jones Jr., in: Slaughter, Classification of bats, 25. - Comments: Type genus: *Hipposideros* J. Gray, 1831. Proposed as tribe and originally included the genera *Hipposideros* J. Gray, 1831;

Aselliscus Tate, 1941; *Cloeotis* Thomas, 1901; *Rhinonicteris* J. Gray, 1847 and *Triaenops* Dobson, 1871 (see Jackson and Groves, 2015: 245).

1994. *Hipposiderina* Koopman, in: Niethammer et al., Chiroptera: Systematics, 60. - Comments: Type genus: *Hipposideros* J. Gray, 1831. Proposed as subtribe and originally included the genera *Hipposideros* J. Gray, 1831; *Anthops* Thomas, 1888 and *Asellia* J. Gray, 1838 (see Jackson and Groves, 2015: 245).

1995. *Coelopsinae:* Pavlinov, Borissenko, Kruskop and Jahonton, Archives of the Zoological Museum, Moscow State University,, 133: 84. - Comments: Mentioned as a synonym of the Hipposideridae by Pavlinov *et al.* (1995: 84). (Lapsus).

2014. *Hippossideridae:* Ndara R., IJISR, 12 (1): 253. Publication date: November 2014. (Lapsus).

2014. *Hippossyderidae:* Ndara R., IJISR, 12 (1): 252. Publication date: November 2014. (Lapsus).

2015. *Hypposideridae:* Lanza, Funaioli and Riccucci, The bats of Somalia and neighbouring areas, 118. (Lapsus).

2018. *Hipossidaridae:* Malekani, Musaba, Gembu, Bugentho, Toengaho, Badjedjea, Ngabu, Mutombo, Laudisoit, Ewango, Van Cakenberghe, Verheyen, Asimonyo, Masudi, Bongo and Ngbolua, Nat. Conserv. Res., 3 (1): 68. Publication date: January 2018. (Lapsus).

TAXONOMY:

Considered a subfamily of the Rhinolophidae by Koopman (1993a: 169), Schutt and Simmons (1998: 28), but see Harrison and Bates (1991: 51), Corbet and Hill (1992: 104), Peterson *et al.* (1995: 66), Hutson *et al.* (2001), Simmons (2005: 365), who consider this to be a valid family. Hoofer and Van Den Bussche (2003: 10 - 12) suggest that the Hipposideridae might not be monophyletic, with *Triaenops* being different, although they state this might be the result of inadequate sampling.

McKenna and Bell (1997) used the name Rhinonycterinae Gray, 1866 for this group, but this has not been accepted by other authors (Simmons, 2005: 365). Although Rhinonycteridae (= Rhinonycterina Gray, 1866) has priority over Hipposideridae as a family-group name, nobody other than Gray (1866b) used the former name until it was resurrected by McKenna and Bell (1997). Miller (1907) used the name Hipposideridae for this group because *Hipposideros* Gray, 1831 has priority over *Rhinonycteris* Gray, 1866 (= *Rhinonicteris* Gray, 1847). Subsequent authors have followed Miller (1907) usage of Hipposideridae/inae, and Simmons (2005: 365) believes that there is little to be gained by replacing it with an unknown name. Simmons (2005: 365) therefore retains Hipposideridae for this group pending action by the International Commission on Zoological Nomenclature.

Due to the recent separation of *Cloetis, Paratriaenops, Rhinonicteris* and *Triaenops* into a distinct family, the above naming issue has resolved itself.

McKenna and Bell (1997) proposed a tribal classification for hipposiderids (which they treated as a subfamily), but many of the groups they defined have subsequently been shown to be paraphyletic (Bogdanowicz and Owen, 1998, Hand and Kirsch, 1998); accordingly, Simmons (2005: 365) did not recognize subfamilies or tribes within Hipposideridae.

Currently (Simmons and Cirranello, 2024b) recognized genera of Hipposideridae: *Anthops* Thomas, 1888, ***Asellia*** Gray, 1838, *Aselliscus* Tate, 1941, *Coelops* Blyth, 1848, ***Doryrhina*** Peters, 1871, ***Hipposideros*** Gray, 1831, ***Macronycteris*** Gray, 1866.

Additionally, there are also the extinct genera †*Miophyllorhina* Hand, 1997; †*Palaeophyllophora* Revilliod, 1917; †*Riversleigha* Hand, 1998, †*Vaylatsia* Sigé, 1990.

COMMON NAMES:

Czech: pavrápencovití, listonosovití. Dutch: Bladneusvleermuizen. English: Old-World leaf-nosed bat, Trident bats, Leaf-nosed bats. French: Hipposidéridés, Phyllorine. German: Rundblattnasen. Italian: Ipposidèridi. Norwegian: Rundbladneser, falske hesteskoneser. Russian: Листоносы, Подковогубы, Ложные подковоносы. Ukrainian: Звичайні листоноси [= Zvychayni lystonosy]. Vietnamese: Họ dơi mũi.

SIMILAR SPECIES:

Key characters for the genera:

Anthops - Head and body is about 50 mm, the tail is very short (less than half as long as the femur), and the forearm length is about 48 - 51 mm. The horseshoe-shape part of the nose leaf has two lateral leaflets, the inner one being quite small and the outer one large. Traces of a small frontal sac are present (Nowak, 1994: 115).

Asellia - Head and body length is about 46 - 62 mm, tail length is 18 - 27 mm (tail protruding up to 7 mm beyond interfemoral membrane), and forearm length is 45 - 52 mm. Posterior component of noseleaf with three short, triangular projections. Only one upper premolar on each side, M^3 greatly reduced (two ridges) (Nowak, 1994: 114, Happold, 2013al: 357).

Aselliscus - Head and body length is about 38 - 45 mm, tail length is 20 - 40 mm (tail extends beyond the membrane, as in *Asellia*), and forearm length is 35 - 45 mm. The upper margin of the transverse noseleaf is divided into three points, and two lateral leaflets margin the horseshoe (Nowak, 1994: 116).

Coelops - Head and body length is 28 - 50 mm, the tail is extremely short or absent, and forearm length is 33 - 47 mm. Lateral leaflets are lacking on the noseleaf, or they are obscured by dense, stiff hairs (Nowak, 1994: 119).
Hipposideros - Head and body is about 35 - 100 mm, tail length is 18 - 70 mm, and forearm length is about 33 - 105 mm. Posterior component of noseleaf roughly elliptical in outline (although the outline of upper margin varies from almost flat to low-arched or even subtriangular), without three projections (Nowak, 1994: 111, Happold, 2013al: 357).
Paracoelops - Head and body length, 45 mm; tail absent, forearm length is about 42 mm. The nose leaf is horseshoe-shaped and surmounted by a round leaf with radial striations (Nowak, 1994: 119).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The Hipposideridae have been found from the Miocene of Songhor (Butler, 1969) and from the Mio-Pliocene of Morocco (Lavocat, 1961). The family goes back to the middle Eocene in Europe (Butler, 1978), where the genus *Palaeophyllophora* is considered to be the oldest representative (Ravel *et al.*, 2016: 412). Early Oligocene to recent in Arabia, early Miocene to recent in Africa, Pleistocene to recent in Asia, late Oligocene to recent in Australia (Hand and Kirsch, 1998). Because they are predominantly cave-dwelling bats, their remains are frequently preserved in Cenozoic limestone sediments (Happold, 2013al: 357). The earliest known *Hipposideros* is from the early Miocene, and the subgenus *Syndesmotis* (into which *H. megalotis* is sometimes placed) appears to have separated from *Hipposideros* in the middle Miocene (Happold, 2013al: 357). The fossils of Hipposideridae from the late Eocene and early Oligocene of France were already distinct from the Rhinolophidae that occurred in the same deposits (Lekagul and McNeely, 1977).

Manthi (2008: 47) reported on the presence of a large and small species of *Hipposideros* at Kanapoi (Kenya) between 4.17 and 4.07 mya. They suggested these bones might have been accumulated by either the barn owl (*Tyto alba*) or the giant eagle owl (*Bubo lacteus*).

Based on phylogenetic analyses, Bogdanowicz and Owen (1998) suggest that the Hipposideridae probably originated somewhere in the Oriental region. In contrast, based on evidence from fossils, Hand and Kirsch (1998) suggest that the family originated in Australia.

Shi and Rabosky (2015: 1537) calculated the family-level stem and crown ages to be respectively 49.9 and 49.3 Mya.

BIOGEOGRAPHY:
The Hipposideridae diverged from the Rhinolophidae from a common ancestor in Africa approximately 42 Mya during the Eocene (Foley *et al.*, 2014: 320). While the family Rhinonycteridae separated from the other Hipposideridae approximately 39 Mya, also in Africa (Foley *et al.*, 2014: 320). The monophyletic *Hipposideros* clade diverged from other Hipposideridae approximately 31 Mya during the Oligocene in Africa (Foley *et al.*, 2014: 320). During the Miocene at about 15 Mya, *Hipposideros* diversified into distinct clades based on geography: these being the African, India and South East Asia clades (Foley *et al.*, 2014: 320).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^1/_2$, $C^1/_1$, $PM^2/_2$, $M^3/_3$ = 30.

Except in *Asellia* and *Hipposideros megalotis*, which have a dental formula of $I^1/_2$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 28.

DETAILED MORPHOLOGY:
Brain
In their comparative study on bat brains, Bhatnagar *et al.* (2016) found that Hipposiderids stand apart from all other examined bats due to their relatively large adenohypophysis

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) mention the 2*n* within the family varies between 24 and 52.

HABITS:
Hipposiderids are often fly-catchers and gleaners but they also forage by slow-hawking, some to a greater extent than others (Happold, 2013al: 358). Unlike most rhinolophids, many hipposiderids forage in small groups (Happold, 2013al: 358).
Hipposiderids are unable to scuttle over the ground, and apparently cannot climb (Happold, 2013al: 358).

DIET:
Hipposiderids are insectivorous: the taxa and size of prey varies according to the size of the bat and the robustness of its teeth (Happold, 2013al: 358).

PARASITES:
Fain (1994: 1280) reports that the Hipposideridae are hosts for four genera of Myobiidae (Acari):

Hipposiderobia with 12 species (parasiting on five genera of bats), *Metabinuncus* also with 12 species (occurring only on the genus *Hipposideros*), *Binunculoides* with one species on *Hipposideros*, and *Triaenomyobia*, with one species on *Triaenops*.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 27 % of the species belonging to this family are confirmed viral carriers.

Coronaviridae
Morales *et al.* (2025: 450) reported that worldwide 31.7 % of all viruses found in the Hipposideridae are coronaviruses.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Central African Republic, Congo (Democratic Republic of the), Kenya, Namibia, Tanzania, Uganda.

Genus ***Asellia*** J. E. Gray, 1838

*1838. *Asellia* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 493. Publication date: 1 February 1838. - Comments: Type species: *Rhinolophus tridens* E. Geoffroy Saint-Hilaire, 1813. - Etymology: From the Greek "*α-*" "alpha privative" and the Greek feminine substantive "*σέλλα*" (sélla), meaning "saddle", referring to the absence of a sella in the noseleaf (see Lanza *et al.*, 2015: 121). Palmer (1904: 124), however, mentions that *Asellia* is an adjective used as a noun, from the Latin "*asellus*", a little ass - probably in allusion to the long, pointed ears. (Current Combination).
1957. *Aseltia:* Harrison, Mammalia, 21 (1): 8. Publication date: March 1957. (Lapsus).
2008. *Ascidia:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 253. (Lapsus).
2023. *Aselia:* Dalhoumi, El Mokni, Ouni, Beyrem and Aulagnier, Diversity, 15 (1108): 5. Publication date: 25 October 2023. (Lapsus).

TAXONOMY:
Allen (1939a: 78) mentioned that *Asellia* was originally described as subgenus of *Hipposideros*.

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Asellia*: *arabica* Benda, Vallo and Reiter, 2011; ***italosomalica*** de Beaux, 1931; ***patrizii*** de Beaux, 1931; ***tridens*** (E. Geoffroy St.-Hilaire, 1813).
Additionally, there is the extinct †*vetus* Lavocat, 1961.

COMMON NAMES:
Czech: trojzubcoví pavrápenci. English: Lesser Trident Bats, Trident Bats, Trident Leaf-nosed Bats. French: Tridents, Asellia, Chauve-souris à 3 endentures. German: Dreizackblattnasen. Italian: Asèllie.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Egypt, Sudan.

Asellia italosomalica de Beaux, 1931

*1931. *Asellia tridens italosomalica* de Beaux, Ann. Mus. civ. Stor. nat. Genova, 55: 190. Publication date: 6 June 1931. Type locality: Somalia: Oddur. [Goto Description]. Holotype: MSNG 30942: ♀, skin and skull. Collected by: Narciso Mosconi Bronzi; collection date: 1929. See Benda *et al.* (2011f: 266). Paratype: MSNG 12232a: ♂, skull and alcoholic. Collected by: Captain Carlo Citerni; collection date: 1911. - Etymology: From the feminine scientific Latin adjective *italosomalica*, meaning "inhabiting Italian Somalia, referring to country where the type specimens were collected (see Lanza *et al.*, 2015: 123)..
1931. *Asellia tridens italo-somalica:* De Beaux, in: 55, Ann. Mus. civ. Stor. nat. Genova, 55: 215. Publication date: 3 October 1931. - Comments: De Beaux (1931) used this spelling in his summary on page 215. All other occurrences in the tekst are without hyphen. I'm assuming this is an hyphenation error. (Lapsus, Alternate Spelling).
? *Asellia italosomalica:* (Current Combination).

TAXONOMY:
Based on morphometric analyses and a K2P genetic distance of 12.3 to 13.7 % with other *Asellia* populations, Benda *et al.* (2011f: 262) distinguish *italosomalica* specimens from Socotra and Somalia as a different, well-defined taxon, which is best considered to be a separate species.

COMMON NAMES:
English: De Beaux's Trident Bat, **Somali Trident Leaf-nosed Bat** (Armstrong *et al.*, 2016: 116). German: Somalische Dreizackblattnase. Italian: Asèllia italosòmala.

CONSERVATION STATUS:
Global Justification
This is a newly established species without enough data on distribution and ecology to be

able to assess it beyond Data Deficient at present (Benda, 2017b).

Assessment History
Global
2016: DD ver. 3.1 (2001) (Benda, 2017b).

Regional
None known.

MAJOR THREATS:
Human disturbance in roost sites and pesticide use against insects are the main threats (Benda, 2017b).

CONSERVATION ACTIONS:
Benda (2017b) report that no specific measures are known to be in place for this species.

GENERAL DISTRIBUTION:
Native: Socotra, Somalia.

POPULATION:
Structure and Density
Benda (2017b) report that no data is available about population size and trend for this species.

Trend
2016: Unknown (Benda, 2017b).

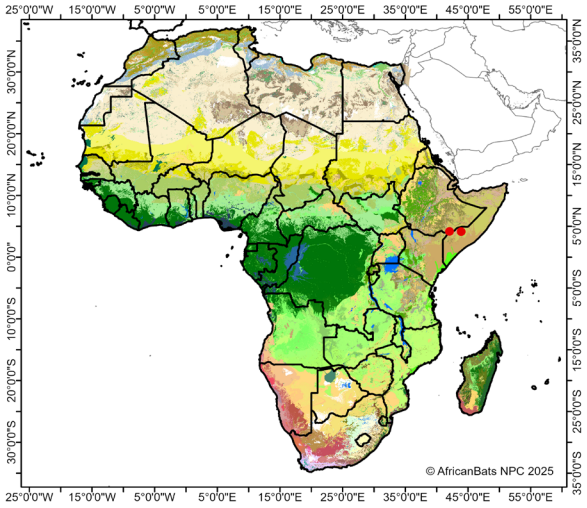

Figure 51. Distribution of *Asellia italosomalica*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Somalia.

Asellia patrizii de Beaux, 1931

*1931. *Asellia patrizii* de Beaux, Ann. Mus. civ. Stor. nat. Genova, 55: 186. Publication date: 6 June 1931. Type locality: Eritrea: Dancalia: Gaare [13 13 N 42 07 E]. [Goto Description]. Holotype: MSNG 31313: ♂, skull and alcoholic. Collected by: Marquis Saverio Patrizi Montoro; collection date: December 1912. See Benda *et al.* (2011f: 267). Paratype: MSNG 31314: ♀, skull and alcoholic. Collected by: Marquis Saverio Patrizi Montoro; collection date: December 1929. See Benda *et al.* (2011f: 267), who mention this specimen along with the holotype, but not explicity as "paratype" (as did De Beaux, 1931: 190). They do mention three further paratypes from the series: MSNG 33203, 33204 [S+B], 31315a, 31315b, collected at Attab (Eritrea), in July 1893 by G. Pestalozza and October 1906 by P. Felter. Paratype: MSNG 31315a: ♂, skull and alcoholic. Collected by: Pietro Felter; collection date: October 1910. Paratype: MSNG 31315b: ♀. Collected by: Pietro Felter; collection date: October 1906. - Etymology: In honour of the Marquis Saverio Patrizi Nero Montoro (1902 - 1978), eminent Italian entomologist, biospeleologist and explorer, collector of zoological material especially in central and eastern Africa, Sardinia and eastern Mediterranean countries (see Lanza *et al.*, 2015: 128). (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: pavrápenec eritrejský. English: Patrizi's Lesser Trident Bat, **Patrizi's Trident Leaf-nosed Bat**. French: Trident de Patrizi, Asellia de Patrizi. German: Patrizis Dreizackblattnase. Italian: Asèllia di Patrìzi.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017e).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017e). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008a; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Mickleburgh *et al.*, 2004ad; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There is very little information, but roost disturbance is a possible threat. However, the species is associated with habitats that are not under significant threat, and has been found in buildings, and so can adapt to human presence

(Mickleburgh *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017e).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008a) and Monadjem *et al.* (2017e) suggest surveys are needed to determine the distribution of this species, both in northeastern Africa and in the Arabian Peninsula. Has been recorded from Awash National Park (Hill and Morris, 1971).

GENERAL DISTRIBUTION:
This species has a restricted known range in northeastern Africa, from central Ethiopia north to Eritrea (Yalden *et al.*, 1996), and also from islands in the Red Sea including Farasan Island and Segid Island (= As-Saqid) of southwestern Saudi Arabia (Moeschler *et al.*, 1990; Harrison and Bates, 1991: 316; Horáček *et al.*, 2000). It probably occurs more widely in this poorly explored region (Mickleburgh *et al.*, 2008a).

Native: Eritrea (Yalden *et al.*, 1996); Ethiopia (Yalden *et al.*, 1996); Saudi Arabia (Moeschler *et al.*, 1990; Harrison and Bates, 1991: 316; Horáček *et al.*, 2000).

ECHOLOCATION:
Al Obaid *et al.* (2023:4) reported an F_{max} of 135.22 (133 - 139) kHz for bats from Saudi Arabia. They also reported F_{start}:134.61 (129 - 138) kHz, F_{end}: 121.5 (108 - 138) kHz and duration: 4.93 (1.59 - 10) ms.

HABITAT:
Dry open terrain such as the semi-desert grassland of the Awash National Park (Hill and Morris, 1971).

ROOST:
It roosts in caves and buildings and in dry open terrain such as the semi-desert grassland of the Awash National Park (Hill and Morris, 1971).

POPULATION:
Structure and Density
Appears to be rare with small roosts. There is a possibility that it will be found in larger roosts, but to date none have been found (Mickleburgh *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017e).

Trend
2016: Unknown (Monadjem *et al.*, 2017e). 2008: Unknown (Mickleburgh *et al.*, 2008a; IUCN, 2009). 2004: Decreasing (Mickleburgh *et al.*, 2004ad; IUCN, 2004).

ACTIVITY AND BEHAVIOUR:
It flies close to the ground catching insects (Mickleburgh *et al.*, 2008a; IUCN, 2009).

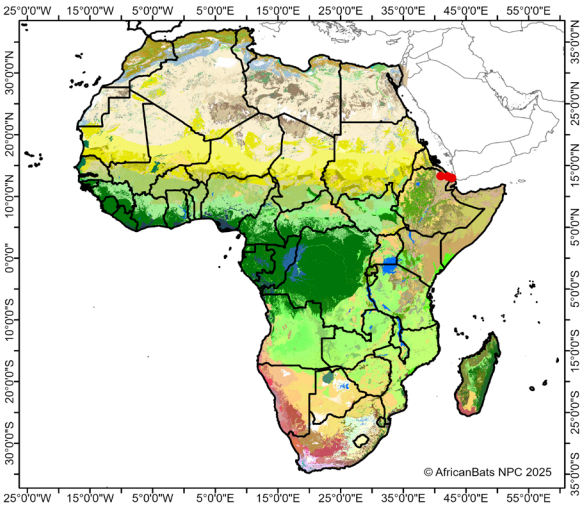

Figure 52. Distribution of *Asellia patrizii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Eritrea, Ethiopia.

Asellia tridens (E. Geoffroy St.-Hilaire, 1813)

*1813. *Rhinolophus tridens* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 20: 260, pl 5. Publication date: 1813. Type locality: Egypt: Qena province: Luxor, near [ca. 25 41 N 32 39 E]. [Goto Description]. Paratype: MNHN ZM-AC-1880-241: complete skeleton. Paratype: MNHN ZM-MO-1986-1069: skull and alcoholic. Collected by: Etienne Geoffroy-Saint-Hilaire. Paratype: MNHN ZM-MO-1986-1070: skull and alcoholic. Collected by: Etienne Geoffroy-Saint-Hilaire. Syntype: MNHN ZM-AC-1880-1880: ad ♀, complete skeleton. Collected by: Etienne Geoffroy-Saint-Hilaire. Number 187a in Rode (1941: 240), who considers this to be an allotype. Other number A.237. Syntype: MNHN ZM-MO-1986-1068: ad ♂, skull and alcoholic. Collected by: Etienne Geoffroy-Saint-Hilaire. Number 187 in Rode (1941: 240), who mentions this specimen as holotype. Furthermore, he remarks that the skull is not removed, so the skull in the atlas, pl. IV, fig. 2, 2', 2" does not correspond to any of the skins in the collection. See also Qumsiyeh (1985: 41). Benda *et al.* (2011f: 267) mention MNHN 1986-1068 as lectotype and indicate this is collected by E. Geoffroy Saint-Hilaire. Other number: A.235. - Comments: Grubb *et al.* (1998: 82) mention p. 265. Kock (1969a: 122), Corbet and Hill (1992: 116) and Horáček *et al.* (2000: 98) only mention "Egypt" as type locality. Kock (1969a: 122) also indicates that E. Geoffroy Saint-Hilaire (1818: 127) restricted the type locality to "Grab der Könige (=Theben, Luxor)".
1855. *Ph[yllorhina] tridens:* Giebel, Die Säugethiere, 987. (Name Combination).
1881. *Phyllorhina tridens murraiana* Anderson, Catalogue of the Mammals in the Indian Museum, vol I: 113. Type locality: Pakistan: Sind: Karachi [24 51 N 67 02 E]. (Name Combination).

1918. *Asellia tridens diluta* K. Andersen, Ann. Mag. nat. Hist., ser 9, 2 (10): 375. Publication date: 1 October 1918. Type locality: Algeria: Algerian Sahara: El Golea [30 35 N 02 53 E]. [Goto Description]. Holotype: NHMUK 1912.11.14.2: ♀. Collected by: Dr. Ernst Johnann Otto Hartert; collection date: 16 May 1912; original number: 42. Presented/Donated by: Nathanial Charles Rothschild. See Andersen (1918: 379). (Name Combination).
1937. *Asellia tridens pallida* Laurent, Mammalia, 1: 111, fig 8. Type locality: Morocco: Anti Atlas: Oued Tata [=Tata] [29 44 N 07 56 W]. [Goto Description]. (Name Combination).
2008. *Ascidia tridens:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 253. (Lapsus).
2023. *Aselia tridens:* Dalhoumi, El Mokni, Ouni, Beyrem and Aulagnier, Diversity, 15 (1108): 5. Publication date: 25 October 2023. (Lapsus).
? *Asellia tridens murraiana:* (Name Combination).
? *Asellia tridens tridens:* (Name Combination).
? *Asellia tridens:* (Current Combination).

TAXONOMY:

Simmons (2005: 366) recognises three subspecies *A. t. diluta* Andersen, 1918 [see discussion below]; *A. t. italosomalica* De Beaux, 1931; and *A. t. murraiana* Anderson, 1881.
Simmons (2005: 366) assigned *A. tridens diluta* to J. Anderson (1881), which would make this form Asian. However, no description is found in J. Anderson's publication, but a description is found in Andersen (1918: 379) as is confirmed by Owen and Qumsiyeh (1987 334), who mention "Andersen, 1918" as author.

Owen and Qumsiyeh (1987: 335) did not examine any specimens from *A. t. italosomalica* De Beaux, 1931, but Benda *et al.* (2011f: 261) consider *italosomalica* to be a separate species, a view that is followed here.

COMMON NAMES:

Arabian: Khaffash. Czech: pavrápenec trojzubcový, wrápenec trojzeykowý, listonos trojzubcový. Dutch: Drietandbladneusvleermuis. English: Geoffroy's Lesser Tident Bat, **Geoffroy's Trident Leaf-nosed Bat**, Trident Leaf-nosed Bat, Trident bat, Trident Rhinolophe. French: Trident du désert, Asellia à trois endentures, Chauve-souris trident, Trident, Rhinolophe trident. German: Dreizackblattnase, Geoffroys Dreizackblattnase, Dreyzahnige Kammnase. Hebrew: פרספון, pasafon, Parsafon.

ETYMOLOGY OF COMMON NAME:

So named because of the three-pronged process at the top of the nose-leaves and noticeably short ears (Taylor, 2005).

CONSERVATION STATUS:

Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Kock *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017m).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017m). 2008: LC ver 3.1 (2001) (Kock *et al.*, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004l; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:

The main threat is the widespread use of pesticides against locusts, while human disturbance in caves and old buildings is affecting some populations (Kock *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017m).

Besides water stress and their aerial hawking feeding style, roosting in caves and trees is an important risk factor linked with climatic change (Sherwin *et al.*, 2012: 174).

CONSERVATION ACTIONS:

Kock *et al.* (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017m) suggest underground roost management is needed in some places and a study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

It presumably occurs in several protected areas (Kock *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017m).

GENERAL DISTRIBUTION:

Asellia tridens ranges widely in the Sahara, through the Arabian Peninsula and the Middle East, to Afghanistan, Pakistan, and India. It is absent from the northern parts of Morocco and Algeria, and Tunisia, and occurs south to Ethiopia and Somalia.

Native: Afghanistan; Algeria (Kowalski and Rzebik-Kowalska, 1991: 64); Burkina Faso (Kangoyé *et al.*, 2015a: 607); Chad; Djibouti; Egypt; Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Gambia (Kock *et al.*, 2002b: 86);

India (Senacha and Dookia, 2013: 21); Iran, Islamic Republic of; Israel; Libyan Arab Jamahiriya; Mali; Mauritania (Brito *et al.*, 2010: 453, Allegrini *et al.*, 2011: 2); Morocco (Aulagnier and Thevenot, 1986: 38; Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 360; Dbiba *et al.*, 2025: 6); Niger; Oman; Pakistan; Saudi Arabia; Senegal; Sudan; Syrian Arab Republic; Tunisia (Horáček *et al.*, 2000: 99; Dalhoumi *et al.*, 2023: 5); Western Sahara.

Presence uncertain: Iraq; Kuwait; Lebanon; Qatar; United Arab Emirates.

A record from Zanzibar (Peters, 1871) has never been confirmed (though often repeated) and may be a MNHN mislabelled specimen. Records from Socotra and Somalia are now considered to belong to *A. italosomalica* (see Benda *et al.*, 2011f).

Detailed morphology:

Brain

Adult hippocampal neurogenesis was studied by Chawana R. *et al.* (2016: 1551).

Gastro-intestinal tract (GIT)

Aylward *et al.* (2019: 1108) reported for six specimens an average weight of 10.67 ± 0.98 g, and a GIT of 0.52 ± 0.11 g (4.83 ± 0.84 %).

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Jones *et al.* (1993)] mention a wing loading value of 9.0 Pa, aspect ratio 7.0 for a wingspan of 31 cm and a wing area of 140 cm^2 and a body mass of 13 g.

Echolocation:

Search-phase call-shape: CF/FM. CF component is sometimes of very low amplitude, but is always present (Pye, 1972). For 11 Egyptian bats, the CF-frequency varied from 115 - 120 kHz; each individual emitted a narrow range of frequencies, and different individuals emitted different ranges of frequencies (ibid.). For 18 Tunisian bats, resting, CF-frequency: 111 - 124 kHz (the CF-frequency varied from bat to bat, individuals kept the frequency constant); band-width of terminal FM component: 19-21 kHz; call-duration 7 - 10 ms; minimum inter-call interval 27 - 215 ms (depending on degree of alertness) (Gustafson and Schnitzler, 1979). Flying bats lowered their emission frequency to compensate for Doppler shifts caused by the flight movement; call-duration: 9 - 11 ms; minimum inter-call interval: 26 ms. For bats in a roost in Gambia containing thousands of individuals, CF-frequency: 108 - 122 kHz (frequency found to be negatively correlated with FA length within sexes); lowest frequency of the terminal FM sweep: 97 kHz: call-duration: 7.5 - 9 ms, inter-call interval: 10 - 20 ms (Jones *et al.*, 1993). In the UAE, Davis (2007: 5) reports a CF-frequency with an FM-ending (117 - 124 kHz).

Benda *et al.* (2012a: 182) provide two sets of data for Iranian *A. tridens*: **1**: F_{start}: 118.4 ± 0.6 (117.5 - 119.0) kHz, F_{end}: 117.1 ± 0.6 (116.3 - 118.0) kHz, F_{peak}: 117.9 ± 0.6 (117.0 - 118.5) kHz, duration: 10.3 ± 2.1 (6.8 - 13.1) ms, and interpulse interval: 32.3 ± 15.7 (13.4 - 55.9) ms; **2** (with bat in resting position): F_{start}: 122.3 ± 0.4 (121.7 - 122.8) kHz, F_{end}: 119.7 ± 4.1 (112.5 - 123.0) kHz, F_{peak}: 122.0 ± 0.4 (121.3 - 122.6) kHz, duration: 9.0 ± 0.4 (8.4 - 9.3) ms, and interpulse interval: 28.0 ± 7.7 (19.3 - 38.4) ms.

From Israel, the following values were reported by Hackett *et al.* (2016: 223) for 56 calls: Pulse duration: 7.97 ± 0.29 ms, F_{start}: 117.74 ± 12.58 (114.2 - 121) kHz, F_{end}: 106.96 ± 10.44 (96.6 - 101.91) kHz, F_{peak}: 116.60 ± 10.69 (107.4 - 120.1) kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats, 2 calls): F_{peak}: 117.9, 116.6 kHz, F_{start}: 118.4, 117.74 kHz, F_{end}: 117.1, 106.96 kHz, and duration: 10.3, 7.97 ms.

Jones and Siemers (2010: 449 - 450) indicate that females emit pulses with a higher frequency than males, and also that juveniles emit lower frequencies than adults (see also Jones *et al.*, 1993; Kunz and Hood, 2000: 420).

Dalhoumi *et al.* (2023: 5) reported F_{end}: 105.22 ± 3.56 (93.4 - 112.3) kHz, F_{max}: 118.90 ± 1.54 (113.0 - 122.3) kHz, duration: 9.47 ± 1.74 (5.7 - 12.8) ms and Interpulse interval: 48.60 ± 13.33 (23.8 - 89.2) ms.for bats from Tunisia.

Molecular Biology:

Karyotype

Baker *et al.* (1974) reported 2*n* = 50, FN = 62, a submetacentric X chromosome and an acrocentric Y chromosome. Baker et al. (1975) reported BA = 14.

Genetics

Bray and Benda (2016: 283) studied concatenated fragments of Cytochrome-*b*, NADH Dehydrogenase 2, and Cytochrome Oxidase 1 genes of primarily Saudi-Arabian bats, but also covered African representatives.

Habitat:

Arid and semi-desert habitats.

Habits:

This is a gregarious and colonial species (Kock *et al.*, 2008b).

ROOST:
It roosts in temples, caves, mines, open-wells, underground irrigation tunnels and old tombs and buildings and in the desert and semi desert vegetation zones it occurs in crevices or in cliffs (Kock *et al.*, 2008b). From Israel, Amichai *et al.* (2012: 96 - 97) report they use abandoned man-made structures (such as military bunkers), where the sexes are initially roosting separately. Later on (October), when their young become independent, this sexual segregation weakens.

From the Erg Chebbi region in Morocco, Ferrández Verdú *et al.* (2019: 5) reported on a colony roosting under large specimens of *Tetraena gaetula* (Emb. & Maire) Beier & Thulin (Zygophyllaceae).

Węgiel *et al.* (2024: 3) reported this species from undamaged domed tombs at the Old Dongola archaeological site (Sudan) where they recorded 1,148 individuals (on a total of 1,652 bats - 69 %). They also indicated that none of the damaged tombs housed bats.

MIGRATION:
In the Dakhla Oasis in Egypt, Benda *et al.* (2014b: 55) found *A. tridens* to be the most common bat during the summer months until the beginning of October, with at least 5,000 individuals divided over several roosts. However, from November to the beginning of April, these roosts were empty (except for a few single animals). In that period, only small colonies were found (70 - 120 ind.), and no animals were observed during the night. Benda *et al.* (2014b) were unable to determine whether the bats disappeared to the Nile Valley (long-distance migration) or whether they moved over short distances to other roosts in the neighbourhood, although there is some evidence that the latter is the case.

DIET:
Amichai *et al.* (2012: 101) report its diet in Israel to consist primarily of Coleoptera and Heteroptera, whereas Lepidoptera, Hymenoptera, Diptera were important additions in different parts of the country. In Iran, Benda *et al.* (2012a: 265) report that Coleoptera - mostly Scarabaeidae, but also Cerambycidae and Curculionidae were dominatingly present, but another faecal sample was dominated by Blattodea. The most frequent representatives of Heteroptera in the diet samples collected on both occasions were bugs of the family Tingidae.

In Libya, Benda *et al.* (2014c: 37) examined the digestive tract of one bat and found it contain 80 % (by volume) Coleoptera (Scarabeidae) and 20 % of Hymenoptera (Formicoidea).

Benarbia and Fentrouci (2017: 44) found the following items in droppings of *A. tridens* in Algeria: Arachnida: Aranea: Araneidae: *Aranea* sp. Ind1; Insecta: Coleoptera: Carabidae: *Megacephala australis*; Chrisomilidae: *Chrisomelida* sp.; Curculionidae: *Curculionida* sp., *Phyllognatnus* sp.; Anthicidae: *Anthicidae* sp. / *Anthicus* sp.; Carabidae: *Cicindella* sp.; Tenebrionidae: *Akis* sp.; Aphodiidae: *Aphodius* sp.; Blatidae: *Blatida* sp.; Hymenoptera: Formicidae: *Messor* sp., *Cataglyphis* sp., *Myrmecina* sp., *Formica* sp.; Vespoidae sp.; Orthoptera: Gryllidae: *Gryllus* sp.; *Ensiphera* sp.; Orthoptera sp.; Odonatoptera; Diptera: Tabanidae sp; Ephemeroptera sp., and Plantea: Planta: Arecaceae: *Phoenix dactilifera*.

The year-round analysis of droppings in Algeria by Loumassine *et al.* (2019: 354) revealed the following composition: Coleoptera (31.07 % - Carabidae, Curculionidae, Chrysomelidae, Tenebrionidae, Aphodidae, Scarabaeidae, and Histeridae), Hymenoptera (21.31 % - Formicidae, Myrmicidae and Vespidae), Diptera (13.78 % - Culicidae and Tabanidae), Orthoptera (11.40 % - Acrididae and Gryllidae), Mantodea, Hemiptera, Isoptera, Ephemeroptera, Blattodea and Odonata. During the autum and winter, Odonata, Scarabaeidae, Blattodea, Acrididae and Myrmicidae were present in large amounts, whereas during the spring and summer Chrysomelidae, Vespidae, Tenebrionidae, Aphodidae and Araneae were more prominent.

POPULATION:
Structure
Unknown.

Density
It is a very common species, found in colonies of up to several hundred in North Africa, and in its Asian distribution it has been found in groups up to 5,000 animals (Kock *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017m).

Trend
2016: Stable (Monadjem *et al.*, 2017m). 2008: Stable (Kock *et al.*, 2008b; IUCN, 2009). 2004: Unknown (Mickleburgh *et al.*, 2004l; IUCN, 2004). *A. tridens* populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

ACTIVITY AND BEHAVIOUR:
Forages over desert and semi-desert vegetation zones, mainly in oases (Kock *et al.*, 2008b).

Forages by slow hawking, has been observed foraging around palm trees and buildings, and over water (Kock *et al.*, 2008b). Pavey (2021: 6) [referring to Amichai *et al.* (2012)] , however, mentions that the prey is generally captured by gleaning from vegetation, and only occasionally by aerial hawking.

REPRODUCTION AND ONTOGENY:
Amichai *et al.* (2012: 96) report that almost all females arrive in their summer roosts in Israel at an advanced stage of pregnancy, and that births take place between the end of June and mid July. There is one young, which is born hairless, with closed eyes and weighting up to 30 % (2.5 - 3 g) of its mother's weight. In the United Arab Emirates, Davis (2007: 5) found females to be pregnant in April-May, and giving birth in June after a gestation period of about 9 to 10 weeks. The lactation period lasts for 40 days.

Intrauterine ultrasonography of pregnant females performed by Amichai *et al.* (2019: 1) showed that the development of the horseshoe is completed (100%) *in-utero*, whereas skull (70%) and forearm (40%) development continues after birth. Neonates already begin emitting precursor echolocation calls two days after birth, and they are able to fly three weeks after birth.

PARASITES:
In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ixodidae: Ixodes vespertilionis Koch, 1844; and Nycteribiidae: *Nycteribia schmidlii schmidlii* Schiner, 1853, *Penicillidia dufourii* (Westwood, 1834).

HAEMOSPORIDA
Austen and Barbosa (2021: 7) mention *Trypanosoma (Megatrypanum) morinorum* from bats from Senegal.

ACARI
Trombiculidae
Neoschoengastia elegans (Vercammen-Grandjean, Rohde and Mesghali, 1970) from Iran. *Myotrombicula aselliae* Vercammen-Grandjean, 1963, *Riedlinia platypygia* Vercammen-Grandjean, 1963, and *R. afghanensis* Vercammen-Grandjean, 1963, all three from Afghanistan (Benda *et al.*, 2012a: 266-267).

Myobiidae
Ugandobia euthrix Fain, 1972 from Saudi Arabia (Fain 1972 [in Benda *et al.*, 2012a: 267]) and *Hipposiderobia heteronycha* (Berlese et Trouessart, 1889) from Saudi Arabia and various parts of Africa (Radford 1949, Fain 1972, 1978 [in Benda *et al.*, 2012a: 267]).

Argasidae
Argas boueti Roubaud and Colas-Belcour, 1933 from various countries in Africa (Roubaud and Colas-Belcour 1933, Hoogstraal 1955 [in Benda *et al.*, 2012a: 267]).

Sándor *et al.* (2021a: 4) reported the presence of *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) [=*Argas boueti*] and *Chiropterargas confusus* (Hoogstraal, 1955), as well as *Carios vespertilionis* Latreille, 1802.

DIPTERA
Streblidae
Raymondia huberi Frauenfeld, 1856 from Tanzania (Haeselbarth *et al.*, 1966: 102), and Iran (Benda *et al.*, 2012a: 266) (see also Shapiro *et al.*, 2016: 254). *Raymondia setosa* Jobling, 1930 from Israel (Haeselbarth *et al.*, 1966: 104).

Nycteriibidae
Nycteribia schmidlii Schiner, 1853 from the Levant (Benda *et al.*, 2012a: 266). *Nycteribia (Listropoda) schmidlii schmidlii* Schiner, 1853 and *Penicillidia (Penicillidia) dufourii* Westwood, 1835 were reported by Bendjeddou *et al.* (2017: 15) from Algeria. *Penicillidia dufourii* Westwood, 1834 from the Levant (Benda *et al.*, 2012a: 266). *Brachytarsina flavipennis* Macquart, 1851 from the Levant (Benda *et al.*, 2012a: 266).

SIPHONAPTERA
Ischnopsyllidae
Chiropteropsylla brockmani Rothschild, 1915 from Iran and Iraq (Benda *et al.*, 2012a: 266). *Rhinolophopsylla unipectinata* (Taschenberg, 1880) from Iraq (Benda *et al.*, 2012a: 266).

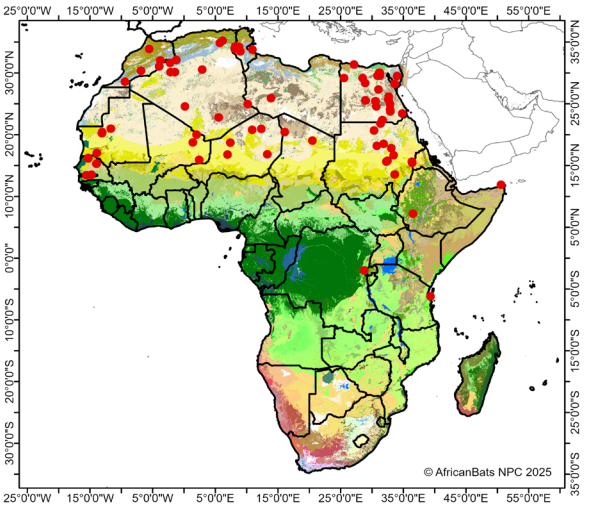

Figure 53. Distribution of *Asellia tridens*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Burkina Faso, Chad, Congo (Democratic Republic of the), Egypt, Ethiopia,

Libya, Mali, Mauritania, Morocco, Niger, Senegal, Somalia, Sudan, Tanzania, The Gambia, Tunisia.

Genus ***Doryrhina*** Peters, 1871

*1871. *Doryrhina* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 314. Publication date: 1871 [Goto Description]. - Comments: Grubb *et al.* (1998: 79) mention p. 324. Type species: *Phyllorrhina cyclops* Temminck, 1853, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246).. - Etymology: From the Greek "*δόρυ*", meaning spear and "*ρινός*", meaning nose, referring to the club-shaped process which is directed forward from the base of the sella, or to the slender and somewhat longer vertical process which projects upward from the margin of the transverse erect nose leaf (see Palmer, 1904: 244).

2021. *Dohyrina:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 1. Publication date: 14 May 2021. (Lapsus).

2021. *Dorirhyna:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 7. Publication date: 14 May 2021. (Lapsus).

TAXONOMY:
Generally considered a synonym of the genus *Hipposideros*, but based on Cyt-*b* analyses, Foley *et al.* (2017: 12) considered *cyclops* to be that different from the other members of this genus to be placed in a separate genus.

Due to the generally recognized close relation between *cyclops* and *camerunensis*, Musila *et al.* (2018a: 21) provisionally placed the latter in the genus *Doryrhina*, but they also indicated that this still needs to be confirmed.

Currently (Simmons and Cirranello, 2024b) recognized species in the genus *Doryrhina*: ***camerunensis*** (Eisentraut, 1956); ***cyclops*** (Temminck, 1853).

MOLECULAR BIOLOGY:
Karyotype
The genus *Hipposideros* s.l. shows an extreme conservatism concerning the 2*n* complement. Almost all species have 32 chromosomes. The only exceptions are the species transferred by Foley *et al.* (2017) to the genus *Macronycteris*, which have 52, and *cyclops*, which has 2*n* = 36.

Doryrhina camerunensis (Eisentraut, 1956)

*1956. *Hipposideros camerunensis* Eisentraut, Zool. Jb. Syst., 84 (3): 526, fig 6 - 8. Publication date: 27 December 1956. Type locality: Cameroon: Buea, near [ca. 04 09 N 09 13 E]. [Goto Description]. Holotype: SMNS 5194: ad ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: 29 April 1954; original number: 505. See Dieterlen *et al.* (2013: 294). Paratype: SMNS 5195: ad ♂, alcoholic (skull not removed). Collected by: Prof. Dr. Martin Eisentraut; collection date: 29 April 1954; original number: 510. See Hutterer (1984: 29 - 30), Dieterlen *et al.* (2013: 294). Paratype: SMNS 5197: ad ♀, skull and alcoholic. Collected by: Prof. Dr. Martin Eisentraut; collection date: 29 April 1954; original number: 511. See Hutterer (1984: 29 - 30), Dieterlen *et al.* (2013: 294). Paratype: ZFMK MAM-1979.0138: ad ♀. Collected by: Prof. Dr. Martin Eisentraut; collection date: 29 April 1954; original number: 506. Exchanged from SMNS in March 1979; SMNS catalog number 5196 (see Hutterer, 1984: 29 - 30; Hutterer and Peters, 2010: 12), Dieterlen *et al.*, 2013: 294). - Etymology: Referring to the country where the type specimen was collected (Cameroon). (Name Combination).

2015. *H[ipposideros] camarunensis:* Gunnell, Winkler, Miller, Head, El-Barkooky, Gawad, Sanders and Gingerich, Hist. Bio., 28 (1 - 2): 163. Publication date: 1 October 2015. (Lapsus).

2018. *Doryrhina camerunensis:* Musila, Monadjem, Webala, Patterson, Hutterer, De Jong, Butynski, Mwangi, Chen and Jiang, Zool. Res. (China), 40 (1): 21 (for 2019). Publication date: 17 October 2018. - Comments: Due to the view that *camerunensis* and *cyclops* are closely related, Musila *et al.* (2018a: 21) provisionally placed this taxon in the genus *Doryrhina*. (Current Combination).

2020. *Doryrhina cf. camerunensis:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

? *Doryrhina cf. camerunensis TD-2020*

TAXONOMY:
Simmons (2005: 369) as part of the *cyclops* species group.

Mickleburgh *et al.* (2008l) in IUCN (2009) report that there is debate as to whether all the records comprise a single species, or whether there might be two or three different species involved. The records from the Democratic Republic of Congo and Kenya could refer to other, possibly undescribed, species.

Musila *et al.* (2018a: 21) provisionally placed *camerunensis* in the genus *Doryrhina* (instead of *Hipposideros*) due to the assumed close relationship of this taxon with *D. cyclops*. They also mentioned that this new assignment needs to be confirmed. Webala *et al.* (2019a: 264; 2019b: 10) mention this taxon in *Doryrhina* without any reservation.

COMMON NAMES:
Chinese: 喀麦隆蹄蝠. Czech: pavrápenec kamerunský. English: Cameroon Leaf-nosed Bat, Greater Roundleaf Bat, Greater Cyclops, Eisentraut's Leaf-nosed Bat. French: Phyllorine du Cameroun, Phyllorine d'Eisentraut. German: Kamerun-Rundblattnase, Kamerun-Blattnase.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing uncertainties as to its taxonomic status, extent of occurrence and ecological requirements (Mickleburgh *et al.*, 2008l; IUCN, 2009; Mickleburgh *et al.*, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) assessed as *Hipposideros camerunensis* (Mickleburgh *et al.*, 2019a). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008l; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004ac; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
If it is a forest-dependent species, then it is probably suffering from ongoing forest loss. If future taxonomic studies show it to be restricted to Mount Cameroon, then it could be seriously threatened by habitat destruction (Mickleburgh *et al.*, 2008l; IUCN, 2009; Mickleburgh *et al.*, 2019a).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008l) [in IUCN (2009)] and Mickleburgh *et al.* (2019a) report that no conservation measures are currently in place. It is not known from any protected areas. Taxonomic studies are urgently needed to determine whether or not the three recorded localities all refer to the same species.

GENERAL DISTRIBUTION:
Doryrhina camerunensis is known only from three localities: Buea in Cameroon (type locality); Shabunda in eastern Democratic Republic of Congo; and at the Kakamega Forest in western Kenya close to Lake Victoria. If it is a single species, then it is likely to be found in future in intervening locations. Its elevational range is from sea-level to 500 m, and probably higher.

Native: Cameroon (Eisentraut, 1956b, 1963, 1973); Congo (The Democratic Republic of the); Kenya (Schlitter *et al.*, 1986).

ECHOLOCATION:
Webala *et al.* (2019b: 15) reported a F value of 50.8 kHz for a male and 51.1 kHz for a female the Kakamega Forest (Kenya). The duration of the calls was 24.5 to 27.7 ms for the male's call and 23.1 to 27.1 ms for the female's.

HABITAT:
The Kakamega specimen was captured in 'Intermediate Evergreen Forest' (Schlitter *et al.*, 1986).

ROOST:
The type specimens were taken from a hollow tree (Eisentraut, 1963).

POPULATION:
Structure and Density
Very little known about the species. It is known form only three records in a general region that is not widely surveyed (Mickleburgh *et al.*, 2008l; IUCN, 2009; Mickleburgh *et al.*, 2019a).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019a). 2008: Unknown (Mickleburgh *et al.*, 2008l; IUCN, 2009).

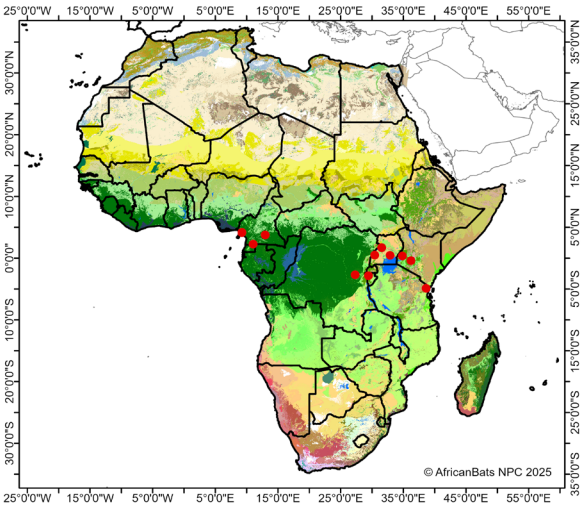

Figure 54. Distribution of *Doryrhina camerunensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burundi, Cameroon, Congo (Democratic Republic of the), Kenya, Tanzania, Uganda.

Doryrhina cyclops (Temminck, 1853)

*1853. *Phyllorrhina cyclops* Temminck, Esquisses zoologiques sur la Côte de Guiné. 1e partie, les Mammifères, 75. Publication date: 1853. Type locality: Ghana: Boutry River [=Butre river] [ca. 04 49 N 01 55 W]. [Goto Description]. Lectotype: RMNH MAM.35973: ad ♂, mounted skin and skull. Collected by: Hendrik Severinus

Pel; collection date: 1841 - 1850. Paralectotype: RMNH MAM.35974: ad ♂, mounted skin and skull. Collected by: Hendrik Severinus Pel; collection date: 1841 - 1850. - Comments: Type locality originally: "sur la rivière Boutry, côte de Guiné". - Etymology: Refers to the one-eyed giants of Greek mythology and alludes to the orifice in the center of the forehead of these bats (see Rosevear, 1965 in Decher and Fahr, 2005: 4).

1897. *Rhinolophus micaceus* de Winton, Ann. Mag. nat. Hist., ser 6, 20 (120): 524. Publication date: 1 December 1897. Type locality: Gabon: 75 mi (112.5 km) from Gaboon: Como River. [Goto Description]. Holotype: NHMUK 1897.12.1.7: ♀. Collected by: George Latimer Bates Esq. Collection date: 6 July 1897; original number: GLB 230. Note: Smoked out of hollow tree.

1899. *Hipposideros cyclops:* de Winton, Ann. Mag. nat. Hist., ser 7, 4 (23): 354. Publication date: 1 November 1899. (Name Combination).

1917. *Hipposideros langi* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 434, text-fig 4 - 6. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Avakubi [01 18 N 27 32 E]. [Goto Description]. Holotype: AMNH 49098: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 24 January 1914; original number: 2481.

1922. *H[ipposideros]. cyclops micaceus:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 47: 2, footnote. (Name Combination).

1922. *Hipposideros cyclops langi:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 47: 2, footnote. (Name Combination).

2017. *Doryrhina cyclops:* Foley, Goodman, Whelan, Puechmaille and Teeling, Acta Chiropt., 19 (1): 12. Publication date: June 2017. (Current Combination).

2020. *Doryrhina cyclops 1:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2020. *Doryrhina cyclops 2:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2021. *Dohyrina cyclops:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 1. Publication date: 14 May 2021. (Lapsus).

2021. *Dorirhyna cyclops:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 7. Publication date: 14 May 2021. (Lapsus).

2021. *Hipposideros cyclosus:* Roemer, Julien and Bas, Methods Ecol. Evol., Suppl. Publication date: 18 September 2021. (Lapsus).

? *Doryrhina cyclops complex sp. lineage 2*

TAXONOMY:

Simmons (2005: 370) includes this taxon in the *Hipposideros cyclops* species group. See Decher and Fahr (2005, Mammalian Species, 763), but see also Foley *et al.* (2017: 12), who transferred it to the genus *Doryrhina*.

COMMON NAMES:

Chinese: 大眼蹄蝠. Czech: pavrápenec Kyklop. English: Cyclops Leaf-nosed Bat, Cyclops Roundleaf Bat, Cyclops Bat. Fang: angon. French: Phyllorine des Cyclopes, Phyllorine cyclope. German: Zyklopen-Rundblattnase, Zyklossen-Blattnase.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bw; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bw; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cn; IUCN, 2004). 1994: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

Although not threatened throughout its range, the species may disappear from many areas that are threatened by deforestation, especially on the extreme limits of its distribution (Decher and Fahr, 2005).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008bw) [in IUCN (2009)] report that the roosting habits of this bat requires very large hollow trees, so conservation of these must be a priority. It is found in some protected areas, for example Kwamgumi Forest Reserve in Tanzania, and the Udzungwa Mountains National Park of Tanzania.

GENERAL DISTRIBUTION:

Doryrhina cyclops has been recorded widely over much of West Africa and Central Africa, with a few scattered records from East Africa. It ranges from Senegal and The Gambia in the west, through most countries in West Africa, to Cameroon, Equatorial Guinea (Rio Muni and Bioko), Gabon, Congo (The Democratic Republic of the) Congo, Central African Republic and Rwanda, being recorded from East Africa in southern Sudan, Uganda and western Kenya, with an isolated population in southeastern Kenya and northeastern Tanzania in coastal forests and Eastern Arc Mountains (Decher and Fahr, 2005: 3). It has been collected at Tongwe Forest near Tanga and Kwamgumi Forest Reserve in Tanzania (K. Howell *pers. comm.* 2004). There is a dubious record from the border area of Chad

and the Central African Republic. It occurs from sea-level up to at least 1,000 m.

Native: Benin; Burkina Faso (Kangoyé *et al.*, 2012: 6024; 2015a: 608); Cameroon (Hill, 1968; Eisentraut, 1973); Central African Republic (Lunde *et al.*, 2001); Congo (Bates *et al.*, 2013: 335); Congo (The Democratic Republic of the); Côte d'Ivoire; Equatorial Guinea (Bioko); Gabon; Gambia; Ghana (Decher and Fahr, 2007: 17); Guinea (Ziegler *et al.*, 2002: 75); Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 52); Kenya (Aggundey and Schlitter, 1984); Liberia; Nigeria (Happold, 1987); Rwanda; Senegal; Sierra Leone; Sudan; Tanzania (Decher and Fahr, 2005: 3; Stanley *et al.*, 2005b), United Republic of; Togo; Uganda.
Presence uncertain: Burundi; Chad.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 6 specimens: Fa: 70.63 ± 1.942 mm, mass: 37.3 ± 3.27 g, wing loading: 11.5 ± 0.53 N/m^2, aspect ratio: 5.5 ± 0.46.

DETAILED MORPHOLOGY:
Brain
Amrein *et al.* (2007) reported from specimens collected in Bénin that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus were found to be absent. They also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. No NeuroD was detected in the hippocampal granule cells (Amrein *et al.*, 2007).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Monadjem *et al.* (2011)] mention a wing loading value of 11.5 Pa, aspect ratio 5.5 for a wingspan of 42 cm and a wing area of 318 cm^2 and a body mass of 37 g.

SEXUAL DIMORPHISM:
Decher and Fahr (2005) [in Kangoyé *et al.* (2015a: 608)] indicate that a pronounced sexual dimorphism exists, with females being larger than males.

ECHOLOCATION:
Monadjem *et al.* (2013b: 351) report a F_{max} of 55.5 (55 - 56) kHz for two specimens from Mount Nimba.

From western Uganda, Monadjem *et al.* (2011: 32) report the following values for 6 calls: F_{min}: 51.24 ± 0.670 kHz, F_{max}: 51.54 ± 0.387 kHz, F_{char}: 51.37 ± 0.459 kHz, F_{knee}: 51.51 ± 0.395 kHz, duration: 14.5 ± 2.02 ms.

In Sierra Leone, Weber *et al.* (2019: 21) reported on two females calling at 54.5 (54.0 - 55.0) kHz.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 48 calls of 2 bats: F_{peak}: 58.9 ± 0.5 (58.7 - 59.7) kHz, F_{min}: 50.5 ± 6.1 (46.5 - 59.7) kHz, F_{max}: 59.5 ± 0.8 (58.9 - 60.7) kHz, duration: 20.0 ± 2.1 (16.6 - 23.2) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a CF-FMd (Constant frequency - Frequency modulation downward) sonotype [as "*Hipposideros cyclosus*" (sic)].

Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003657_UUAODTLMRU.WAV, https://chirovox.elte.hu/sounds/A003658_PMHGLOHRQY.WAV, https://chirovox.elte.hu/sounds/A003659_IYAAAUDEQQ.WAV, https://chirovox.elte.hu/sounds/A003660_LFVMCSLHAG.WAV

MOLECULAR BIOLOGY:
Karyotype
Koubínová *et al.* (2010b) report for one female from Senegal, 2*n*= 36, Fna= 62 (as "*Hipposideros cyclops*"), while the chromosomal complement comprised 15 metacentric or submetacentric, and three small acrocentric pairs.

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Monadjem *et al.* (2016y: 365) recorded it from two forested sites in the Mount Nimba area, between 480 and 730 m. Bakwo Fils *et al.* (2021b: 6) reported on one specimen collected in undisturbed Afromontane forest in Cameroon.

ROOST:
Killick-Kendrick (1973: 641) reported on pygmy flying squirrels (*Idiurus macrotis* Miller, 1898) collected from hollow trees, which were associated with "*Hipposideros cyclops*".

POPULATION:
Structure and Density
It is a reasonably common species in some areas (Mickleburgh *et al.*, 2008bw; IUCN, 2009).

Trend
2008: Decreasing (Mickleburgh *et al.*, 2008bw; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
One female, carrying a furred female infant, was captured in December 2005 at Uzungwa Scarp Forest Reserve, Tanzania (Trentin and Rovero, 2011: 50).

Two lactating females were reported on 26 and 28 May from Sierra Leone by Weber *et al.* (2019: 24).

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2013a: 17416) report the presence of the hemosporidian parasite *Plasmodium cyclopsi* Landau and Chabaud, 1978 in three out of four investigated bats. Up until now, *Macronycteris cyclops* is the only known host species for this parasite. *Plasmodium* sp. (Hip_cy_L1_1) was reported from Liberia by Arnuphapprasert *et al.* (2020: Suppl.).
Lutz *et al.* (2016: 9) examined three *M. cyclops* specimens from East Africa and found all of them infected with *Nycteria* sp.
Perkins and Schaer (2016: Suppl.) also mention *Dionisia bunoi* Landau, Chabaud, Miltgen and Baccam, 1980 from bats from Gabon, *Nycteria* sp. from Uganda, *Plasmodium cyclopsi* from Gabon and Liberia.
Landau *et al.* (1980a: 272), furthermore, mentioned a third atypical hematozoon: *Trypanosoma lizae* Miltgen and Landau, 1979.
Tsague *et al.* (2021: 3) tested 10 bats from the Centre province in Cameroon of which 6 were infected by *Nycteria* sp, and Tsague *et al.* (2024: Suppl.) reported seven Cameroonian bats co-infected by *Trypanosoma* sp. and *Nycteria* sp.
T. vespertilionis was found in bats from the CAR by Babyesiza *et al.* (2025: 4).

DIPTERA
Streblidae
Raymondia brachyphysa Jobling, 1956 from Abidjan, Côte d'Ivoire (Haeselbarth *et al.*, 1966: 102; Shapiro *et al.*, 2016: 254). *Raymondia intermedia* Jobling, 1936 in Côte d'Ivoire (Haeselbarth *et al.*, 1966: 102).

VIRUSES:
Matonaviridae
Rubivirus
Bennett *et al.* (2020a: 424) discovered the ruhugu virus (RuhV) from Ugandan "*Hipposideros cyclops*", where it was found in 5 our of 9 males (55.6 %) and 5 out of 11 females (45.5 %).

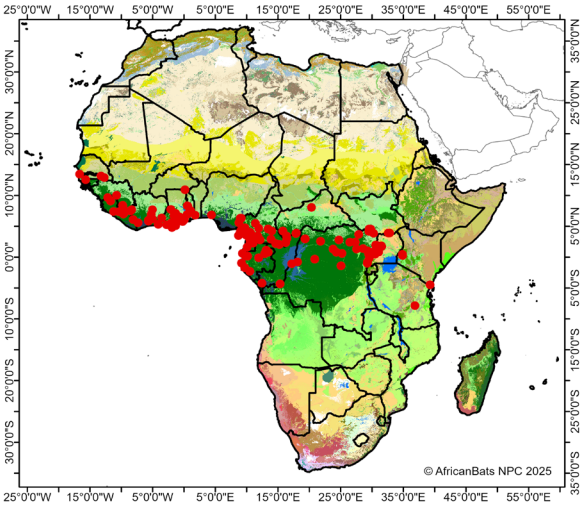

Figure 55. Distribution of *Doryrhina cyclops*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Senegal, Sierra Leone, South Sudan, Tanzania, The Gambia, Togo, Uganda.

Genus ***Hipposideros*** J. E. Gray, 1831

*1831. *Hipposideros* J. E. Gray, Zool. Misc., 1: 37. Publication date: 1831. - Comments: Type species: *Vespertilio speoris* Schneider, 1800, by subsequent designation by Sclater (1901: 166) (see Meester *et al.*, 1986: 41; Jackson and Groves, 2015: 245). - Etymology: From the Greek "*ἵππος*", meaning horse and "*σίδηρος*", meaning iron (=horse-iron, horseshoe), an allusion to the shape of the noseleaf (see Palmer, 1904: 327). - Phonetics: hip-oh-sid'-er-os.

1834. *Hipposiderus* J. E. Gray, Proc. zool. Soc. Lond., 1834, II (xviii): 53. Publication date: 26 September 1834. - Comments: Unjustified emendation (see Meester *et al.*, 1986: 41; Pavlinov *et al.*, 1995: 84; Decher and Fahr, 2005: 1; Jackson and Groves (2015: 245). Blanford (1888: 638) claims the name *Hipposiderus* was published by Gray (1831: 37), but this is in error. (Emendation).

1837. *Phyllorrhina* Bonaparte, Icon. Fauna Ital, 1, fasc 21: 3. - Comments: Type species: *Rhinolophus diadema* É. Geoffroy, 1813, by subsequent designation by Sclater (1901: 116) (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 245). Fenton and Rautenbach (1998: 535) and Allen (1939a: 79) indicated that it was described as a subgenus of *Rhinolophus*. Not preoccupied by *Phyllorhina* Leach, 1816. Jelle Zijstra (pers. comm., 26/03/2023) Indicated that the usage of a double "r" makes this name available as as subgenus of *Hipposideros*.

1838. *Phyllorhina:* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 492. Publication date: 1 February 1838. - Comments: Type species: *Rhinolophus diadema* E. Geoffroy Saint Hillaire, 1813. Preoccupied by *Phyllorhina* Leach, 1816 (see Pavlinov *et al.*, 1995: 84; although they do not explicitly mention its preoccupation), although

also see Fenton and Rautenbach (1998: 535), who refers to Bonaparte (1837) to refute this. Fenton and Rautenbach (1998: 535) and Allen (1939a: 79) indicated that it was described as a subgenus of *Rhinolophus*. - Etymology: From the Greek "*φύλλον*", meaning leaf and "*ρίς*" or "*ρινος*", meaning nose, referring to the nose-leaf (see Palmer, 1904: 535).

1849. *Hypposideros:* Layard, J. Ceylon Branch R. Asiat. Soc., 2 (2) 5: 190. (Lapsus).

1866. *Chrysonycteris* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 82. Publication date: May 1866. - Comments: Type species: *Hipposideros fulvus* Gray, 1838, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246). - Etymology: From the Greek "*χρυδός*", meaning gold and "*νυκτερις*", meaning bat, referring to the briljant golden yellow fur (see Palmer, 1904: 189).

1866. *Gloionycteris* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 82. Publication date: May 1866. - Comments: Type species: *Rhinolophus armiger* Hodgson, 1835, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246). - Etymology: From the Greek "*γλοιός*", meaning gum and "*νυκτερις*", meaning bat, referring to the large glandular elevations on the sides of the forehead (see Palmer, 1904: 297).

1866. *Rhinophylla* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 82. Publication date: May 1866. - Comments: Type species: *Phyllorrhina labuanensis* Tomes, 1859, by monotypy (see Jackson and Groves, 2015: 246). Preoccupied by *Rhinophylla* Peters, 1865 (Chiroptera, Phyllostomidae) (see Pavlinov *et al.*, 1995: 84).

1866. *Speorifera* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 82. Publication date: May 1866. - Comments: Type species: *Rhinolophus vulgaris* Horsfield, 1823 (=*Rhinolophus larvatus* Horsfield).

1871. *Cyclorhina* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 326. Publication date: 1871. - Comments: Type species: *Phyllorrhina obscura* Peters, 1861 and *Phyllorrhina doriae* Peters, 1871. Meester *et al.* (1986: 42) retain only *Phyllorhina obscura* Peters as type species, by subsequent designation by Moreau *et al.* (1946: 208), Tate (1941a: 354), Corbet and Hill (1992: 105) (see Jackson and Groves, 2015: 246). Not *Cyclorhina* J. Hall and Clarke, 1894 (Brachiopoda, Rhynchonellata, Rhynchonellida, Machaerariidae) (see Jackson and Groves, 2015: 246). - Etymology: From the Greek "*κύκλος*", meaning circle, and "*ρις*" or "*ρινός*", meaning nose (see Palmer, 1904: 208).

1871. *Ptychorhina* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 325. Publication date: 1871. - Comments: Type species: *Rhinolophus caffer* Sundevall, 1846, by monotypy (according to Decher and Fahr, 2005: 1) or by subsequent designation by Palmer (1904: 597) (according to Jackson and Groves, 2015: 246).

1871. *Sideroderma* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 324. Publication date: 1871. - Comments: Type species: *Phyllorrhina fuliginosa* Temminck, 1853, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246). - Etymology: From the Greek "*σίδηρος*", meaning iron and "*δέρμα*", meaning skin, referring to the dark brown or reddish colour of the fur (see Palmer, 1904: 630).

1871. *Syndesmotis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 329. Publication date: 1871. - Comments: Type species: *Phyllorhina megalotis* Heuglin, 1862, by monotypy (see Jackson and Groves, 2015: 247).

1871. *Thyreorhina* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 327. Publication date: 1871. - Comments: Type species: *Phyllorrhina coronata* Peters, 1871, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246). - Etymology: From the Greek "*θυρεός*", meaning a large, oblong shield and "*ρις*" or "*ρινός*", meaning nose, referring to the upper noseleaf with thickened edge (see Palmer, 1904: 678).

1902. *Syndesmotus* C.O. Waterhouse, Index Zoologicus. - Comments: Objective synonym of *Syndesmotis* Peters, 1871 (see Simmons, 2005) or incorrect subsequent spelling of *Syndesmotis* Peters, 1871 (see Jackson and Groves, 2015: 247). - Etymology: From the Greek "*σύνδεσμος*", meaning bond or fastening and "*ούς*" or "*ώτός*", meaning ear (see Palmer, 1904: 656).

2016. *Hipposieros:* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 42. Publication date: 9 May 2016. (Lapsus).

2017. *Hipposidereos:* Hammond, Tan and Johnson, Protein Sci., 26: 1727. Publication date: 5 June 2017. (Lapsus).

2019. *Hipposederos:* Zeghbib, Herczeg, Kemenesi, Zana, Kurucz, Urbán, Madai, Földes, Papp, Somogyi and Jakab, Sci. Reps., 9 (15706): 2. Publication date: 31 October 2019. (Lapsus).

2024. *Hipposiderous:* Adesoji, George, Sulayman, Uwanibe, Olawoye, Igbokwe, Olanipekun, Adeleke, Akindoyin, Famakinwa, Adamu, Terkuma, Ezekiel, Eromon, Happi, Fadare, Shittu and Happi, Sci. Reps., 14 (6899): 5. Publication date: 22 March 2024. (Lapsus).

? *Hipposideros sp. caffer-ruber*

? *Hipposideros sp. caffer-ruber DMR-2017*

? *Hipposideros sp.:*

TAXONOMY:

For review of the genus see Hill (1963a), on which the above synonymy and the treatment that follows are largely based, followed by Meester *et al.* (1986); Koopman (1993a: 170). Hill (1963a) recognizes seven species groups, five are recognized in Africa *speoris*, *bicolor*, *cyclops*, *commersoni*, and *megalotis* (Simmons, 2005: 367 - 379). However, see also Bogdanowicz and Owen (1998: 38), who indicate that recent species are not expressed accurately by current systematic arrangements based on the supraspecific groupings proposed by Hill (1963a), and that the genus *Hipposideros* might be a paraphyletic taxon. This is confirmed by Foley *et al.* (2014: 324), who indicate that *H. commersoni* and *H. vittatus* pose a problem here. Without these species, the monophyly of the remaining *Hipposideros* species is supported by all of their analyses. Foley *et al.* (2017: 2) furthermore indicate that the species groups, currently recognized in the genus, have yet to be thoroughly evaluated using molecular data.

One of the most controversial groups in the African *Hipposideros* representatives is the *caffer/ruber* complex. Vallo *et al.* (2009: 196) subdivided this in four main groups, of which three are again subdivided in two lineages, and which were tentatively called: A1, A2, B1, B2, C1, C2, and D. These lineages would represent at least five species. Monadjem *et al.* (2013b: 345)

separated two further lineages in southern African *H. caffer*: A1a and A2b, and two in Senegalese *H.* cf. *ruber*: D1 and D2; and one in Ghanian (E2) and Liberian and Côte d'Ivorian *H.* cf. *ruber*: (E1).

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Hipposideros*: ***abae*** J.A. Allen, 1917; *alongensis* Bourret, 1942 – Vietnam; *antricola* (Peters, 1862) – Palawan (Philippines); *armiger* (Hodgson, 1835) – Northern India, Nepal, Burma, south and southeastern China, Vietnam, Laos, Cambodia, Thailand, Malay Peninsula, Taiwan (Simmons, 2005: 367); *ater* Templeton, 1848 – Sri Lanka; India to western Malaysia, through Philippines, Indonesia, and New Guinea to northern Queensland, north Northern Territory, and north Western Australia (Australia) (Simmons, 2005: 367); ***beatus*** K. Andersen, 1906; *bicolor* (Temminck, 1834) – Laos, Vietnam, southern Thailand and Malaysia to Borneo and the Philippines, Java, Sumbawa, Seralu, Sumba, Savu, Roti and Timor Isls (Indonesia) and adjacent small islands (Simmons, 2005: 368); *boeadii* Bates, Rossiter, Suyanto and Kingston, 2007 – SE Sulawesi (Indonesia); *breviceps* Tate, 1941 – Mentawai Isls (Indonesia) (Simmons, 2005: 368); ***caffer*** (Sundevall, 1846); *calcaratus* (Dobson, 1877) – central New Guinea (Simmons, 2005: 368); *cervinus* (Gould, 1854) – western Malaysia, Sumatra, and Mindanao (Philippines) to the Mollucca Isls, Vanuatu, and northeastern Australia (Simmons, 2005: 369); *cineraceus* Blyth, 1853 – Pakistan and India to Burma, Thailand, Laos, Vietnam, Sumatra and Borneo, adjacent small islands including Kangean Isls (Indonesia) (Simmons, 2005: 369); *coronatus* (Peters, 1871) – northeastern Mindanao (Philippines) (Simmons, 2005: 369); *corynophyllus* Hill, 1985 – central New Guinea (Simmons, 2005: 370); *coxi* Shelford, 1901 – Sarawak (Borneo, Malaysian part) (Simmons, 2005: 370); *crumeniferus* (Lesueur and Petit, 1807) – Timor (Indonesia) (Simmons, 2005: 370); ***curtus*** G.M. Allen, 1921; *demissus* K. Andersen, 1909 – San Cristobal Isl (Solomon Isls) (Simmons, 2005: 370); *diadema* (E. Geoffroy Saint Hilaire, 1813) – Burma and Vietnam through Thailand, Laos, western Malaysia and Indonesia (including Sumatra, Borneo and Bali) to New Guinea, Bismarck Arch., Solomon Isls and northeastern Australia, Philippines, Nicobar Isls (Simmons, 2005: 370); *dinops* K. Andersen, 1905 – Solomon Isls; Bougainville Isl (Paua New Guinea) (Simmons, 2005: 370); *doriae* (Peters, 1871) – western Malaysia, Sarawak and Sabah (Malaysia), Borneo and Sumatra (Indonesia) (Simmons, 2005: 371); *durgadasi* Khajuria, 1970 – central India (Simmons, 2005: 371); *dyacorum* Thomas, 1902 – Borneo (including Sarawak, Malaysia), Peninsular Thailand (Simmons, 2005: 371); *edwardshilli* Flannery and Colgan, 1993 – northwestern Papua New Guinea (Simmons, 2005: 371); *einnaythu* Douangboubpha, Bumrungsri, Satasook, Soisook, Hla Bu, Aul, Harrison, Pearch, Thomas and Bates, 2011 – Myanmar; ***fuliginosus*** (Temminck, 1853); *fulvus* Gray, 1838 – Afganistan, India, Sri Lanka, Pakistan to Vietnam (Simmons, 2005: 371); *galeritus* Cantor, 1846 – Sri Lanka and India through southeast Asia (including Burma, Thailand and Peninsular Malaysia) to Java and Borneo, Sanana Isl (Sula Group, Moluccas Isls) (Simmons, 2005: 372); *gentilis* K. Andersen, 1918 – N India (incl. Manipur), Bangladesh, through Myanmar and Thailand (part) to N Malaya; *grandis* G. M. Allen, 1936 – Myanmar, Thailand, Vietnam, Cambodia; India; *griffini* Thong, Puechmaille, Denzinger, Dietz, Csorba, Bates, Teeling, and Schnitzler, 2012 – Vietnam; *halophyllus* Hill and Yenbutra, 1984 – Thailand (Simmons, 2005: 372); *hypophyllus* Kock and Bhat, 1994 – southern India (Simmons, 2005: 372); *inexpectatus* Laurie and Hill, 1954 – northern Sulawesi (Indonesia) (Simmons, 2005: 372); *inornatus* McKean, 1970 – Northern Territory (Australia) (Simmons, 2005: 373); ***jonesi*** Hayman, 1947; *khaokhouayensis* Guillén-Servent and Francis, 2006 – Laos, Vietnam; *kingstonae* Wongwaiyut, Karapan, Saekong, Francis, Guillén-Servent, Senawi, Khan, Bates, Jantarit and Soisook, 2023 – S Thailand, peninsular Malaysia, Sabah; *kunzi* Murray, Khan, Kingston, Akbar and Campbell, 2018 – Malay Peninsula between 03 12 N and 10 41 N; ***lamottei*** Brosset, 1985; *lankadiva* Kelaart, 1850 – Sri Lanka, southern and central India (Simmons, 2005: 373); *larvatus* (Horsfield, 1823) – northern and eastern India and Bangladesh; Yunnan, Kwangsi and Hainan (China), Burma, Thailand, Cambodia, Laos and Vietnam, western Malaysia to Sumatra, Java, Borneo and adjacent small islands including Kangean Isls (Indonesia) (Simmons, 2005: 373); *lekaguli* Thonglongya and Hill, 1974 – Thailand, peninsular Malaysia, Luzon (Philippines) (Simmons, 2005: 373); *lylei* Thomas, 1913 – Burma, Vietnam, Thailand, western Malaysia (Simmons, 2005: 374); *macrobullatus* Tate, 1941 – Sulawesi, Seram (Molucca Isls) and Kangean Isls (Indonesia) (Simmons, 2005: 374); *madurae* Kitchener and Maryanto, 1993 – Madura Island, central Java (Indonesia) (Simmons, 2005: 374); *maggietaylorae* J.D. Smith and Hill, 1981 – New Guinea, Bismarck Arch (Simmons, 2005: 374); ***marisae*** Aellen, 1954; ***megalotis*** (Heuglin, 1861); *muscinus* (Thomas and Doria, 1886) – New Guinea (Simmons, 2005: 374); *nequam* K. Andersen, 1918 – Malaysia (Simmons, 2005: 375); *nicobarulae* Miller, 1902 – Nicobar islands;

obscurus (Peters, 1861) – Philippines except Palawan region (Simmons, 2005: 375); *orbiculus* Francis, Kock, and Habersetzer, 1999 – Sumatra (Indonesia), Peninsular Malaysia (Simmons, 2005: 375); *papua* (Thomas and Doria, 1886) – Biak and Numfoor Isls, western New Guinea and northern Molucca Isls (Simmons, 2005: 375); *pelingensis* Shamel, 1940 – Peleng Isl and Sulawesi (Indonesia) (Simmons, 2005: 375); *pendlebury* Chasen 1936 – S Thailand; *pomona* K. Andersen, 1918 – Bangladesh and India to Burma, Thailand, Laos, Cambodia, Vietnam, southern China and western Malaysia (Simmons, 2005: 375); *poutensis* J.A. Allen, 1906 – N Myanmar, S China (incl. Hainan), N Vietnam to C Vietnam along the coast (Cham Islands); *pygmaeus* (G.R. Waterhouse, 1843) – Philippines except Palawan region (Simmons, 2005: 376); *ridleyi* Robinson and Kloss, 1911 – Peninsular Malaysia, Singapore, northern Borneo (Simmons, 2005: 376); *rotalis* Francis, Kock, and Habersetzer, 1999 – Laos (Simmons, 2005: 376); ***ruber*** (Noack, 1893); *scutinares* Robinson, Jenkins, Francis, and Fulford, 2003 – Laos, Vietnam (Simmons, 2005: 376); *semoni* Matschie, 1903 – northern Queensland (Australia), eastern New Guinea (Simmons, 2005: 376); *sorenseni* Kitchener and Maryanto, 1993 – central and western Java (Indonesia) (Simmons, 2005: 376); *speoris* (Schneider, 1800) – India, Sri Lanka (Simmons, 2005: 377); *stenotis* Thomas, 1913 – Northern Territory, north Western Australia and northern Queensland (Australia) (Simmons, 2005: 377); *sumbae* Oei, 1960 – Sumba, Roti, Sumbawa, Flores, Semau and Savu Isls (Indonesia) (Simmons, 2005: 377); ***tephrus*** (Cabrera, 1906); *turpis* Bangs, 1901 – Peninsular Thailand and Vietnam; Ryukyu Isls (Japan) (Simmons, 2005: 377); *wollastoni* Thomas, 1913 – western and central New Guinea (Simmons, 2005: 378).

Additionally, there are extinct species such as the African †***besaoka*** Samonds 2007 and †***kaumbului*** Wesselman 1984.

COMMON NAMES:
Czech: praví pavrápenci. English: Leaf-nosed Bats, Leafnosed Bats, Roundleaf Bats. French: Phyllorhines. German: Altwelt-Rundblattnasen. Italian: Ipposidèri.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The approximate fossil date for crown *Hipposideros* is set by Shi and Rabosky (2015: 1532) to 40.4 Mya.

At Songhor, Butler (1969, 1978) found *Hipposideros* sp. from Early Miocene deposits.

BIOGEOGRAPHY:
During the Miocene at about 15 Mya, *Hipposideros* diversified into distinct clades based on geography: these being the African, Indian and Southeast Asian clades (Foley *et al.*, 2014: 320).

MOLECULAR BIOLOGY:
Genetics
An analysis of *cytb* sequences by Kundu *et al.* (2023: 7) indicated that most of the African species they included (*abae, caffer beatus, fuliginosus, lamottei* and *ruber*) form a monophyletic group, the only exception being *Hipposideros jonesi*.

PARASITES:
HAEMATOSPORIDA
Schaer *et al.* (2017: 2) examined 23 *Hipposideros* specimens from South Sudan, of which 1 (4 %) was infected by *Hepatocystis*.

ACARI
Trombiculidae
Zajkowska *et al.* (2018: 121) [referring to Vercammen-Grandjean and Fain (1958)] mentioned a *Myotrombicula bidentipalpis* Vercammen-Grandjean and Fain, 1958 on a *Hipposideros* sp. from Congo.

DIPTERA
Nycteribiidae
Dick *et al.* (2023: 78) mentioned that *Penicillidia (Penicillidia) pachymela* Speiser, 1901 has been found on *Hipposideros* sp.

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
During Febuary 2008 in Ghana, Pfefferle *et al.* (2009) tested fecal samples of various *Hipposideros* species of the *caffer*/*ruber* complex, where the specific identification needs to be confirmed, and therefore is presented here - Pfefferle *et al.* (2009) as *Hipposideros caffer ruber* tested 40 fecal samples, 10 tested positive for coronavirus (CoV) RNA, while 4 were positive for group 1 CoV and 6 for group 2 CoV. Pfefferle *et al.* (2009) as *Hipposideros* cf. *ruber* tested 8 fecal samples which tested negative for coronavirus (CoV) RNA, from Booyem A cave. While from Booyem B cave [identified as *H* cf. *ruber* two morphotypes], in Ghana 11 fecal samples, 2 samples tested positive for coronavirus (CoV) RNA, while the one was positive for group 1 CoV and the other for group 2 CoV (Pfefferle *et al.*, 2009).

Drexler *et al.* (2013a: 50) and Hu *et al.* (2015: 5) indicate that *Hipposideros* betacoronaviruses

detected in Africa (Ghana, Kenya, and Nigeria) and Asia are clearly distinct from SARS-related coronaviruses.

27.6 % (?; 16 out of 68) of the Kenyan *Hipposideros* specimens tested by Tao *et al.* (2017: 3, Suppl.) were positive for CoV. 33.3 % (7 out of 21) of the Guinean specimens tested by Lacroix *et al.* (2020: 7) were positive for CoV.

Meta Djomsi *et al.* (2023: 1) tested 291 *Hipposideros* specimens from the DRC, Cameroon and Guinea and found that 61 (20.9 %) tested positive for CoV.

Filoviridae
Marburgvirus
Markotter *et al.* (2020: 6) mention this virus from non-specified *Hipposideros* spp.

Flaviviridae
Raulino *et al.* (2022: 256) found antibodies against Denque and West Nile.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that one out of eight examined Kenyan *Hipposideros* sp. specimens tested positive for *Paramyxovirus* sequences. This was also the case for one out of 39 specimens from Cameroon, and one out of three Nigerian specimens.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 16 Tanzanian *Hipposideros* sp. specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Togaviridae
Raulino *et al.* (2022: 256) reported antibodies against O'nyong nyong virus from these bats.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Congo (Democratic Republic of the), Gabon, Ghana, Guinea, Kenya, Liberia, Madagascar, Namibia, Niger, Nigeria, Senegal, Somalia, South Sudan, Tanzania, Togo, Uganda, Zambia.

Hipposideros abae J.A. Allen, 1917

*1917. *Hipposideros abæ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 432. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 49123: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 13 December 1911; original number: 1715. - Etymology: Referring to the locality where the type specimen was collected (Aba). (Current Combination).
2021. *Hipposideros cf. abae:* Yuzefovich, Artyushin and Kruskop, Diversity, 13 (5) 218: 3. Publication date: 19 May 2021. (Name Combination).
? *Hipposideros abae:* (Current Spelling).

TAXONOMY:
Simmons (2005: 367) places it in the *speoris* species group. Patterson *et al.* (2020: 121) place it in the *ruber* subgroup of the *bicolor* group.

COMMON NAMES:
Czech: pavrápenec abánský. English: Aba Roundleaf Bat, Aba Leaf-nosed Bat. French: Phyllorhine d'Aba. German: Aba-Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008at; IUCN, 2009; Monadjem *et al.*, 2017aq).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017aq). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008at; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bq; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There are no known major threats to this species. It appears to have taken advantage of forest clearance by moving into formerly forested land (Mickleburgh *et al.*, 2008at; IUCN, 2009; Monadjem *et al.*, 2017aq).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008at) [in IUCN (2009)] and Monadjem *et al.* (2017aq) report that no specific conservation measures are in place, but it occurs in Comoe National Park in Côte d'Ivoire, and

presumably also in other protected areas across its wide range.

GENERAL DISTRIBUTION:
Hipposideros abae is patchily distributed in a range which extends from Guinea-Bissau in West Africa (also the most northerly record) to northern Uganda (also the most eastern and southerly record) (Simmons, 2005: 367). It is a lowland species found below 1,000 m.

Native: Benin (Benda *et al.*, 2023a: 27), Burkina Faso (Koopman *et al.*, 1978: 4; Kangoyé *et al.*, 2015a: 608); Cameroon; Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire; Ethiopia (Kruskop *et al.*, 2016: 57); Ghana; Guinea (Weber and Fahr, 2007); Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 56); Liberia; Nigeria; Sierra Leone; Sudan; Togo; Uganda (Kityo and Kerbis, 1996: 61).

Presence uncertain: Benin; Chad; Mali.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Young (1975: 76) indicates that two distinct colour phases can be found: rufous (orange) and grey.

ECHOLOCATION:
In Sierra Leone, Weber *et al.* (2019: 21) recorded the call of one female with CF at 103.0 kHz.

In Benin, Roemer *et al.* (2021: Suppl.) categorized the bat's call as a CF-FMd (Constant frequency - Frequency modulation downward) sonotype.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003).

ROOST:
It roosts in caves and rocky crevices or on the undersides of boulders, but apparently not in houses (Happold, 1987). For Guinea, Weber and Fahr (2006: 4) indicate that *H. abae* largely or exclusively depends on the availability of caves as day roosts.

POPULATION:
Structure and Density
Is thought to be sparsely distributed throughout its range, and to roost in small colonies (approximate group size in the dozens, not hundreds) (Mickleburgh *et al.*, 2008at; IUCN, 2009; Monadjem *et al.*, 2017aq).

Trend
2016: Unknown (Monadjem *et al.*, 2017aq). 2008: Unknown (Mickleburgh *et al.*, 2008at; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
One female captured on 24 May in Sierra Leone was lactating (Weber *et al.*, 2019: 23).

PARASITES:
ACARI
Fain (1959d: 239) described *Psorergates (Psorergatoides) hipposideros* (Acari: Psoridatidae) from a *H. abae* captured near Bunia, Ituri, DRC.

DIPTERA
Streblidae
Ascodipteron jonesi Jobling 1952 from the wing at Njala, Sierra Leone (Haeselbarth *et al.*, 1966: 106).

VIRUSES:
Coronaviridae
Alphacoronavirus
SARS-CoV (subgenus *Duvinacovirus*)
During Febuary 2008 in Ghana, 16 fecal samples for coronavirus (CoV) RNA from two localities tested negative Pfefferle *et al.*, 2009). Corman *et al.* (2015: 11859) tested 242 Ghanaian bats and found 19 (7.8 %) to test positive for 229E-related coronaviruses. Baldwin (2015: 38) also mentioned that juvenile bats had higher rates of infections by multiple coronaviruses than adults. Meyer *et al.* (2024: 4) found CoV 229E-like, CoV 2b and CoV 2bBasal viruses in Ghanaian bats.

Hepeviridae
Drexler *et al.* (2012b: 9137) reported two positive feacal samples out of a total of 57 examined (3.51 %) from Ghana. Johne *et al.* (2014: 223, 224) suggested to place the Bat hepatitis E virus found in *H. abae*, as well as Hepevirus-species occurring in other bat families into a separate genus: *Chiropteranhepevirus*, a name that was officially changed to *Chirohepevirus* (see Wang and Yang, 2022: 5).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) reported that none of the 80 specimens they examined from Ghana tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

Phenuiviridae
Phlebovirus
de Jong *et al.* (2011: 11), Luis *et al.* (2013: Suppl.), and Willoughby *et al.* (2017: Suppl.) report the occurrence of Rift Valley fever virus.

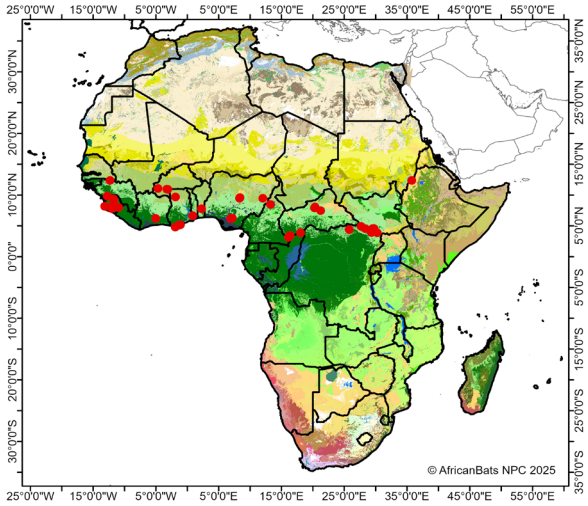

Figure 56. Distribution of *Hipposideros abae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Ghana, Guinea, Nigeria, Senegal, Sierra Leone, South Sudan, Togo.

†*Hipposideros africanum* Ravel, 2016

*2016. *Hipposideros (Pseudorhinolophus) africanum* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 372, figs 8 - 10. Publication date: 30 September 2016. Type locality: Tunisia: Kassérine province: Djebel Chambi National Park: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: The name refers to the African continent and underlines the geographic importance as the genus was herethereto only reported from Europe (see Ravel et al., 372).

2019. *Hipposideros africanuum:* Brown, Cashmore, Simmons and Butler, Palaeontology, 62 (5): Suppl. Publication date: 25 March 2019. (Lapsus).

GENERAL COMMENTS:
This fossil species is generally assigned to the subgenus *Pseudorhinolophus* Schlosser, 1887.

TAXONOMY:
This taxon is generally included in the (sub)genus *Pseudorhinolophus* Schlosser, 1887 (Chornelia and Hughes, 2022: 12).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

†*Hipposideros amenhotepos* Gunnell, Winkler, Miller, Head, El-Barkooky, Gawad, Sanders and Gingerich, 2015

*2015. *Hipposideros (Pseudorhinolophus) amenhotepos* Gunnell, Winkler, Miller, Head, El-Barkooky, Gawad, Sanders and Gingerich, Hist. Bio., 28 (1-2): 162, figs 4, 5, 6 (for 2016). Publication date: 1 October 2015. Type locality: Egypt: Eastern Desert: Khasm El-Raqaba [28.451 N 31.834 E]. Holotype: CGM 83763. Right M1. - Comments: The paper was published online on 1 October 2015, and in print on 17 February 2016. - Etymology: Named after Amenhotep IV (= Akhenaten), an Egyptian 18th Dynasty pharaoh, whose capital city of Amarna was located in the Eastern Desert not far from the type locality of this species (see Gunnell *et al.*, 2015b: 162).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene (Tortonian - Brown *et al.*, 2019: Suppl.).

Hipposideros beatus (K. Andersen, 1906)

*1906. *Hipposiderus beatus* K. Andersen, Ann. Mag. nat. Hist., ser 7, 17 (99): 275, 279. Publication date: 1 March 1906. Type locality: Equatorial Guinea: Rio Muni: Benito River, 15 mi (24 km) from [01 31 N 09 52 E]. [Goto Description]. Holotype: NHMUK 1900.2.5.45: ad ♀, alcoholic (skull not removed). Collected by: George Latimer Bates Esq. Collection date: February 1899. (Current Combination).

1957. *Hipposideros beatus maximus* Verschuren, Exploration du Parc national du Garamba, 7: 365. Type locality: Congo (Democratic Republic of the): Garamba National Park: Pidigala-Nord, Source area of [04 38 N 29 42 E]. Holotype: RBINS 4037: ad ♂. Collected by: Gaston-François de Witte *et al.*; collection date: 23 April 1952; original number: 4565. Paratype: RBINS 4038: ad ♂. Collected by: Gaston-François de Witte *et al.*; collection date: 8 March 1952; original number: 4379. Paratype: RBINS 4039: ad ♀. Collected by: Gaston-François de Witte *et al.*; collection date: 23 April 1952; original number: 4765. Paratype: RBINS 4040: ad ♂. Collected by:

Gaston-François de Witte *et al.*; collection date: 18 April 1952; original number: 4579. Paratype: RBINS 4041: ad ♂. Collected by: Gaston-François de Witte *et al.*; collection date: 14 May 1952; original number: 4634. Paratype: RBINS 4042: ad ♂. Collected by: Gaston-François de Witte *et al.*; collection date: 19 May 1952; original number: 4658. Paratype: RBINS 4043: ad ♂. Collected by: Gaston-François de Witte *et al.*; collection date: 20 May 1952; original number: 4662. Paratype: RBINS 4044: ad. Collected by: Gaston-François de Witte *et al.*; collection date: 22 May 1952; original number: 4668.

2020. *Hipposideros beatus 1:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2020. *Hipposideros beatus 2:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2021. *Hypposideros beatus:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 9. Publication date: 14 May 2021. (Lapsus).

? *Hipposideros beatus beatus:* (Name Combination).

? *Hipposideros beatus:* (Current Spelling).

TAXONOMY:

Simmons (2005: 368) places it in the *bicolor* species group, and Patterson *et al.* (2020: 121) in the *ruber* subgroup of the *bicolor* group.

COMMON NAMES:

Castilian (Spain): Murciélago de Nariz de Hoja. Czech: pavrápenec guinejský. English: Benito Roundleaf Bat, Benito Leaf-nosed Bat, Dwarf Leaf-nosed Bat. French: Phyllorine naine, Phyllorhine de Benito. German: Benito-Rundblattnase, Benito-Blattnase.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bz; IUCN, 2009; Monadjem *et al.*, 2017bm).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bm). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bz; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ck; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

Habitat loss is the major threat to this species (Mickleburgh *et al.*, 2008bz; IUCN, 2009; Monadjem *et al.*, 2017bm).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008bz) [in IUCN (2009)] and Monadjem *et al.* (2017bm) report that it occurs in the Mount Allen National Park (Equatorial Guinea), and Garamba National Park (Democratic Republic of Congo), and presumably in several other protected areas.

GENERAL DISTRIBUTION:

Hipposideros beatus has been recorded from Sierra Leone eastwards across the forest zone west and central Africa, as far east as the Sudan/Democratic Republic of Congo border. There are records from Sierra Leone, Guinea, Liberia, Côte d'Ivoire, Ghana, Togo, Nigeria, Cameroon, Equatorial Guinea, Congo, Democratic Republic of Congo and Sudan. A previous report of this species in Central African Republic is in error, though it might occur in the south of that country.

Native: Cameroon (Eisentraut, 1973); Congo (The Democratic Republic of the); Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana (Decher and Fahr, 2007: 16); Guinea; Guinea-Bissau (Rainho and Ranco, 2001: 59); Kenya (Webala *et al.*, 2019b: 13); Liberia; Nigeria (Happold, 1987); Sierra Leone; Sudan; Togo.

Presence uncertain: Central African Republic.

Bates *et al.* (2013: 338) reject the presence of *H. beatus* in the Republic of Congo, because previous authors (e.g., Malbrant and Maclatchy, 1949; Dowsett *et al.*, 1991) indicated it would be 'likely' to occur in that country.

ECHOLOCATION:

Monadjem *et al.* (2013b: 351) report the F_{max} to be 129.0 kHz at Mount Nimba.

Heller and Volleth (2016: 4) report different bandwidths for *H. beatus* specimens from various parts of Africa: Côte d'Ivoire: 139 - 147 kHz (Happold, 2013ap), Mount Nimba: 129 kHz (Monadjem *et al.*, 2013b), Lake Tumba, DRC: 108 and 129 kHz (2 specimens; see Novick, 1958), and Irangi, DRC: 109.2 kHz (their study). This 20 kHz difference makes them suggest that two cryptic species might be present.

In Kenya, Webala *et al.* (2019b: 15) report F_{max}: 114.8 - 123.7 kHz, duration: 7.0 - 9.1 ms for three females and F_{max}: 124.0 kHz, duration: 8.0 - 8.4 ms for two males.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 162 calls of 4 bats: F_{peak}: 129.4 ± 4.0 (127.8 - 138.6) kHz, F_{min}: 114.3 ± 8.4 (107.4 - 129.3) kHz, F_{max}: 132.1 ± 4.5 (129.0 - 140.6) kHz, duration: 5.4 ± 1.5 (3.6 - 8.5) ms.

Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003652_KKRKEXFMEH.WAV, https://chirovox.elte.hu/sounds/A003654_POORECISLB.WAV, https://chirovox.elte.hu/sounds/A003672_QRQCGYCRWA.WAV

HABITAT:
In Nigeria, it is widely distributed in the rainforest zone (Happold, 1987). Monadjem *et al.* (2016y: 365) also report its wide distribution in forested habitats in the Mount Nimba area, on altitudes between 420 and 700 m.

POPULATION:
Structure and Density
It has a patchy distribution, typically found in small familial groups, but can be found in groups of up to 20 individuals. There is no information on overall abundance (Mickleburgh *et al.*, 2008bz; IUCN, 2009; Monadjem *et al.*, 2017bm).

Trend
2016: Decreasing (Monadjem *et al.*, 2017bm).
2008: Decreasing (Mickleburgh *et al.*, 2008bz; IUCN, 2009).

MATING:
Brosset (1982: 5) mentions that this species' social structure is monogamous as family groups consist of one adult male and female and their young. The parents stay together until the start of the next breeding season, when new pairs are formed (see also Heller *et al.*, 1993: 376).

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023: 79) reported they found *Phthiridium inopinata* (Theodor, 1957) on *Hipposideros beatus* clade 1 specimens from the Kakamega Forest (Kenya).

VIRUSES:
Poxviridae
Orthopoxvirus
Mande (2019: 7) reported a seropositive case of Mokeypoxvirus in a *H. beatus* from the DRC.

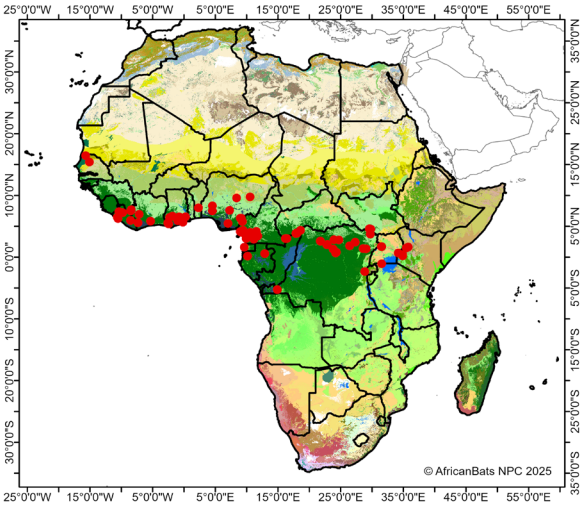

Figure 57. Distribution of *Hipposideros beatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Senegal, Tanzania, Uganda.

Hipposideros caffer (Sundevall, 1846)

*1846. *Rhinolophus caffer* Sundevall, Öfvers. kongl. Sv. Vet.-Akad. Förhandl., 3 (4): 118. Publication date: 1846. Type locality: South Africa: KwaZulu-Natal: Port Natal [=Durban], near [ca. 29 52 S 31 00 E]. [Goto Description]. Syntype: NHMUK 1848.6.2.16: skull only. "Cotype" from Stockholm Museum, labeled "*Hipposideros caffer typicus*" locality Natal. Syntype: NHMUK 1849.11.22.11: skin only. Syntype: NRM 100279:; collection date: 1845. Syntype: NRM 631054:; collection date: 4 July 1841. Syntype: NRM 631055:; collection date: 14 May 1840. Syntype: RMNH MAM.27330: ad, mounted skin (skull not removed). Collected by: Johan August Wahlberg; collection date: 1838 - 1856. - Comments: Type locality originally mentioned as "Circa Port-Natal inventus". - Etymology: From the masculine scientific Latin adjective *càffer* "Kafir", referring to the southern African locality where the type specimen was collected (see Lanza *et al.*, 2015: 139).

1852. *Phyllorrhina caffra* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 39, pl 8. Publication date: 1852. Type locality: Mozambique: Ibo island. (Name Combination, Alternate Spelling).

1852. *Phyllorrhina gracilis* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 36, pl 7, fig 1 - 4; pl 13, fig 14 - 15. Publication date: 1852. Type locality: Mozambique: Lower Zambesi River: Tete [16 10 S 33 35 E, 230 m]. [Goto Description]. Holotype: ZMB 364/85624: ♂. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847; original number: An 16311. See Turni and Kock (2008: 38) [skin & skull: ZMB 364 + skeleton: ZMB 85624].

1852. *Phyllorrhina patellifera* Peters, Naturw. Reise Mossamb., Säugethiere, p 39. Type locality: Mozambique: Ibo island. - Comments: Manuscript name, cited by Peters (1852: 39, 40).

1898. *Phyllorhina angolensis* Seabra, J. Sci. mat. phys. nat., ser 2, 5: 256. Publication date: December 1898. Type locality: Angola: Rio Coroca [=Curoca river] [15 43 S 11 55 E]. Syntype: NHMUK 1906.1.3.2. - Comments: Meester *et al.* (1986: 43) indicate "Benguela, Angola, restricted by Hill and Carter (1941: 40), who point out that the name is based on four specimens from Benguela, housed in the Museu Bocage, Lisbon, and one from Rio Coroca, Angola, in the British Museum (Natural History). Koopman (in litt.) points out that, as the Museu Bocage had been destroyed by fire, the Rio Coroca specimen may be the only remaining of the type series.".

1917. *Hipposideros nanus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 434. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 49426: ad ♀, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 24 September 1912; original number: 1689. Allen (1917: 434) erroneously mentioned 24 October 1912 as collection date, see Goodwin (1953: 245).

1924. *Hipposideros caffer aurantiaca* de Beaux, Atti Soc. Lig. Sci. Nat. Geogr, 3: 155. Type locality: Somalia: Basso Giuba [=Lower Juba river]: Belet Mamu. - Comments: Lanza *et al.* (2015: 139) indicate that the correct spelling shoud actually be "*aurantiacus"* as the generic name ("*Hipposideros*") is a masculine name.

1965. *Hipposideros cafer cafer:* Dalquest, J. Mamm., 46 (2): 257. Publication date: May 1965. (Lapsus).

2015. *H[ipposideros] cafer:* Gunnell, Winkler, Miller, Head, El-Barkooky, Gawad, Sanders and Gingerich, Hist. Bio., 28 (1 - 2): 163. Publication date: 1 October 2015. (Lapsus).

2016. *Hipposideros cf. caffer* Monadjem, Richards and Denys, Acta Chiropt., 18 (2): 365. Publication date: December 2016. - Comments: .

2020. *Hipposideros caffer 1:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicate that this is the same form as the *Hipposideros caffer* A2 lineage mentioned by Vallo *et al.* (2009) and *Hipposideros caffer tephrus* mentioned by Monadjem *et al.* (2013b). (Name Combination).

2020. *Hipposideros caffer 2:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2020. *Hipposideros caffer 3:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2020. *Hipposideros caffer 4:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicate that this is the same form as the *Hipposideros caffer* A1 lineage mentioned by Vallo *et al.* (2009) and the A1a and A1b lineages mentioned by Monadjem *et al.* (2013b). (Name Combination).

2020. *Hipposideros caffer 5:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicate that this is the same form as the *Hipposideros caffer* B lineage mentioned by Vallo *et al.* (2009). (Name Combination).

2020. *Hipposideros caffer 6:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

2020. *Hipposideros caffer 7:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicates that this is the same form as the *Hipposideros ruber* B2 lineage mentioned by Monadjem *et al.* (2013b). (Name Combination).

2020. *Hipposideros caffer 8:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).

? *Hipposideros caffer angolensis:* (Name Combination).

? *Hipposideros caffer caffer:*

? *Hipposideros caffer centralis:*

? *Hipposideros caffer complex sp. lineage 1*

? *Hipposideros caffer complex sp. lineage 2*

? *Hipposideros caffer complex sp. lineage 3*

? *Hipposideros caffer complex sp. lineage 7*

? *Hipposideros caffer complex sp. lineage 8*

? *Hipposideros caffer nanus:* (Name Combination).

? *Hipposideros caffer:* (Name Combination, Current Combination).

TAXONOMY:

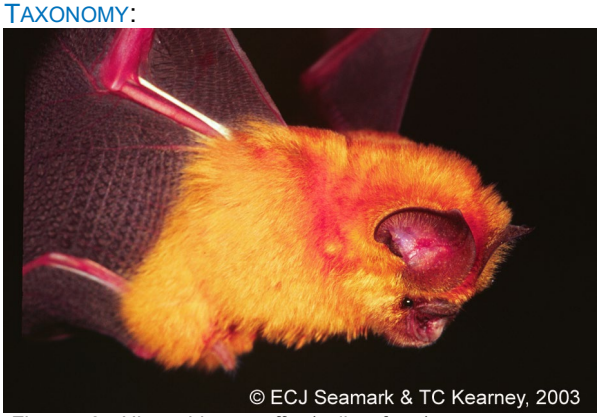

Figure 58. *Hipposideros caffer* (yellow form).

Meester *et al.* (1986) state that further extralimital [to Southern Africa] subspecies may include *centralis* Andersen, 1906, *tephrus* Cabrera, 1906, *nanus* J.A. Allen, 1917 (Koopman, 1975), and also *guineensis* Andersen, 1906, and *niapu* J.A. Allen, 1917 (Hill, 1963a). Most recent authors appear to regard *ruber* Noack, 1893, as a separate species (Kock, 1969a; Hayman and Hill, 1971; Ansell, 1978; Corbet and Hill, 1980, Koopman, 1982). Although Hill (1963a) and Koopman (1975 regard *ruber* as only subspecifically distinct from *caffer*. Simmons (2005: 368) places *H. caffer* within the *bicolor* species group. Vallo *et al.* (2007: 257) consider *tephrus* to be a separate species, based on cytochrome *b* analysis. Reviewed by Vallo *et al.* (2009).

Based on analyses of mitochondrial DNA, Vallo *et al.* (2009: 196) subdivided *H. caffer* s.l. in four major lineages (A, B, C and D), of which A to C were subdivided into two sublineages (1 and 2). Sizewise, A represents small sized specimens (*caffer* and *tephrus*), whereas the three other lineages represent larger sized forms (*ruber* morphotype, Fa > 48 mm). Monadjem *et al.* (2013b: 344) introduced lineage E (with two sublineages), which also represents a larger form. To this, Patterson *et al.* (2020) added some additional sublineages from East Africa.
Baldwin *et al.* (2021: 1394) analysed *cytb* of bats from the *H. caffer* complex from Ghana, which led to a further subdivision (A: "*caffer*" 1 to 4; B::"*caffer*" 5 to 8 + cf. *lamottei*; C: "*ruber*" 1 to 4; D: aff. *ruber*, including D3 and D4). They suggest (p. 1398) that at least four species should be recognized within the *H. caffer* complex, whereby lineage A1 should be assigned to *H. caffer tephrus* (although the German summary mentions . *H. tephrus*). The identification of the East African lineages A2 and A3 remains unclear, but lineage A4 from South Africa represents *H. caffer* s.s. Lineages B and C are provisionally assiged to "*H.* cf. *ruber*" and lineage D to "*H.* aff. *ruber*".

Patterson *et al.* (2020: 121) place it in the *ruber* subgroup of the *bicolor* group.

COMMON NAMES:
Afrikaans: Sundevall se bladneusvlermuis, Sundevall-bladneusvlermuis, Sundevallse blaarneusvlermuis, Kaapse Blaarneusvlermuis. Azande (DRC): Nkulo. Chinese: 松氏蹄蝠. Czech: pavrápenec natalský, listonos africký, pavrápenec africký. English: Sundevall's Leaf-nosed Bat, Common African Leaf-nosed Bat, Lesser Leaf-nosed bat, Sundevall's Roundleaf Bat, Cape Leaf-nosed bat, Sundevall's African Leaf-nosed Bat, South African Lesser Leaf-nosed Bat. French: Phyllorhine de Cafrerie, Phyllorhine de Sundevall, Rhinolophe de Cafrerie. German: Sundevalls Rundblattnase, Sundevall's Blattnase, Gewöhnliche Rundblattnase. Italian: Ipposìdero càfro. Kiluba (DRC): Kasusu. Malawian: Liputiputi, Ndemiya, Namzeze. Nyungwe (Malawi): Kalemawalema (not specific). Portuguese: Morcego de nariz enfolhado da cafraria. Tshokwe (Angola): Kafukufuku, Kafukufuku-mulá. Ukrainian: Листоніс південноафриканський [= Lystonis pivdennoafrykans'kyy].

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category (Kock *et al.*, 2008c; IUCN, 2009; Richards *et al.*, 2020).

Assessment History
Global
2019: LC ver 3.1 (2001) (Richards *et al.*, 2020). 2008: LC ver 3.1 (2001) (Kock *et al.*, 2008c; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ae; IUCN, 2004). 1994: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016t). 2004: DD ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
Human disturbance to roosting sites (caves) could have a negative effect (Kock *et al.*, 2008c; IUCN, 2009; Richards *et al.*, 2020).

Sherwin *et al.* (2012: 174) consider aerial hawking and water stress to be the major risk factors linked to climatic change.

CONSERVATION ACTIONS:
Kock *et al.* (2008c) [in IUCN (2009)] and Richards *et al.* (2020) report that no specific conservation measures are in place. Occurs in protected areas throughout its range.

GENERAL DISTRIBUTION:
Hipposideros caffer is a very wide-ranging species, occurring from the south-western Arabian Peninsula (including Yemen) and across most of sub-Saharan Africa (except for central forested regions) (Simmons, 2005: 368). This species has also been recorded in southern Algeria, central Niger, eastern Chad, the Senegal/Mauritania border. Elevation ranges from sea level to 2,500 m in this area.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,581,888 km^2. In South Africa, its distribution is strongly associated with the mean temperature of the coldest quarter (Babiker Salata, 2012: 49).

Specimens from Morocco need verification as these may be attributed to *H. tephrus* (Cabrera, 1906). A supposed record from southern Algeria requires confirmation.

Specimens identified by Fahr *et al.* (2006a) as *H. caffer* from Mount Nimba might need to be reassigned, as this species is restricted to southern Africa and possibly eastern Africa, south of Kenya/Tanzania (Vallo *et al.*, 2009: 193;

Monadjem *et al.*, 2016y: 365; Richards *et al.*, 2020: 2).

Native: Angola (Crawford-Cabral, 1989; Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 536); Benin; Botswana (Monadjem *et al.*, 2010d: 536); Burkina Faso; Burundi; Cameroon; Chad; Congo (Bates *et al.*, 2013: 335); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 536); Côte d'Ivoire; Equatorial Guinea; Eritrea; Eswatini (Monadjem *et al.*, 2010d: 537, Monadjem *et al.*, 2021: 5); Ethiopia; Gabon (Brosset, 1966c); Gambia; Ghana; Guinea; Guinea-Bissau (Seabra, 1900c; Monard, 1939;; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 50); Kenya; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d:536); Mali; Mauritania; Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 360); Mozambique (Lopes and Crawford-Cabral, 1992; Monadjem *et al.*, 2010d: 536; Monadjem *et al.*, 2010c: 380); Namibia (Monadjem *et al.*, 2010d: 536); Niger; Nigeria (Menzies, 1973); Rwanda; Saudi Arabia; Senegal; Sierra Leone; Somalia; South Africa (Taylor, 2000: 140; Monadjem *et al.*, 2010d: 537); Sudan; Tanzania (including the islands of Pemba, Unguja, and Mafia [see O'Brien, 2011: 287]); Togo; Uganda (Kityo and Kerbis, 1996: 61); Yemen; Zambia (Ansell, 1969; Ansell, 1978; Ansell, 1986; Cotterill, 2002b: 5; Monadjem *et al.*, 2010d: 537); Zimbabwe (Monadjem *et al.*, 2010d: 537).

Presence uncertain: Algeria; Liberia.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Menzies (1973) [in Young (1975: 76) indicates that, in some colonies in northern Nigeria, rufous bats get a grey fur during the moulting season, and subsequently change back to rufous. Young (1975: 76) also mentions that the majority of *H. caffer* specimens in Angola and south-west Africa (Namibia) is grey, whereas in eastern Africa, the rufous phase is more common.

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 5 *H.* cf. *caffer* specimens: Fa: 51.50 ± 1.398 mm, mass: 10.2 ± 1.10 g, wing loading: 5.2 ± 0.27 N/m^2, aspect ratio: 5.8 ± 0.10.

DETAILED MORPHOLOGY:
Brain
Tambusso and Fariña (2015: Suppl.) mention a brain mass of 0.32 g for an average body mass of 10.7 g.

Amrein *et al.* (2007), from specimens collected from Bénin, reported moderate proliferating cell activity, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus, with doublecortin (DCX) they detected highest levels of young migrating neuron in the subgrannular layer of the hippocampus. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. No NeuroD was detected in the hippocampal granule cells (Amrein *et al.* (2007).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.6 Pa, aspect ratio 6.3 and tip shape index of 3.17 for a wingspan of 25 cm and a wing area of 100 cm^2 and a body mass of 6 g.

ECHOLOCATION:
At Irangi (Kivu province, DRC), Heller (1992: 77) was able to distinguish *H. caffer* from *H. ruber* as the prior emitted calls at a much higher frequency: 137 - 160 kHz (versus 130 - 140 kHz in *ruber*).

In Guinea, Fahr and Ebigbo (2003) reported a constant frequency component of 160.2 - 164.1 kHz (these may not represent *H. caffer*, see Vallo *et al.*, 2009). In Kenya, Taylor *et al.* (2005) reported a maximum frequency of 157 ± 0.2 kHz, using a Pettersson D980 detector. From the same country, Eisenring *et al.* (2016: SI 2.) reported the following values: F_{peak}: 144.0, HF: 149.4, F_{min}: 110.9, DT: 0.1, DF: 38.5, and IPI: 0.0. At Sengwa in Zimbabwe, Fenton (1986a) reported a F_{max}: 141.5 ± 2.7 kHz, whereas previously Jacobs (1996) and Fenton and Bell (1981) had reported a F_{max} 138 kHz from the same locality. In South Africa, Fenton (1986a) reported a F_{max} of 145.4 ± 2.5 kHz from Levuvhu, while Taylor (1999b) using a Pettersson D980 detector reported a similar F_{max} 145 ± 0.2 kHz from Jozini Dam. Monadjem *et al.* (2007a), using an Anabat detector, reported a F_{max} of 143.0 ± 1.43 kHz from various localities in Swaziland. See also Pye (1972, O'Shea and Vaughan, 1980). Monadjem *et al.* (2010c: 381) reported from Mozambique that the peak echolocation frequencies of two individuals were recorded at 145 kHz (ANABAT).

Monadjem *et al.* (2007a) also reported sexual dimorphism in the call with males emitting a higher call than females (males 145.0 ± 0.76 kHz, females 142.9 ± 1.39 kHz).

For 13 calls from Swaziland, Taylor *et al.* (2013b: 19) reported the following parameters: F_{max}: 142.9 ± 0.96 (140.4 - 144.1) kHz, F_{min}: 123.2 ± 6.40 (108.9 - 130.3) kHz, F_{knee}: 141.5 ± 0.95 (139.3 -

142.9) kHz, F_{char}: 142.0 ± 1.00 (139.8 - 143.5) kHz, duration: 4.2 ± 0.28 (3.7 - 4.7) ms. Monadjem *et al.* (2017c: 180) indicated that calls from this species could not be detected at a distance of more than 0.5 m, using an Anabat detector. They also reported the following values: F_{min}: 121.2 ± 5.88 (109.1 - 127.3) kHz, F_{knee}: 141.4 ± 1.97 (138.7 - 144.3) kHz, F_c: 141.7 ± 1.69 (139.5 - 144.0) kHz, duration: 4.8 ± 1.08 (3.7 - 6.7) ms.

Monadjem *et al.* (2011: 32) reported on 3 calls from *Hipposideros* cf. *caffer* from western Uganda: F_{min}: 144.11 ± 6.373 kHz, F_{max}: 151.73 ± 1.661 kHz, F_{char}: 146.88 ± 3.909 kHz, F_{knee}: 151.13 ± 1.650 kHz, duration: 2.8 ± 1.18 ms.

In the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded the following parameters: F_{char}: 143.00 ± 1.64 kHz, F_{max}: 143.28 ± 1.63 kHz, F_{min}: 124.99 ± 5.92 kHz, F_{knee}: 143.14 ± 1.64 kHz, duration: 7.41 ± 0.91 ms, with 12.29 ± 7.81 calls/sec. In southern KwaZulu-Natal and Eastern Cape (RSA), Moir (2020: 29) and Moir *et al.* (2021a: 371) recorded 49 calls from 2 bats: F_{max}: 148.64 ± 0.03 (148.62 - 148.67) kHz, F_{min}: 136.46 ± 3.04 (134.31 - 138.61) kHz, F_{char}: 145.93 ± 0.54 (145.55 - 146.31) kHz, F_{knee}: 148.1 ± 0.08 (148.04 - 148.16) kHz an duration: 5.06 ± 1.29 (4.15 - 5.97) ms. From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 27.90 ± 2.50 kHz, F_{max}: 33.20 ± 8.00 kHz, F_{min}: 25.70 ± 2.20 kHz.

In Kenya, Webala *et al.* (2019b: 15) reported echolocation data from nine localities, where F_{max} varied between 148.9 and 153.6 kHz for seven unsexed bats, 145.0 and 155.8 kHz for eight males, and 145.5 and 150.9 kHz for six females. The call durations varied respectively between 6.7 and 9.7, 5.4 and 10.6, and 5.0 and 9.7 ms.

For Ghana, Baldwin *et al.* (2021: 1395) reported the following mean and 95 % CI values for the four lineages they identified in *H. caffer* s.l.: A: 29 ♀♀: 151.4 (150.9 - 152.0) kHz, 12 ♂♂: 153.1 (152.3 - 153.6) kHz; B: 6 ♀♀: 124.3 (123.1 - 125.6) kHz, 11 ♂♂: 125.9 (125.4–126.4) kHz; C: 12 ♀♀: 135.8 (134.6 - 136.9) kHz, 10 ♂♂: 136.7 (134.5 - 138.9) kHz; D: 50 ♀♀: 131.9 (131.5 - 132.4) kHz, 59 ♂♂: 134.3 (133.6 - 134.9) kHz.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 50 calls of 6 bats: F_{max}: 155.64 ± 10.3 kHz, F_{min}: 146.03 ± 27.97 kHz, F_{knee}: 153.78 ± 11.95 kHz, F_{char}: 151.15 ± 10.77 kHz, slope: -1522.71 ± 23,168.41 OPS, duration: 2.26 ± 3.24 ms. Four calls from the Venatia mine recorded by Cory-Toussaint and Taylor (2022; Table S1) had a duration of 4.93 ± 0.38 ms, F_{min}: 101.99 ± 12.46 kHz, F_{max}: 143.50 ± 0.39 kHz, F_{knee}: 142.24 ± 1.34 kHz and F_{char}: 141.76 ± 0.93 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 14 *Hipposideros caffer* calls from the Kruger Park (RSA): F_{min}: 124.6 ± 15.9 (99.1 140.4) kHz, duration: 4.6 ± 1.3 (3.2 7.5) ms, F_{max}: 142.8 ± 3.1 (134.7 145.1) kHz, F_{knee}: 141.1 ± 3.4 (132.1 143.9) kHz, F_{char}: 139.2 ± 3.6 (130.6 142.7) kHz,

For 30 calls from a single *Hipposideros caffer* from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 138.78 ± 1.33 kHz, F_{knee}: 141.14 ± 1.63 kHz, F_{min}: 125.04 ± 9.51 kHz, F_{max}: 143.60 ± 1.19 kHz, Bandwidth: 18.55 ± 9.79 kHz, Duration: 6.21 ± 1.28 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 145.4 kHz and duration: 8 ms.

In Benin, the bat's call was categorized as a CF-FMd (Constant frequency - Frequency modulation downward) sonotype by Roemer *et al.* (2021: Suppl.).

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 143.00 ± 1.64 kHz, F_{max}: 143.28 ± 1.63 kHz and F_{min}: 124.99 ± 5.92 kHz.

For one call from Zambia Taylor-Boyd *et al.* (2025: 116) report the following values: Interpulse interval: 96.4 ms; F_{max}: 148.1 kHz; Start slope: -0.1 kHz/ms; End slope: -36.9 kHz/ms; Ledge duration: 0.4 ms.

For two caves in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data for *Hipposideros* cf. *caffer*: Boundou cave: 7 FF: F_{pmin}: 141 ± 4.2 kHz, F_{pmax}: 138.3 ± 13.2 kHz, F_{pmean}: 133.2 ± 11.6 kHz, F_{ppeak}: 135.7 ± 15 kHz, F_{flat}: 73.3 ± 9.7 kHz, F_{knee}: 72.7 ± 9.4 kHz, F_{mean}: 73 ± 9.7 kHz, Duration: 4.3 ± 1.1 ms; 8 MM: F_{pmin}: 136.1 ± 15.1 kHz, F_{pmax}: 149 ± 7.8 kHz, F_{pmean}: 139.6 ± 5.7 kHz, F_{ppeak}: 142.8 ± 9.1 kHz, F_{flat}: 79.7 ± 9.2 kHz, F_{knee}: 79.7 ± 9.4 kHz, F_{mean}: 79.7 ± 9.3 kHz, Duration: 4.2 ± 0.7 ms. Mont Belo cave: 3 FF: F_{pmin}: 133.5 ± 0 kHz, F_{pmax}: 145.2 ± 8.8 kHz, F_{pmean}: 134.9 ± 2.1 kHz, F_{ppeak}: 109.7 ± 47.2 kHz, F_{flat}: 55.3 ± 0.2 kHz, F_{knee}: 39.5 ± 27.8 kHz, F_{mean}: 56.6 ± 0.1 kHz, Duration: 6.2 ± 2.5 ms; 5 MM: F_{pmin}: 126.3 ± 23.4 kHz, F_{pmax}: 147.7 ± 3.6 kHz, F_{pmean}: 132.3 ± 20.7 kHz, F_{ppeak}: 134.5 ± 21.7 kHz, F_{flat}: 52.8 ± 3.9 kHz, F_{knee}: 53 ± 3.4 kHz, F_{mean}: 52.5 ± 4.3 kHz, Duration: 5.2 ± 3.6 ms.

MOLECULAR BIOLOGY:
Genetics
Vallo *et al.* (2009).

Budinski *et al.* (2024: 66) distinguished three mtDNA lineages in the Ghanaian *Hipposideros caffer/ruber* complex. They also differed significantly in their echolocation calls.

Karyotype
Đulić and Mutere (1974), Peterson and Nagorsen (1975), Rautenbach *et al.* (1993) and Porter *et al.* (2010) all reported 2*n* = 32, FN = 60, and BA = 30. Peterson and Nagorsen (1975) and Rautenbach *et al.* (1993) also agreed on an acrocentric Y chromosome. However, Đulić and Mutere (1974) reported a metacentric X chromosome, Peterson and Nagorsen (1975) reported a subtelocentric X chromosome, and Rautenbach *et al.* (1993) reported a submetacentric X chromosome. For Ethiopian bats, Tolera *et al.* (2021: 125) mention 2*n* = 32 and FN = 60 with all autosomal being metacentrics (except for four pairs of submetacentrics) and a medium sized acrocentric X chromosome and a very small acrocentric Y chromosome (In the abstract, however, they mention FN = 60/62).

HABITAT:
This species occurs in savanna, bushveld and coastal forest, and is usually associated with rivers and other water resources (Taylor, 2000: 140).

In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported that i Hipposideros cf. *caffer* was only found in disturbed habitats in the Afromontane forest biome, but this was based on one specimen only.

HABITS:
Happold and Happold (2023: 93) indicate that these bats can take off from the ground and can briefly hover and they turn by banking and by stalling-and-twisting.

ROOST:
Weber and Fahr (2006: 4) indicate that *H. caffer*, in Guinea, largely or exclusively depends on the availability of caves as day roosts. In the Durban area, Taylor *et al.* (1999: 70) reported it roosting in a tunnel of the Songweni Dam.

In Taita-Tawa county (Kenya), Jackson *et al.* (2023: 5) reported the use of one building as roost, which was not shared with other bat species.

DIET:
In their study of *H. caffer* bats from Skukuza (Kruger National Park, RSA), Dunning and Krüger (1996: 708) found that they overwhelmingly fed upon tympanate Lepidoptera, whereby relative numbers of noctuid, pyralid, and arctiid moths taken by the bats were proportional to the representation of these families in the general population of moths in the area. They also took much less moths belonging to the Geometridae, and arctiid moths that were able to produce clicking sounds.

Taylor *et al.* (2017b: 245, 252 - 254) reported the diet from bats from the Limpopo province (RSA) to include: one unidentified beetle and seven genera or species of moths belonging to four families: *Sena* sp., *Mimallo amilia DHJ01*, *Xenopseustis* sp., *Pericyma atrifusa*, *Tycomarptes* sp., *Maurilia arcuata*.

From Sudwala (RSA), Jacobs (2000: 201) reported the following proportions of preys: Lepidoptera (65.6 ± 46.3), Coleoptera (19.1 ± 40.0), Isoptera (14.5 ± 35.6), Hemiptera (0.5 ± 1.2) and unknown (0.3 ± 0.6).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention *H. caffer* as a possible prey of the Lanner falcon (*Falco biarmicus* Temminck, 1825), Peregrine falcon (*Falco peregrinus* Tunstall, 1771) and Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850).

Based on Fenton *et al.* (1981), Gual-Suárez and Medellín (2021: Suppl.) reported that this species accounted for 1.1 % of the food items taken by *Nycteris grandis*.

POPULATION:
Structure and Density
Are extremely gregarious and capable of forming huge colonies where there is adequate roosting space. In Nigeria, at Shagunu (Menzies, 1973), a colony of about 1,000 individuals inhabited a cave five meters wide, 1-2 m high and 10-15 m deep. In Gabon they live in colonies of 200-1,000 and one exceptionally large cave contained an estimated 500,000 bats (Brosset, 1966c; Happold, 1987).

Trend
2019: Decreasing (Richards *et al.*, 2020). 2008: Decreasing (Kock *et al.*, 2008c; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
For Uganda, Mutere (1968) reported pregnancies between December and March and births in April.

Bernard and Meester (1982: 131) studied the reproductive cycle in *H. caffer* in Natal and found that follicular development began in February, with copulation and ovulation taking place from late April onwards. The duration of the gestation period was about 220 days (zygote: 21 days, embryo: 123 days and foetus: 76 days). Parturition took place in December, after which there was a lactation period until January, during which the bats were anoestrus.

Pakenham (1984: 9, 31) mentioned pregnant females on Zanzibar in October and on Pemba in February.

Menzies (1973) claimed it can take up to two months before a blastocyst gets implanted, but this was revoked by Racey (1982: 83), who indicated that some of Menzies' illustrations proved otherwise.

In NE Gabon, Brosset and Saint Girons (1980: 226) found that *H. caffer* was reproducing with a boreal cycle (giving birth in March) in some caves, whereas in others they were following an austral cycle (giving birth in October). A line separating both groups seemed to run just north of the equator. For the northern group, mating occurred in November-December. In both groups, the single young was weaned after three and a half months. In the caves, where the females were following a boreal cycle, the males were in full spermatocytogenesis at the beginning of October. The spermiogenesis was starting in that period and this phase ended between 25 and 30 November. In the other caves, the males were in sexual rest between August and January.

Meinig (2010: 391) indicates that the gestation period differs according with latitude. In bats from South Africa it would last for seven months, whereas for tropical bats, it would take only four months.

MATING:
H. caffer has a polygnynous mating system (Webber *et al.*, 2017: Suppl.).

PARASITES:
Adam and Landau (1973a: 5) report that *H. caffer* was rarely infected by a protozoan parasite of the genus *Polychromophilus* (Haemoproteidae). The bats were also found to carry low numbers of the nycteribiid flies *Penicillidia fulvida* Bigot, 1885 and *Nycteribia schmidlii scotti* Falcoz, 1923, of which the prior was a major carrier of *Polychromophilus* sporozoites. Perkins and Schaer (2016: Suppl.) reported the presence of *Polychromophilus murinus* (Dionisi, 1899).

One of the 47 bats collected by Lutz *et al.* (2021: Suppl.) in Kenya carried *Polychromophilus* parasites.

Wünschmann *et al.* (2010: 178) refer to Boulard (1975), who reported the first case of renal coccidiosis in a bat (on *H. caffer* and *Rhinolophus* sp.) from Sierra Leone and the Congo, and caused by *Klossiella killicki* Boulard, 1975.

Teixeira and Camargo [in Lima *et al.* (2013: 13)] described *Trypanosoma livingstonei* from two bats from Mozambique: *Rhinolophus landeri* (type host) and *H. caffer* (additional host) [see also Barbosa *et al.*, 2016: 215 and Cai *et al.*, 2019: Suppl.]. This *Trypanosoma* species was also reported by Babyesiza *et al.* (2025: 4) from bats from the CAR and Uganda.
Austen and Barbosa (2021: 7) mention *Trypanosoma (Megatrypanum) leleupi* from the DRC, and (p. 151) *Gahrliepia grenieri* Taufflieb, 1965 and *Gahrliepia nana* (Oudemans, 1910) from South Africa.

Vercammen-Grandjean and Fain (1958: 10, 12, 14, 20, 22, 30, 33) described *Trombigastia (Ascoschongastoïdes) ascoschongastoïdes*, *Trombigastia (Ascoschongastoïdes) berghei*, *Trombigastia (Scapularia) scapularia*, *Trombigastia (Trombigastia) laarmani*, *Trombigastia (Trombigastia) vinckei*, *Trombigastia (Trombigastia) minor*, and *Myotrombicula bidentipalpis* (Acari: Trombiculidae) from 77 *H. caffer centralis* specimens collected at Irangi, DRC. Fain (1959d: 239) described *Psorergates (Psorergatoides) hipposideros* (Acari: Psoridatidae) from a *H. caffer centralis* captured in Kakontwe cave, Jadotville (= Likasi), DRC.

Reviewing African chiggers (Acari: Trombiculidae), Stekolnikov (2018a: 26; 2018b: 268) indicated that *Gahrliepia nana* (Oudemans, 1910) was described from *H. caffer* from Durban, where it was also the type host for *Austracarus polydiscum* (Oudemans, 1910) (Stekolnikov, 2018a: 43). Stekolnikov (2018a: 49, 50, 117, 119, 121, 154, 160, 179) also reported *Whartonia atracheata* Taufflieb and Mouchet, 1959, *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957, *Trombigastia ascoschoengastoides* Vercammen-Grandjean and Fain, 1958, *Trombigastia berghei* Vercammen-Grandjean and Fain, 1958, *Trombigastia laarmani* Vercammen-Grandjean and Fain, 1958, *Trombigastia minor* Vercammen-Grandjean and Fain, 1958, *Trombigastia scapularia* Vercammen-Grandjean and Fain, 1958, *Trombigastia vinckei* Vercammen-Grandjean and Fain, 1958, *Microtrombicula*

irangiensis Vercammen-Grandjean, 1965; *Microtrombicula minutissima* (Oudemans, 1910), and *Myotrombicula bidentipalpis* Vercammen-Grandjean and Fain, 1958.

Zajkowska *et al.* (2018: 145) mentions *Austracarus polydiscum* (Oudemans, 1910) from a *Hipposideros caffer* from South Africa.

Periglischrus moucheti Till, 1958 (Acari: Spinturnicidae) was reported by McKechnie *et al.* (2013: 112).

Cierocka *et al.* (2022: 10) mentioned the presence of *Psorergatoides hipposideros* Fain, 1959 (Acari: Psorergatidae) in wing membranes of *Hipposideros caffer* specimens from the DRC.

DIPTERA

Streblidae

Brachytarsina africana (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100), *Brachytarsina alluaudi* (Falcoz, 1923) in Botswana (Haeselbarth *et al.*, 1966: 101), Gabon (Obame-Nkoghe *et al.*, 2016: 5), *Brachytarsina longiarista* (Jobling, 1949) in Sierra Leone (Haeselbarth *et al.*, 1966: 101), *Raymondia alulata* Speiser, 1908 (Shapiro *et al.*, 2016: 253), *Raymondia aspera* Maa, 1968 in Mozambique (Shapiro *et al.*, 2016: 254), *Raymondia hardyi* in South Africa (Shapiro *et al.*, 2016: 254). *Raymondia huberi* Frauenfeld, 1856 may be associated but remains to be confirmed (Jobling, 1954 [in Haeselbarth *et al.* (1966: 102)]). *Raymondia huberi* Frauenfeld, 1856 group in Gabon (Obame-Nkoghe *et al.*, 2016: 5). *Raymondia intermedia* Jobling, 1936 (Shapiro *et al.*, 2016: 255). *Raymondia seminuda* Jobling, 1954 from Sierra Leone, the Congo, Tanzania, Zimbabwe, South Africa (Haeselbarth *et al.*, 1966: 103; Shapiro *et al.*, 2016: 255). *Raymondia setiloba* Jobling, 1954 from Katanga (Haeselbarth *et al.*, 1966: 104; Shapiro *et al.*, 2016: 256 [host as *H. caffer-ruber* complex]). *Raymondia waterstoni* Jobling, 1931 (Haeselbarth *et al.*, 1966: 104; Shapiro *et al.*, 2016: 256 [host as *H. caffer-ruber* complex]). *Raymondioides leleupi* Jobling, 1954 from Duékoué, Côte d'Ivoire (Haeselbarth *et al.*, 1966: 104). *Ascodipteron jonesi* Jobling, 1952 from Sudan, the Congo, Uganda and Tanzania (Haeselbarth *et al.*, 1966: 106). *Ascodipteron megastigmatos* Jobling, 1956 from Duékoué, Côte d'Ivoire (Haeselbarth *et al.*, 1966: 106). *Ascodipteron semirasum* Maa, 1965 from Botswana, but Maa (1965) doubts the correctness of the host-identification (Haeselbarth *et al.*, 1966: 106).
A *Brachytarsina allaudi* captured on a Gabonese "*H. caffer* complex" bat was carrying a *Polychromophilus melanipherus* blood parasite (Szentiványi *et al.*, 2019a: Suppl.).

Theodor (1968) described *Raymondia allisoni* Theodor, 1968 from a *H. caffer* from Ghana, but Shapiro *et al.* (2016: 253) indicate that the bat species is probably not correct and they assigned it to the *H. caffer-ruber* complex. Shapiro *et al.* (2016: 255) also mention *Raymondia pagodarum* Speiser, 1900 from the species complex in Uganda (but here the original host was referred to as *H. ruber*), as well as *Raymondia simplex* Jobling, 1955 (from the DRC). Shapiro *et al.* (2016: 256) furthermore mention an unnamed *Raymondia* species (sp. A) from Congo. Szentiványi *et al.* (2019a: Suppl.) indicated that a Gabonese "*H. caffer* complex" bat was parasitized by a *Raymondia huberi* group bat fly, which was carrying the blood parasite *Polychromophilus melanipherus*.
Lutz *et al.* (2021: Suppl.) collected *Raymondia* sp. from bats collected in Kenya.

Nycteribiidae

Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108; Duron *et al.*, 2014: 2108; Obame-Nkoghe *et al.*, 2016: 5, Júnior *et al.* (2020: Suppl.). *Nycteribia scissa sudanica* Theodor, 1957 from Ethiopia, the Sudan and the Congo (Haeselbarth *et al.*, 1966: 108). *Nycteribia integra* Theodor and Moscona, 1954 (Haeselbarth *et al.*, 1966: 109). *Nycteribia ovalis* Theodor, 1957 from Sierra Leone (Haeselbarth *et al.*, 1966: 110). *Nycteribia tecta* Theodor, 1957 from Zimbabwe and South Africa, but Haeselbarth *et al.* (1966: 110) suggests these may represent a distinct subspecies. *Penicillidia pachymela* Speiser, 1901, from Somalia, Sudan, Kenya, Tanzania, the Congo, Guinea and the Cameroon Mts (Haeselbarth *et al.*, 1966: 114), and Zambia (Blackwell, 1980: 145 - itself infected by the fungus *Arthrorhynchus nycteribiae* (Peyritsch) Thaxter) (see also de Groot *et al.*, 2020: Suppl.). *Eucampsipoda africana* Theodor, 1955 and *Penicilidia fulvida* (Bigot, 1885), found both on bats from the *H. caffer* complex in Gabon (Obame-Nkoghe *et al.*, 2016: 5).

Haelewaters *et al.* (2018: 794) also mention the Nycteribiid *Penicillidia pachymela* Speiser, 1900, which might be the host for the fungus *Arthrorhynchus nycteribiae* (Peyr.) Thaxt. This bat fly was also found by Lutz *et al.* (2021: Suppl.) on Kenyan bats, as well as *Nycteribia schmidlii*.

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Hipposideros caffer* or "*Hipposideros caffer*": *Nycteribia schmidlii scotti* Falcoz, 1923, *Penicillidia*

(Penicillidia) fulvida (Bigot, 1885), *Penicillidia (Penicillidia) pachymela* Speiser, 1901 and *Phthiridium tectum* (Theodor, 1957). *P. pachymela* was also found on *Hipposideros caffer* clade 1 from Nakuru National Park (Kenya).

CESTODA

Hymenolepididae

Jenzen and Howell (1983: 135) referred to Edungbola (1981), who mentioned *Vampirolepsis kerivoulaei* (Hübscher, 1937) from a bat from Nigeria

VIRUSES:

In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Hipposideros caffer*: Astroviruses, Coronaviruses and Paramyxoviruses.

Willoughby *et al.* (2017: Suppl.) report the following viruses: Chikungunya virus, Human coronavirus 229E, Rift Valley fever phlebovirus.

Astroviridae

10 of 57 bats from Mozambique, tested by Hoarau *et al.* (2018: 2) were positive for Astroviruses.

Coronaviridae - Coronaviruses

Alphacoronavirus

SARS-CoV (subgenus *Duvinacovirus*)

Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in five individuals from Limpopo Province, South Africa. None were tested positive (0/5), neither did nine individuals from Oriental Province, DRC (0/9). See also note under "viruses" for the genus as possiblitiy.

Pfefferle *et al.* (2009) report the detection of several alpha- and betacoronaviruses from *H.* cf. *caffer/ruber*. The alphacoronaviruses were related to the human coronavirus HCoV-229E, and Porcine coronaviruses.

Joffrin *et al.* (2020: 6) reported alphacoronaviruses from bats from Mozambique.

Betacoronavirus

Anthony *et al.* (2017b: Suppl.) mention the beta-coronaviruses Predict_CoV_43 and Predict_CoV_44 (see also Nziza *et al.*, 2019: 157).

Both alpha- and betacoranoviruses were reported from Zimbabwe by Bourgarel *et al.* (2018: 255).

Schmid *et al.* (2023: 1, 3) investigated coronavirus presence in four *Hipposideros* species in Ghana (*H. abae* and *H. caffer* B, C and D), and found *H. caffer* D to be the most heavily infected with CoV-229E and SARS-related CoV-2B. Meyer *et al.* (2024: 4) furthermore found *H. caffer* D specimens to be infected by CoV-2bBasal viruses.

Filoviridae

Marburgvirus

This virus was reported by Nieto-Rabiela *et al.* (2019: Suppl.).

Hepadnaviridae

Roundleaf bat HBV

Detected in the lung and liver of *H.* cf. *caffer/ruber* from Gabon.

Herpesviridae

Viruses belonging to the Gammaherpesvirinae were reported by Harima *et al.* (2023: 7) from Zambia.

Nairoviridae

Orthonairovirus

Only three of the 36 *H.* cf. *caffer* specimens from Gabon tested by Müller *et al.* (2016: 3) were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae

Drexler *et al.* (2012a: Suppl. Table S1) indicated that one of the 80 *H.* cf. *caffer* specimens they examined from Ghana tested positive for *Morbillivirus*. Of the 337 specimens from Gabon they identified as belonging to *H.* cf. *caffer/ruber*, two tested positive for *Morbillivirus* and one for *Rubulavirus*.

Mortlock *et al.* (2015: 1841) reported that two out of six examined South African *H. caffer* specimens tested positive for *Paramyxovirus* sequences.

Markotter *et al.* (2020: 6) reported the presence of Human orthorubulavirus-related viruses of the genus *Orthorubulavirus*.

In *H. caffer* bats from Zimbabwbe, Bourgarel *et al.* (2018: 255) identified viruses belonging to the genus *Jeilongvirus*.

Phenuiviridae

Phlebovirus

de Jong *et al.* (2011: 11) and Luis *et al.* (2013: suppl.) report the occurrence of Rift Valley fever virus (RVFV), either by virus isolation or molecular evidence (see Fagre and Kading, 2019: 5).

Reoviridae
Rotavirus
Simsek *et al.* (2021: 4) found *Rotavirus A* in *H. caffer* specimens from Gabon.

Togaviridae
Alphavirus
de Jong *et al.* (2011: 10) and Luis *et al.* (2013: suppl.) reported Chikungunya virus occurring on *H. caffer*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

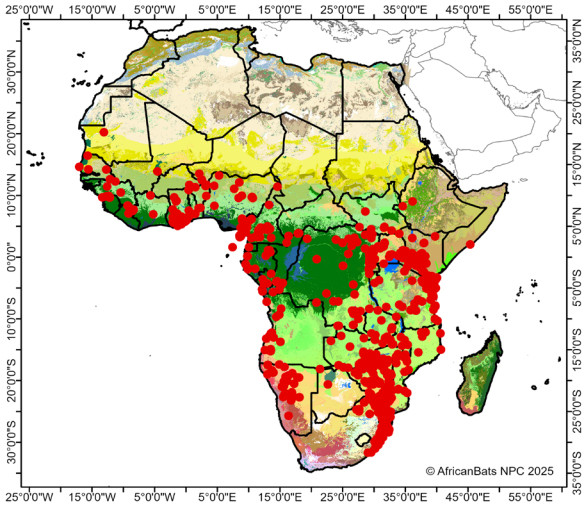

Figure 59. Distribution of *Hipposideros caffer*.

Hipposideros cf. centralis Andersen, 1906

*2016. *Hipposideros cf. centralis:* Kruskop, Benda, Vasenkov and Lavrenchenko, Lynx, 47: 56.

TAXONOMY:
Generally, this taxon is considered to be a subspecies of *H. ruber*, but Kruskop *et al.* (2016: 57) consider the large-sized NE African individuals from the *H. caffer* group to represent a separate species, although they indicate that a genetic comparison with specimens from Uganda and NE DRC is still required.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

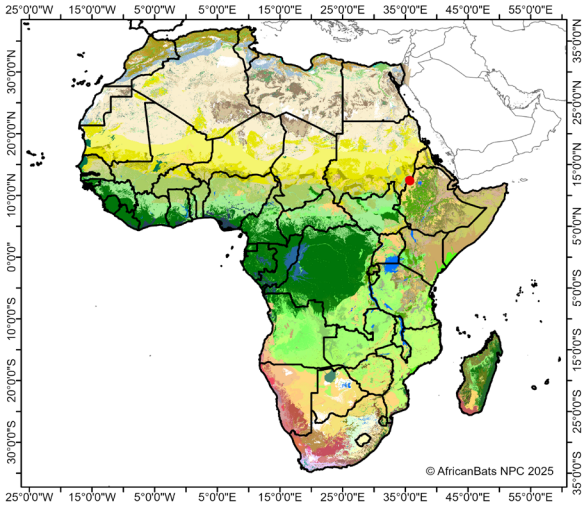

Figure 60. Distribution of *Hipposideros* cf. *centralis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

Hipposideros curtus G.M. Allen, 1921

*1921. *Hipposideros curtus* G.M. Allen, Rev. Zool. afr., 9 (2): 194. Publication date: December 1921. Type locality: Cameroon: Littoral province: on the Sanaga River: Sakbayeme [04 02 N 10 35 E]. [Goto Description]. Holotype: MCZ 19305: ad ♀, alcoholic (skull not removed). Collected by: Reverend George W. Schwab; collection date: 1920. See Helgen and McFadden (2001: 142). - Comments: The cover of issue 9 (2) mentions 15 October 1921 as publication date, but the actual date might be December 1921. (Current Combination).

1937. *Hipposideros sandersoni* Sanderson, Animal Treasure, 290 (fig), p 296. Publication date: September 1937. Type locality: Cameroon: near Mamfe [05 47 N 09 18 E]. - Comments: ("bluish-grey and small"). The type locality (Mamfe) was originally situated in Nigeria but is currently located in Cameroon.

TAXONOMY:
Simmons (2005: 370) placed it as part of the *bicolor* species group. Includes *sandersoni* (Hill, 1963a: 60).

The taxonomic relationship between *Hipposideros curtus* and *H. vittatus* is unclear and needs further investigation (Mickleburgh *et al.*, 2008dj; IUCN, 2009).

COMMON NAMES:
Czech: pavrápenec krátkoocasý. English: Short-tailed Leaf-nosed Bat, Short-tailed Roundleaf Bat. French: Phyllorine à queue courte. German: Kurzschwanz-Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN A2c ver 3.1 (2001)) based on a suspected past population size reduction of more than 50% over the past 15 years (three generations; generation length = 5 years; Pacifici *et al.*, 2013). The population decline is continuing due to loss of some previously known roosts,
confirmed occupancy of only one out of 35 caves assessed in Nigeria, the limited availability of undisturbed roosts, the species being limited by quality forest, and ongoing deforestation within its range significantly reducing the area of occupancy (Tanshi, 2020).

Assessment History
Global
2019: EN A2c ver 3.1 (2001) (Tanshi, 2020). 2008: VU B2ab(iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2008dj; IUCN, 2009). 2004: VU A3c ver 3.1 (2001) (Mickleburgh *et al.*, 2004da; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Tanshi (2020) report that this species is threatened by the continued degradation and clear-cutting of its forest habitat. Although protected, forests where the species is known in Nigeria are threatened by wildfire outbreaks arising from slash and burn agriculture in surrounding farm lands (I. Tanshi, *pers. obs* in Tanshi (2020)). Similarly, the species is heavily dependent on undisturbed caves and has been known to desert previously occupied caves due to disturbance or cave destruction (Mickleburgh *et al.*, 2008dj; IUCN, 2009; Tanshi, 2020). Some of the few previously known roosts have been lost (Happold, 2013ar). A search of 35 cave-like boulder roosts in Afi Mountain Wildlife Sanctuary and Cross River National Park (both in Nigeria), yielded just one roosting group of *H. curtus*, the lack of additional groups is thought to be due to the nature and intensity of fruit bat hunting that currently occurs in these parks (Tanshi, 2020).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dj) [in IUCN (2009)] report that this species has not been recorded from any protected areas. There is an urgent need to protect any important roosting site, and to maintain suitable foraging habitat in the vicinity of these. Further field surveys are needed to locate additional populations of this species, and to determine if the species is present in Nigeria.

Conservation Actions
Tanshi (2020) suggests the following five actions:1) Protection of the single known roost of the species in Cross River National Park is now urgent. Cave roost protection depends on preventing all forms of disturbance of this last known roost including ending fruit bat hunting in Afi Mountain Wildlife Sanctuary and Cross River National Park. 2) Elimination of wildfire outbreaks in both AMWS and CRNP is crucial for maintaining good foraging grounds for the species. 3) Investigation of the human social dimension to cave roost disturbance and destruction. 4) Extensive surveys and roost searches across the species range is essential for expanding the reach of conservation efforts and understanding its conservation ecology. 5) Confirm the status of other previously known cave roosts.

Research needed
Tanshi (2020) suggest the following research is need: - Population size, distribution and trends: Intensive understory forest surveys and cave searches across previously known and other localities (for example those identified in distribution niche models) are essential for identification of additional populations and roosts. More surveys, as well as additional ecological and biogeographical studies, are needed to identify potential areas for conservation of this species.

GENERAL DISTRIBUTION:
Hipposideros curtus is restricted to southwestern Cameroon and Equatorial Guinea (both Bioko island and Rio Muni). The species might be

present in Nigeria; however, this needs confirmation. It is a lowland species found at elevations from sea-level to 500 m.

Native: Cameroon (Eisentraut, 1973); Equatorial Guinea (Bioko) (Juste B. and Ibáñez, 1994b); Nigeria (Tanshi *et al.*, 2022a: 317).

ECHOLOCATION:
From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 79 calls of 2 bats: F_{peak}: 97.0 ± 4.5 (91.7 - 100.9) kHz, F_{min}: 90.0 ± 4.6 (84.6 - 95.1) kHz, F_{max}: 98.2 ± 5.0 (93.1 - 102.6) kHz, duration: 11.0 ± 0.4 (9.3 - 11.4) ms.

HABITAT:
Grunwald *et al.* (2025: 294) indicated that *Hipposideros curtus* is a moist lowland species relying on undisturbed caves.

ROOST:
Tanshi *et al.* (2022a: 330) mentioned that potential roosts include cave-like boulder systems. One in the Cross River National Park was occupied during three consecutive years, and consisted of a single chamber about 0.5 × 2 × 4 m (H × W × L) with an entrance height of ca. 30 cm, perched on ca. 3 m high boulder and ventilated with a roof exit. The roost was occupied by 10 to 15 animals, probably of mixed sex.

POPULATION:
Structure and Density
This is a rarely encountered species that had not been captured or observed in the wild since the 1970s until recent surveys conducted in Nigeria (I. Tanshi, *unpub data* in Tanshi (2020)). It appears to occur in small and fragmented populations with only a few (ca 10-15) individuals sharing a roost. Its population is considered to be decreasing due to deforestation, habitat degradation and cave roost disturbance and destruction (I. Tanshi, pers. obs in Tanshi (2020)).

Trend
2019: Decreasing (Tanshi, 2020). 2008: Decreasing (Mickleburgh *et al.*, 2008dj; IUCN, 2009).

PARASITES:
PROTOZOA
Tsague *et al.* (2024: Suppl.) found 13 Cameroonian bats to be infected by *Trypanosoma* sp.

VIRUSES:
Coronaviridae
Gonzalez and Banerjee (2022: 8) reported HCoV-229E from this bat.

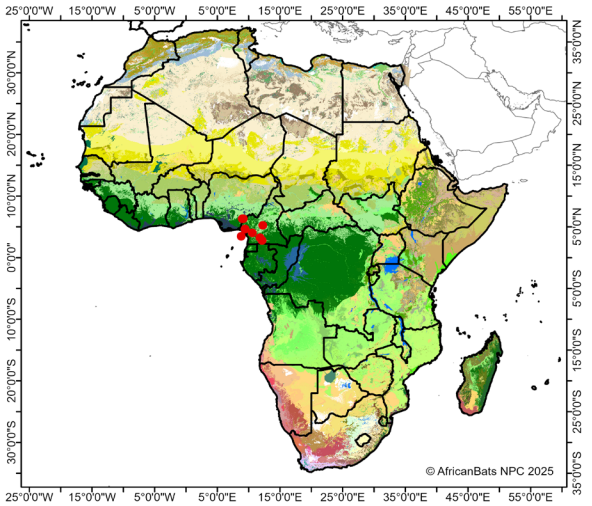

Figure 61. Distribution of *Hipposideros curtus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Equatorial Guinea, Nigeria.

Hipposideros fuliginosus (Temminck, 1853)

*1853. *Phyllorrhina fuliginosa* Temminck, Esquisses zoologiques sur la Côte de Guiné. 1e partie, les Mammifères, 77. Publication date: 1853. Type locality: Ghana: "Ghana". [Goto Description]. Holotype: RMNH MAM.35972: ad ♀, mounted skin and skull. Collected by: Hendrik Severinus Pel; collection date: 1841. - Comments: Temminck (1853: 78), Allen (1939a: 81) and Grubb *et al.* (1998: 79) mentioned the type locality as "La côte de Guiné", whereas Jentink (1888b: 167) gave it as 'Côte d'Or, Pays des Aschantes.'). Temminck (1853: viii) also indicated that M. Pel went to the Ashanti county and visited its capital Coumassie [=Kumasi]. However, on page 88 (discussing *Felis celidogaster*), Temminck mentions: "Patrie. La côte de Guiné, où on la voit rôder de temps en temps; mais elle est plus abondante dans le pays des Aschantes." This indicates that both are different places. On page 135 (*Sciurus leucostigma*) he mentions "Patrie. La Guiné, sur les bords de la rivière Boutry et·dans les forêts de la côte jusqu'aux confins du pays des Aschantes." The Butre river is situated in southwestern Ghana, which suggests that the type locality for *fuliginosus* is on the coast of Ghana (probably somewhere between Butre and Kumasi).
1895. *Phyllorhina fuliginosa:* Bocage, J. Sci. mat. phys. nat., ser 2, 4 (8): 4. Publication date: December 1895. (Name Combination).
2014. *Hipposideros fuliganosas:* Chawana, Alagaili, Patzke, Spocter, Mohammed, Kaswera, Gilissen, Bennett, Ihunwo and Manger, Neuroscience, 277: 725. Publication date: 26 September 2014. (Lapsus).
2016. *Hipposideros fulginosus:* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 42. Publication date: 9 May 2016. (Lapsus).
? *Hipposideros fuliginosus:* (Current Combination).

TAXONOMY:
Simmons (2005: 371) as part of the *bicolor* species group. Patterson *et al.* (2020: 121) include it in the *ruber* subgroup of the *bicolor* group.

Populations from central Africa may well represent a different species from those in western central (west of about 15°) and the Ethiopian records represent another, possibly undescribed, species (Mickleburgh *et al.*, 2008da in IUCN, 2009) based on J. Fahr *pers. comm.*). Herkt *et al.* (2017: Appendix S9) indicate that genetic tests evaluating the distinct species status are still lacking, and no clear major geographic gap between both putative species ranges can be discerned.

COMMON NAMES:
Czech: pavrápenec sazový. English: Sooty Leaf-nosed Bat, Sooty Roundleaf Bat, Dusky leaf-nosed bat. French: Phyllorine sombre, Phyllorine fuligineuse, Phyllorhine fuligineux. German: Temmincks Rundblattnase, Rußfarbene Rundblattnase.

SIMILAR SPECIES:
Grunwald *et al.* (2025: 295) indicate that *Hipposideros fuliginosus* is difficult to distinguish morphologically from *H. ruber*, but the latter is slightly smaller (Fa: 52.0 ± 1.5 mm versus 56.92 ± 0.82 mm)

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008da; IUCN, 2009; Monadjem *et al.*, 2017bn).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bn). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008da; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004cp; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The major threat to this species is deforestation or degradation of its habitat. Presumably this is largely a result of logging operations and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008da; IUCN, 2009; Monadjem *et al.*, 2017bn).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008da) [in IUCN (2009)] and Monadjem *et al.* (2017bn) report that although there are no specific conservation measures in place for this bat, it is presumably present in several protected areas. There is a specific need to maintain large trees as roosting sites for the species. Further studies are needed into the taxonomy, distribution, natural history and possible additional threats to this species.

GENERAL DISTRIBUTION:
Hipposideros fuliginosus has been recorded in West Africa and Central Africa. It ranges from Guinea and Sierra Leone in the west, and has been recorded from Liberia, Côte d'Ivoire, Ghana and Nigeria. In Central Africa it is distributed in southern Cameroon, with scattered records from Gabon, Central African Republic, northern parts of Democratic Republic of the Congo and western Uganda. It is generally a lowland species, being recorded up to 500 m asl.

Native: Cameroon (Eisentraut, 1973); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 538); Côte d'Ivoire; Gabon; Ghana (Decher and Fahr, 2007: 16); Guinea (Fahr and Ebigbo, 2003: 128; Decher *et al.*, 2016: 265); Guinea-Bissau (Rainho and Ranco, 2001: 58); Liberia (Koopman, 1989b; Koopman *et al.*, 1995); Nigeria; Sierra Leone; Uganda.

Presence uncertain: Central African Republic; Congo; Equatorial Guinea.

DETAILED MORPHOLOGY:
Brain
Adult hippocampal neurogenesis was studied by Chawana R. *et al.* (2016: 1551).

ECHOLOCATION:
In Guinea Fahr and Ebigbo (2003) reported the frequency of the CF-component at 122.5 ± 1.3 (120.0 - 123.3) kHz.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 61 calls of 2 bats: F_{peak}: 109.9 ± 0.2 (109.7 - 110.1) kHz, F_{min}: 92.6 ± 6.0 (86.7 - 98.8) kHz, F_{max}: 111.1 ± 0.1 (111.0 - 111.2) kHz, duration: 6.0 ± 1.6 (2.8 - 9.2) ms.

HABITAT:
In their study on the influence of African cocoa farms, Ferreira *et al.* (2023: 1) found that this species was only present in high shade farms.

POPULATION:
Structure and Density
There is little information on its overall abundance. It is usually found in small groups, but sometimes in congregations of up two hundred bats (Mickleburgh *et al.*, 2008da; IUCN, 2009; Monadjem *et al.*, 2017bn).

Trend
2016: Decreasing (Monadjem *et al.*, 2017bn).
2008: Decreasing (Mickleburgh *et al.*, 2008da; IUCN, 2009).

PARASITES:
PROTOZOA
Tsague *et al.* (2024: Suppl.) found multiple Cameroonian bats being infected by either *Trypanosoma* cf. *livingstonei* or another unidentified (possibly new) *Trypanosoma* sp.

DIPTERA
Streblidae
Raymondia huberi huberi Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254). *Raymondia seminuda* Jobling, 1954 in southern Nigeria (Haeselbarth *et al.*, 1966: 103).

VIRUSES:
Circoviridae
Vidovszky *et al.* (2023: Suppl.) found Human associated cyclovirus 2 in bats from the DRC.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that three out of 21 examined *H. fuliginosus* specimens from the DRC tested positive for *Paramyxovirus* sequences.

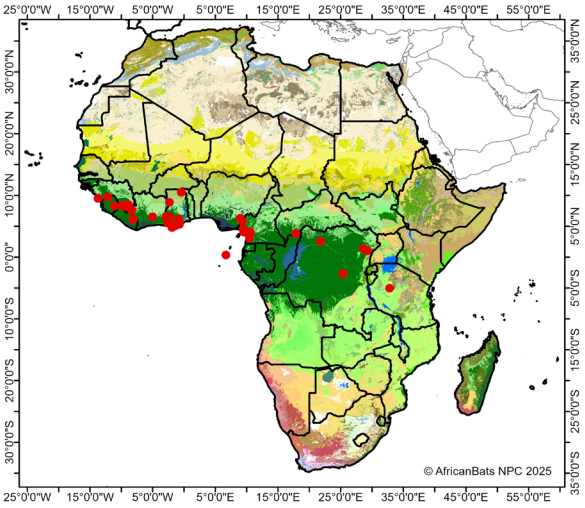

Figure 62. Distribution of *Hipposideros fuliginosus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Guinea, Liberia, Nigeria, São Tomé and Príncipe, Senegal, Sierra Leone, Tanzania.

Hipposideros jonesi Hayman, 1947

*1947. *Hipposideros jonesi* Hayman, Ann. Mag. nat. Hist., ser 11, 14 (109): 71, fig 1. Publication date: 19 November 1947. Type locality: Sierra Leone: Makeni [08 57 N 12 02 W]. [Goto Description]. Holotype: NHMUK 1947.629: ad ♀, skull and alcoholic. Collected by: Theo Simpson Jones; collection date: 12 December 1946; original number: 42. - Etymology: In honour of Mr. T.S. Jones, the collector of the type specimen. (Current Combination).

TAXONOMY:
Simmons (2005: 373) as part of the *bicolor* species group. Patterson *et al.* (2020: 121) place it in the *speoris* group.

COMMON NAMES:
Czech: pavrápenec Jonesův. English: Jones' Leaf-nosed Bat, Jones' Roundleaf Bat, Jones's Roundleaf Bat, Western Africa leaf-nosed bat. French: Phyllorine de Jones, Phyllorine d'Afrique occidentale. German: Jones' Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened (NT ver 3.1 (2001)) as its global population is suspected to have declined by ca 25% over the past 10 years (two generations) and will continue to decline at a similar rate over the next 5 years (one generation; generation length = 5 years, Pacifici *et al.* (2013)) making it close to qualifying under criterion A4c. Its extent of occurrence (EOO), area of occupancy (AOO), and habitat are projected to continue to decline, especially its cave and mine roost habitats, due to continuing threats from cave/mine losses due to mining and disturbance,

and forest loss and degradation (Cooper-Bohannon *et al.*, 2020b).

Assessment History
Global
2019: NT A2c ver 3.1 (2001) (Cooper-Bohannon *et al.*, 2020b). 2008: NT ver 3.1 (2001) Mickleburgh *et al.*, 2008au; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004br; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is generally threatened by the disturbance of roosting caves and might additionally be threatened by subsistence hunting although this needs to be confirmed (Mickleburgh *et al.*, 2008au; IUCN, 2009; Fahr, 2013n). Nkrumah *et al.* (2018: 755) indicate that *H. jonesi* is a generalist in the Kwamang agro-ecosystem of Ghana, and as such, might not be sensitive to increased disturbance. However, they also mention that their results need to be cautiously interpreted. While Cooper-Bohannon *et al.* (2020b) suggests that species is threatened by past and continued deforestation of its foraging habitats, largely through logging and mining operations and conversion of land to agricultural use.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008au) [in IUCN (2009)] and Cooper-Bohannon *et al.* (2020b) report that there appear to be no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. There is a need to conserve important roosts for this species. Additional studies are needed into the distribution, natural history (population size and trends) and threats to this species.

GENERAL DISTRIBUTION:
Hipposideros jonesi is a West African endemic, closely associated with caves. It has been recorded from Sierra Leone and Guinea to Mali, Burkina Faso, Ghana and Nigeria. It is found between sea level and 1,400 m asl.

Native: Benin (Benda *et al.*, 2023a: 27),;Burkina Faso (Kangoyé *et al.*, 2015a: 608); Côte d'Ivoire; Ghana; Guinea (Decher *et al.*, 2016: 265); Liberia (Fahr, 2007a: 104); Mali; Nigeria (Happold, 1987); Sierra Leone (Hayman, 1947d; Grubb *et al.*, 1998).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Young (1975: 76) indicates that two distinct colour phases can be found: rufous (orange) and grey.

MOLECULAR BIOLOGY:
Karyotype
Koubínová *et al.* (2010b) report for on a single male from Senegal, 2*n*= 32, Fna= 60 and FN= 64, these included 30 biarmed autosomes, including four metacentric, eight submetacentric and three subtelocentric, eight submetacentric and three subtelocentric pairs. A secondary constriction situated near the centromere was observed in one pair of the medium-sized submetacentric autosomes (approximately the 9th largest pair). The X chromosome was identified as a large metacentric element, the Y chromosome as a medium submetacentric.

HABITS:
Lawer and Darkoh (2016: 429) found that this bat's activity declined with increasing lunar illumination, indicating that bright moonlight suppresses the nocturnal activities of both insectivorous bats and insects. They also found a negative association between wind speed and overal insectivorour bat activity (p. 430).

ROOST:
Weber and Fahr (2006: 4) indicate that in Guinea *H. jonesi* largely or exclusively depends on the availability of caves as day roosts.

DIET:
In the Kwamang agro-ecosystem in Ghana, E.K. Badu (in Nkrumah *et al.*, 2018: 755) found that the diet of *H. jonesi* consists of nearly 100 % Lepidoptera.

POPULATION:
Structure and Density
This species forms roosts of only a few animals, usually in the dozens rather than hundreds (Mickleburgh *et al.*, 2008au; IUCN, 2009; Cooper-Bohannon *et al.*, 2020b). There is a pronounced geographic morphological variation among subpopulations, suggesting that there may be little movement of animals between populations (Mickleburgh *et al.*, 2008au; IUCN, 2009; Cooper-Bohannon *et al.*, 2020b).

Trend
2019: Decreasing (Cooper-Bohannon *et al.*, 2020b). 2008: Decreasing (Mickleburgh *et al.*, 2008au; IUCN, 2009).

VIRUSES:

Botourmiaviridae

Ourmiavirus was found by Hermida Lorenzo *et al.* (2021: 6) in bats from Guinea.

Circoviridae

Viruses of this family were reported from Guinean bats by Hermida Lorenzo *et al.* (2021: 6).

Coronaviridae

Meyer *et al.* (2024: 4) reported that Ghanaian bats were infected by Cov 2b viruses.

Flaviviridae

From Guinean bats, Hermida Lorenzo *et al.* (2021: 6) reported the presence of Pestivirus.

Paramyxoviridae

Hermida Lorenzo *et al.* (2021: 6) reported Lophuromys jeilongvirus 1, Bat paramyxovirus and Rhinolophus ferrumequinum paramyxovirus from Guinean bats.

Parvoviridae

Unclassified parvoviridae were reported by Hermida Lorenzo *et al.* (2021: 6) from Guinea.

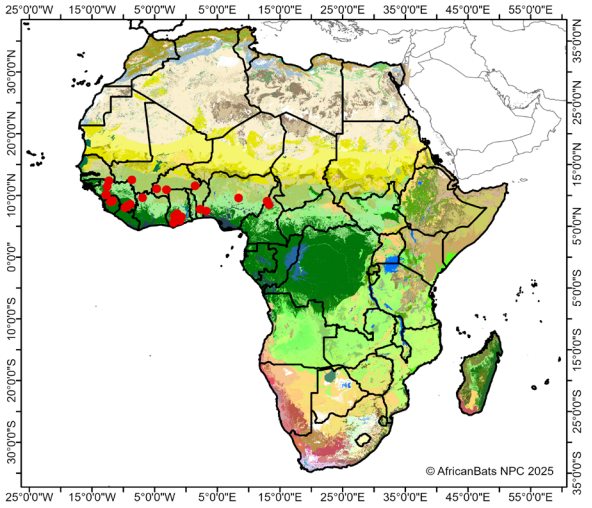

Figure 63. Distribution of *Hipposideros jonesi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Guinea, Liberia, Mali, Nigeria, Senegal, Sierra Leone.

†***Hipposideros kaumbului*** Wesselman, 1984

*1984. *Hipposideros kaumbului* Wesselman, Contributions to vertebrate evolution, 7: 59. Type locality: Ethiopia: Locality 28, lower Member S, Shungura Formation. - Etymology: This taxon is named in honour of John Kaumbulu Kimau, a Wakamba tribesman from Kikoko, Kenya, who worked with Henry ("Hank") Barnard Wesselman as his field assistant following the 1972 and 1973 field seasons and helped with the task of handpicking almost 20 tons of screenwashed residues (Wesselman, 1984: 59). (Current Combination).

TAXONOMY:
Wesselman (1984: 59) suggests that this taxon may be ancestral to "*Hipposideros commersoni*" (= *Macronycteris commersoni*. Rakotoarivelo *et al.* (2019: 14), however, indicate that many different taxa included in the *commersoni*) group are morphologically very similar to each other, yet genetically quite distinct

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late Pliocene (2.08 Mya) (Wesselman, 1984: 59; Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Native: Ethiopia, Kenya.

Hipposideros lamottei Brosset, 1985

*1985. *Hipposideros lamottei* Brosset, Mammalia, 48 (4): 548 (for 1984). Publication date: 1985. Type locality: Guinea: Mount Nimba: Pierré Richaud [07 41 N 08 22 W]. [Goto Description]. Holotype: MNHN ZM-MO-1984-487: ad ♂. Collected by: André Brosset; collection date: December 1983. Paratype: MHNG |TS478|: ad ♂. Collected by: André Brosset; collection date: December 1983. Paratype: MNHN ZM-MO-1984-488: ad ♂. Collected by: André Brosset; collection date: December 1983. Paratype: MNHN ZM-MO-1984-489: ad ♂. Collected by: André Brosset; collection date: December 1983. (Current Combination).

2020. *Hipposideros cf. lamottei:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicate that this is the same form as the *Hipposideros ruber* B1 lineage mentioned by Monadjem *et al.* (2013b). (Name Combination).

TAXONOMY:
Simmons (2005: 373) *bicolor* species group. Patterson *et al.* (2020: 121) place it in the *ruber* subgroup of the *bicolor group*.

Distinction from *H. ruber* is not entirely clear (Koopman, 1993a: 173; Koopman *et al.*, 1995; Simmons, 2005: 373). Monadjem *et al.* (2013b: 341) state that, morphologically, *H. lamottei* falls within the *caffer/ruber* group.

Baldwin *et al.* (2021: 1399) indicate that the West African forest specimens identified as "cf. *lamottei*" by Patterson *et al.* (2020; 138) should rather be assigned another name as *H. lamottei* lives in montane savannah habitats at Mount Nimba.

Benda *et al.* (2023a: 40) mentioned that the Beninese specimens they identified as "cf. *lamottei*" were previously identified as the B1 sublineage of *Hipposideros ruber* or *Hipposideros* aff. *ruber*, and should probably be assigned to a separate, undescribed species or a morphological transition between *Hipposideros ruber* s.l. and *Hipposideros lamottei*.

COMMON NAMES:
Czech: pavrápenec nimbánský. English: Lamotte's Leaf-nosed Bat, Lamotte's Roundleaf Bat, Mount Nimba Leaf-nosed Bat. French: Phyllorine de Lamotte, Phyllorine du Mont Nimba. German: Mount Nimba-Rundblattnase, Lamottes Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Critically Endangered (CE B1ab(i,iii,v) ver 3.1 (2001)) as its extent of occurrence (EOO) is smaller than 100 km^2 (Monadjem and Cooper-Bohannon, 2020). The species is only known from a single location (Mount Nimba) where there are only four (4) known roosts, all in abandoned mines within an active mine site (Monadjem and Cooper-Bohannon, 2020). There is significant risk of continuing decline in the extent and quality of its roosts in the abandoned mines and foraging habitat due to deforestation (Mickleburgh *et al.*, 2008av; IUCN, 2009; Monadjem and Cooper-Bohannon, 2020).

Kouame *et al.* (2012: 2748) indicate that *H. lamottei* is a highly threatened species, which only occurs in one single KBA [= Key Biodiversity Area] in the Upper Guinea Forest: Mount Nimba. While Collen *et al.* (2011: 2616) rank it on position 62 (as only African mainland Chiropteran) out of 100 mammal species requiring urgent conservation attention.

Assessment History
Global
2019: CE B1ab(i,iii,v) ver 3.1 (2001) (Monadjem and Cooper-Bohannon, 2020). 2008: CE B1ab(I,ii,iii,iv,v)+2ab(I,ii,iii,iv,v) ver 3.1 (2001) (Mickleburgh *et al.*, 2008av; IUCN, 2009). 2004: CR B1ab(iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2004bs; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is believed to be highly threatened because of extensive iron ore mining activities underway, and planned, within its limited range on Mount Nimba. It is probably additionally threatened by general deforestation in parts of its range. Indiscriminate subsistence hunting of bats for food occurs in caves on Mount Nimba and likely impacts this species (Mickleburgh *et al.*, 2008av; IUCN, 2009; Monadjem and Cooper-Bohannon, 2020).

CONSERVATION ACTIONS:
Although it is present within the Mount Nimba Strict Nature Reserve World Heritage Site (Mickleburgh *et al.* (2008av) [in IUCN (2009)]), its only known roosts are within an active mining concession (Monadjem and Cooper-Bohannon, 2020). There is a need to enforce the protection of this area. Additional surveys are needed to learn more about the distribution, population size and trend, ecology, and threats to this species (Mickleburgh *et al.*, 2008av) [in IUCN (2009)]; Monadjem and Cooper-Bohannon, 2020). Given the extensive mining, logging and agricultural expansion in the area it is also recommended to engage key stakeholders and work with local communities and government authorities given they have an endemic rare species in the area. Specific research is needed to understand disturbance and if protection or gating of a mine is viable (Monadjem and Cooper-Bohannon, 2020).

GENERAL DISTRIBUTION:
Known only from Mt. Nimba on Guinea-Liberia border, but probably more widespread. However, Fahr (2007a: 104) and Decher and Fahr (2007: 5) indicate that specimens from Liberia, Ghana, Sierra Leone and Cameroon (mentioned by Koopman *et al.*, 1995 and Grubb *et al.*, 1998) were re-identified as belonging to *H. caffer*. They restrict the distribution of *lamottei* to the Guinean side of Mt. Nimba. It has been recorded between 500 and 1,400 m asl.

Benda *et al.* (2023a: 27) report *Hipposideros* cf. *lamottei* from Benin.

Native: Guinea (Brosset, 1985; Denys *et al.*, 2013: 284).

ECHOLOCATION:
Monadjem *et al.* (2013b: 351) report a F_{max} of 119.0 (118 - 120) kHz for two specimens from Mount Nimba.

HABITAT:
Chakravarty *et al.* (2024: 7) considers this species to be a "highland dwelling species".

POPULATION:
Structure and Density
The global population is limited to one location within an active mining concession and is assumed to be declining (Monadjem and Cooper-Bohannon, 2020). There are only 1-2 dozen museum specimens are currently known, all from the Guinean side of Mount Nimba. However, counts of bats exiting the four known roost sites (mine adits) estimated between 50 and 200 individuals in each roost, at most, a total 400 individuals were present during these counts (A. Monadjem and A. Dower, *unpub data* in Monadjem and Cooper-Bohannon (2020)). Whether other roosting populations exist and where these may be located, are unknown. Certainly this species existed before mining commenced and therefore must have used some other natural roosting sites (Monadjem and Cooper-Bohannon, 2020).

Trend
2019: Decreasing (Monadjem and Cooper-Bohannon, 2020). 2008: Decreasing (Mickleburgh *et al.*, 2008av; IUCN, 2009).

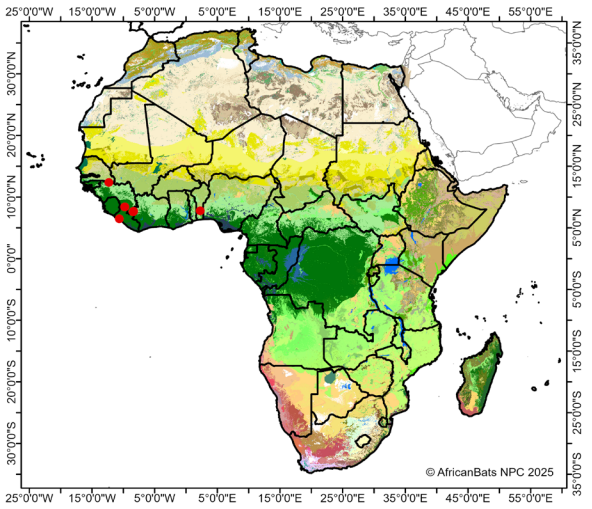

Figure 64. Distribution of *Hipposideros lamottei*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Guinea, Liberia, Senegal.

Hipposideros marisae Aellen, 1954

*1954. *Hipposideros marisae* Aellen, Rev. suisse Zool., 61 (24): 474. Type locality: Côte d'Ivoire: Duékoué: White Leopard Rock. [Goto Description]. Holotype: [Unknown] |TS82|: ad ♂. Collection date: 13 May 1953; original number: 400. See Aellen (1954: 474). Holotype: MHNG 924.090: ♂, alcoholic (skull not removed). Collected by: Dr. Villy Aellen; collection date: 13 May 1953; original number: 400. - Comments: Type locality original: roche de la Panthère Blanche. - Etymology: In honour of Mrs. Aellen (Aellen, 1954: 474). (Current Combination).

TAXONOMY:
Simmons (2005: 374) as part of the *bicolor* species group. Monadjem *et al.* (2013b: 346) indicate that *H. marisae* is a sistergroup to *H. jonesi*, which Patterson *et al.* (2020: 121) confirm by placing both in the *speoris* group.

COMMON NAMES:
Czech: pavrápenec Aellenův. English: Marisa's Leaf-nosed Bat, Aellen's Leaf-nosed Bat, Aellen's Roundleaf Bat. French: Phyllorine d'Aellen. German: Marisas Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (A4c ver 3.1 (2001)) as its global population is suspected to have declined by >30% over the past 10 years (two generations) and is expected to continue declining at the same rate over the next 5 years (one generation; generation length = 5 years, Pacifici *et al.*, 2013). The species' extent of occurrence (EOO), area of occupancy (AOO), and habitat is projected to continue to decline due to continuing threats from forest loss and degradation and cave/mine loss, degradation, and disturbance (Cooper-Bohannon *et al.*, 2020c).

Assessment History
Global
2019: VU A4c ver 3.1 (2001) (Cooper-Bohannon *et al.*, 2020c). 2008: VU B2b(ii,iii,iv,v) ver 3.1 (2001) (Mickleburgh *et al.*, 2008aw; IUCN, 2009). 2004: EN A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004bt; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is threatened by general deforestation, mining operations on Mount Nimba, the disturbance of roosting caves (Mickleburgh *et al.*, 2008aw; IUCN, 2009), and the loss of old mine adits to ongoing mining operations. Due to its small size it is unlikely to harvested for food. Disturbance at roost sites are also likely to be significant threats to this species (Fahr, 2013p). This species also occurs in areas of high population density, so persecution and human-bat conflict likely to be a significant threat (Cooper-Bohannon *et al.*, 2020c).

CONSERVATION ACTIONS:
This species is endemic to Africa, and found within the Mount Nimba Strict Nature Reserve World Heritage Site (Mickleburgh *et al.*, 2008aw) in IUCN (2009)] in Guinea as well as the East Nimba Nature Reserve in Liberia, and Gola Forest in Sierra Leone. Cooper-Bohannon *et al.* (2020c) recommended that there is a need to protect important roost sites and areas of suitable forest habitat. Further studies are needed into the distribution, population size and trend, ecology and significant threats to this species. Given the extensive mining, logging and agricultural expansion and potential cave disturbance in the area it is also recommended to engage key stakeholders and work with local communities and government authorities given they have an endemic rare species in the area. Specific research is needed to understand disturbance and if protection or gating of important maternity roosts is viable.

GENERAL DISTRIBUTION:
This West African species has been recorded from seven localities in Guinea, Liberia (central and western uplands), and Côte d'Ivoire, and two localities in Sierra Leone. It may range into Ghana, although there is no record from this country (Grubb *et al.*, 1998). It is a lowland species recorded between sea level and 650 m asl.

Native: Côte d'Ivoire (Aellen, 1954); Guinea; Liberia (Kuhn, 1965; Hill, 1982a; Wolton *et al.*, 1982; Koopman *et al.*, 1995; Monadjem and Fahr, 2007: 53); Sierra Leone (Weber *et al.*, 2019: 22 - first record). Presence uncertain: Ghana.

ECHOLOCATION:
Monadjem *et al.* (2013b: 351) report F_{max} to be 146.0 kHz at Mount Nimba.

In Sierra Leone, Weber *et al.* (2019: 21) recorded two females calling at 142.5 (141.0 - 144.0) kHz and two males at 146.5 (146.0 - 147.0) kHz.

HABITAT:
Weber *et al.* (2019: 22) indicate that this is an extremely rare species, which might depend on suitable caves as day roost and forest habitats.

POPULATION:
Structure and Density
It is generally considered to be a very rare species (Mickleburgh *et al.*, 2008aw; IUCN, 2009). Monadjem *et al.* (2013b: 342), occurring in low numbers. For example, at Mount Nimba, an old mine adit was occupied by five adult individuals, while in a neighbouring adit there were a further two individuals (Monadjem *et al.*, 2016y). The global population is suspected to have declined in the past and will continue to decline due to loss and degradation of the species habitat, especially the loss of cave and mine roosts (Cooper-Bohannon *et al.*, 2020c).

Trend
2019: Decreasing (Cooper-Bohannon *et al.*, 2020c). 2008: Decreasing (Mickleburgh *et al.*, 2008aw; IUCN, 2009).

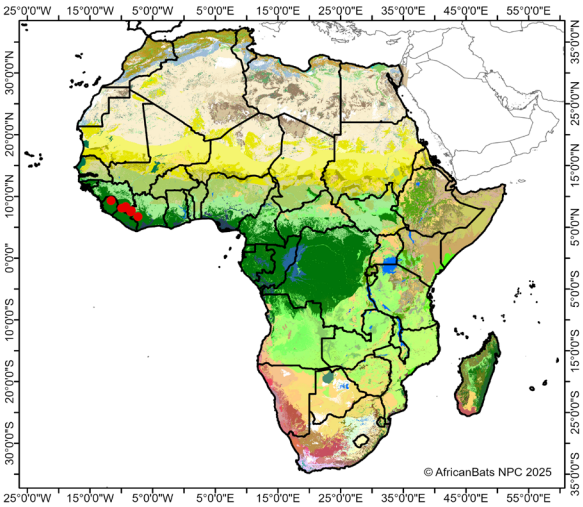

Figure 65. Distribution of *Hipposideros marisae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Guinea, Liberia, Sierra Leone.

Hipposideros megalotis (Heuglin, 1861)

*1861. *Phyllorrhina megalotis* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 8. Publication date: 1861. Type locality: Eritrea: Bogos country [=Keren region] [ca. 15 45 N 38 20 E]. [Goto Description]. Holotype: SMNS 984: ad ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See:

Dieterlen *et al.* (2013: 294). - Comments: Type specimen: SMNS, ???. Horáček *et al.* (2000: 98) mention "Monatsber. Königl. Preuss. Akad. Wiss. Berlin: 329". Nancy Simmons (pers. comm.) checked this and rejected this reference. - Etymology: From the Greek adjective "*μέγα*" (méga), meaning "big" and the neuter Greek substantive "*οὖς*" (genitive "*ὠτός*", "*ûs*", "*ōtós*"), meaning "ear" referring to the large ears of the species (see Lanza *et al.*, 2015: 145).

? *Hipposideros megalotis:* (Name Combination, Current Combination).

TAXONOMY:

Placed in the subgenus *Syndesmotis* by Legendre (1982), Gaucher and Brosset (1990) and Horáček *et al.* (2000: 98) include it with a question mark). Horáček *et al.* (2000: 98) as part of the *megalotis* species group, followed by Simmons (2005: 374).

Patterson *et al.* (2020: 121) placed it as only species in the *megalotis* group.

COMMON NAMES:

Chinese: 串耳蹄蝠. Czech: pavrápenec ušatý. English: Large-eared Leaf-nosed Bat, Ethiopian Large-eared Leaf-nosed Bat, Ethiopian Large-eared Roundleaf Bat, Big-eared leaf-nosed bat. French: Phyllorine à grandes oreilles d'Ethiopie, Phyllorine à grandes oreilles. German: Großohr-Rundblattnase. Italian: Ipposìdero orecchiùto.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) because, although it is seldom recorded, it has a relatively wide distribution, is tolerant of a range of habitats, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ax; IUCN, 2009; Monadjem *et al.*, 2017as).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017as). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008ax; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bu; IUCN, 2004). 2000: LR/nt (Hilton-Taylor, 2000). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

The threats to this species remain poorly known. Its is suspected to be threatened by habitat loss resulting from the conversion of land to agricultural use, and by disturbance of roosting sites (Mickleburgh *et al.*, 2008ax; IUCN, 2009; Monadjem *et al.*, 2017as).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008ax) [in IUCN (2009)] and Monadjem *et al.* (2017as) report that there are no direct conservation measures in place for this species. It is not known if the species is present in any protected areas. Additional studies are needed into the distribution, abundance, general ecology and threats to this little-known species.

GENERAL DISTRIBUTION:

Hipposideros megalotis has been reported from Eritrea (including the type locality of Keren (Heuglin, 1861)), Ethiopia (including Sidamo in southern Ethiopia (Hayman and Hill, 1971)), Kenya (where it has been recorded from the localities of Kinangop and Nakuru (Hayman, 1954)), Somalia, Djibouti (Heuglin, 1861; Pearch *et al.*, 2001) and from Jeddah in Saudi Arabia (Gaucher and Brosset, 1990). It has been reported at elevations of up to 2,000 m asl.

Native: Djibouti (Heuglin, 1861; Pearch *et al.*, 2001); Eritrea (Heuglin, 1861); Ethiopia (Hayman and Hill, 1971); Kenya (Hayman, 1954); Saudi Arabia (Gaucher and Brosset, 1990).

Presence uncertain: Somalia (Senna, 1905).

POPULATION:

Structure and Density

Little is known about the population of this species. Very few animals have ever been recorded (Mickleburgh *et al.*, 2008ax; IUCN, 2009; Monadjem *et al.*, 2017as).

Trend

2016: Unknown (Monadjem *et al.*, 2017as). 2008: Unknown (Mickleburgh *et al.*, 2008ax; IUCN, 2009).

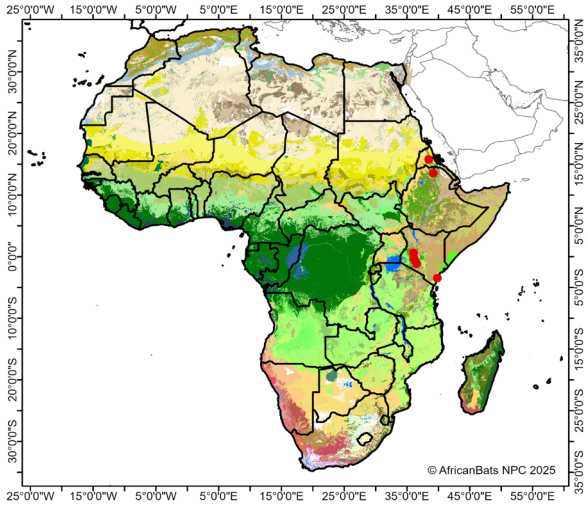

Figure 66. Distribution of *Hipposideros megalotis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Eritrea, Ethiopia, Kenya.

Hipposideros ruber (Noack, 1893)

*1893. *Phyllorhina rubra* Noack, Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere, 7: 586, pl 18, fig 14, 15. Publication date: 23 December 1893. Type locality: Tanzania: Eastern province: Ngerengere River [ca 07 00 S 38 00 E]. [Goto Description]. Holotype: ZMB 89571: ♂, skin only. Collected by: Dr. Mehmed Emin Pasha; collection date: 20 May 1890. Formerly Noack collection number 5, see Turni and Kock (2008: 38). - Comments: Noack (1893: 586) and Allen (1939a: 81) mentioned the type locality as "Lugerrunjere Fluss, Tanganyika Territory". Grubb *et al.* (1998: 80) mention the type locality as "Lugerrunjere Fluss = Ngerengere River, Tanzania - probably Ngerengere village, 32 miles east of Morogor according to Swynnerton, 1945, Proc. Zool. Soc. Lond., 115: 69". - Etymology: From the Latin "*ruber*" meaning red.

1906. *Hipposiderus caffer centralis* K. Andersen, Ann. Mag. nat. Hist., ser 7, 17 (99): 275, 277. Publication date: 1 March 1906. Type locality: Uganda: Entebbe [Ntebbi] [00 04 N 32 28 E, 3 800 ft]. [Goto Description]. Holotype: NHMUK 1899.8.4.8: ad ♂, skin only. Collection date: 5 April 1893. Presented/Donated by: Sir Frederick John Jackson.

1906. *Hipposiderus caffer guineensis* K. Andersen, Ann. Mag. nat. Hist., ser 7, 17 (99): 275, 278. Publication date: 1 March 1906. Type locality: Gabon: 70 mi (105 km) from Gaboon: Como River. [Goto Description]. Holotype: NHMUK 1897.12.1.11: ad ♀, skin only. Collected by: George Latimer Bates Esq. Collection date: 3 June 1897; original number: GLB 215. Note: caught under large rock, Fang name- Otan. - Comments: Considered a valid subspecies by Grubb *et al.* (1998: 80).

1917. *Hipposideros caffer niapu* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 431. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): NE Congo: Niapu [02 25 N 26 28 E]. [Goto Description]. Holotype: AMNH 49414: ad ♂, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 27 January 1914; original number: 2322. Topotype: MCZ 17224: ♂, alcoholic (skull not removed). Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 27 February 1914.

2016. *Hipposideros aff. ruber:* Nkrumah, Vallo, Klose, Ripperger, Badu, Drosten, Kalko, Tschapka and Oppong, Acta Chiropt., 18 (1): 239. Publication date: June 2016. - Comments: Nkrumah *et al.* (2016b: 3) indicate that this is the same form as "*H. ruber* lineage D from Vallo *et al.* (2009: 196), and which is evolutionarily distant to *Hipposideros ruber* s. str. from East Africa. (Name Combination).

2016. *Hipposideros cf. ruber (lineage C1)* Monadjem, Richards and Denys, Acta Chiropt., 18 (2): 365. Publication date: December 2016. - Comments: .

2016. *Hipposideros cf. ruber (lineage E1)* Monadjem, Richards and Denys, Acta Chiropt., 18 (2): 366. Publication date: December 2016. - Comments: .

2018. *H[ipposideros] rubber:* Malekani, Musaba, Gembu, Bugentho, Toengaho, Badjedjea, Ngabu, Mutombo, Laudisoit, Ewango, Van Cakenberghe, Verheyen, Asimonyo, Masudi, Bongo and Ngbolua, Nat. Conserv. Res., 3 (1): 67. Publication date: January 2018. (Lapsus).

2018. *Hip[posideros] caffer rufer:* Bourgarel, Pfukenyi, Boué, Talignani, Chiweshe, Diop, Caron, Matope, Missé and Liégeois, Infec. Gen. Evol., 58: 255. Publication date: 10 January 2018. (Lapsus).

2019. *Hipposideros caffer rubber:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

2020. *Hipposideros cf. ruber (lineage D1)* Mamba, Dalton, Mahlaba, Kropff and Monadjem, Mammalia, 85 (2): 133 (for 2021). Publication date: 8 December 2020.

2020. *Hipposideros ruber 1:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicates that this is partially the same form as the *Hipposideros ruber* C1 lineage mentioned by Vallo *et al.* (2009) and the *Hipposideros* cf. *ruber* C1a and C1b lineages mentioned by Monadjem *et al.* (2013b). (Name Combination).

2020. *Hipposideros ruber 2:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicates that this is partially the same form as the *Hipposideros ruber* C1 lineage mentioned by Vallo *et al.* (2009). (Name Combination).

2020. *Hipposideros ruber 3:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicates that this is the same form as the *Hipposideros ruber* C2 lineage mentioned by Vallo *et al.* (2009) and the *Hipposideros* cf. *ruber* C2 lineage mentioned by Monadjem *et al.* (2013b). (Name Combination).
2020. *Hipposideros ruber 4:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. (Name Combination).
2020. *Hippposideros cf. ruber:* Patterson, Webala, Lavery, Agwanda, Goodman, Kerbis Peterhans and Demos, ZooKeys, 929: 126. Publication date: 22 April 2020. - Comments: Patterson *et al.* (2020: 138) indicates that this is the same form as the *Hipposideros ruber* D lineage mentioned by Vallo *et al.* (2009) and the *Hipposideros* cf. *ruber* D1, D2, E1 and E2 lineages mentioned by Monadjem *et al.* (2013b). (Name Combination).
? *Hipposideros caffer guineensis:*
? *Hipposideros caffer ruber:* (Name Combination).
? *Hipposideros centralis:* (Name Combination).
? *Hipposideros cf. ruber*
? *Hipposideros ruber centralis:* (Name Combination).
? *Hipposideros ruber complex sp. lineage 1*
? *Hipposideros ruber complex sp. lineage 2*
? *Hipposideros ruber complex sp. lineage 4*
? *Hipposideros ruber guineensis:* (Name Combination).
? *Hipposideros ruber niapu:* (Name Combination).
? *Hipposideros ruber ruber:* (Name Combination).
? *Hipposideros ruber:* (Name Combination, Current Combination).

TAXONOMY:
Simmons (2005: 376) recognised it as part of the *bicolor* species group, and indicated that the subspecies limits are problematic, and it possible that this species complex includes more than one species. Vallo *et al.* (2007: 257; 2009: 193) indicate that two sympatric lineages exist in *ruber* based on analysis of complete sequences of the mitochondrial gene for cytochrome *b*, with possibly a third form in West Africa. Mitochondrial DNA analyses on specimens from the Niokolo Koba National Park in Senegal indicated that two distinct lineages of *H.* aff. *ruber* exists in that area (Vallo *et al.*, 2011b: 84).

Patterson *et al.* (2020: 121) place it in the *ruber* subgroup of the *bicolor* group.

Decher *et al.* (2016: 265) indicate that they provisionally include all Simandou records (Guinea), previously named *H. caffer* or *H. ruber* in *H.* cf. *ruber*.

Based on 11 cytochrome *b* microsatellite loci, Baldwin *et al.* (2014: 1) called the West African bats "*Hipposideros* aff. *ruber*" as these differed from East African *H. ruber* s. str., indicating it might represent a separate species. Nkrumah *et al.* (2016a: 240) also used the name "*H.* aff. *ruber* for their Ghanaian specimen (assigned to the D gentotype lineage), which is rather distant from *H. ruber* s.str. from East Africa. Nkrumah *et al.* (2017: 348) assigned their Ghanaian bats to *H.* cf. *ruber* as these include multiple genetic lineages.

Examining cyt *b* sequences from various parts of Africa led Mande (2019: 5) to distinguish four clades: (a) restricted to the DRC, (b) spread from Liberia, through Cameroon, the DRC to Uganda, (c) occurring in Cameroon, Equatorial Guinea and São Tomé and Príncipe, and (d) restricted to Senegal.

Benda *et al.* (2023a: 42; 2025: 61) called *Hipposideros* [cf.] *ruber* a parataxon, which includes several separate species - at least two in West Africa - possessing the *ruber* morphotype of the *H. caffer* group sensu Koopman (1975). The ruber morphotype is a large-sized form (with condylobasal length > 15.5 mm)

Benda *et al.* (2025: 65) indicate that there might be a nomenclatural problem as *ruber* - as originally described - is a medium-sized form and the large-sized form (currently also designated as *ruber*) has to be assigned a new/different name, which they tentatively name "aff. *ruber*".

COMMON NAMES:
Chinese: 诺氏蹄蝠. English: Noack's Leaf-nosed Bat, Noack's Roundleaf Bat, Red Leaf-nosed Bat. French: Phyllorine rouge, Phyllorine de Noack. German: Noacks Rundblattnase, Kamerun-Blattnase. Malawian: Liputiputi, Ndemiya, Namzeze.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ay; IUCN, 2009; Monadjem *et al.*, 2017at).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017at). 2008: LC ver 3.1 (2001) (Mickleburgh *et*

al., 2008ay; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bv; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is locally threatened by the loss and conversion of suitable habitat. It is also threatened in parts of its range by collection for subsistence use (Mickleburgh *et al.*, 2008ay; IUCN, 2009; Monadjem *et al.*, 2017at).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ay) [in IUCN (2009)] and Monadjem *et al.* (2017at) report that in view of its wide range it seems likely that the species is present in a number of protected areas. It has been recorded from the Manga Forest Reserve of Tanzania (Doggart *et al.*, 1999b). No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Hipposideros ruber is a widespread species recorded throughout much of West, Central, and East Africa and part of southern Africa including Angola, southern Democratic Republic of the Congo, northern and eastern Zambia, southern Malawi and northwestern Mozambique. It is found between sea level and 2,300 m asl.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 625,018 km^2.

Native: Angola (Hayman, 1963; Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 538); Benin; Burkina Faso (Kangoyé *et al.*, 2015a 608); Burundi (Hayman *et al.*, 1966); Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Chad; Congo (Bates *et al.*, 2013: 318 - 1st authenticated records); Congo (The Democratic Republic of the) (Allen, 1917; Römer, 1862; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 538) ; Côte d'Ivoire; Equatorial Guinea; Ethiopia; Gabon; Gambia (Emms and Barnett, 2005: 50); Ghana (Decher and Fahr, 2007: 13 - 15); Guinea (Fahr and Ebigbo, 2003: 128; Denys *et al.*, 2013: 283; Decher *et al.*, 2016: 265 mention it as "*Hipposideros cf. ruber*"; Weber and Fahr, 2007); Guinea-Bissau; Kenya; Liberia (Monadjem and Fahr, 2007: 50); Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 538); Mali; Mozambique (Monadjem *et al.*, 2010d: 538; Monadjem *et al.*, 2010c: 381); Niger; Nigeria (Happold, 1987; Rwanda (Hayman *et al.*, 1966); Saõ Tomé (Rainho *et al.*, 2010a: 28); Senegal; Sierra Leone; Sudan; Tanzania , United Republic of (Cunneyworth, 1996b; Doggart *et al.*, 1999b); Togo; Uganda (Kityo and Kerbis, 1996: 61); Zambia (Monadjem *et al.*, 2010d: 538).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Menzies (1973: 932) mentioned that the "*Hipposideros caffer guineensis*" bats he collected in Nigeria had a dirty, yellowish gold to bright, reddish golden pelage during most of the year. Only in May and July, he found gray bats. Some of the bats collected during these months had a golden coloured body, but gray shoulders, suggesting that the hair on the shoulders molted before that on the rest of the body. He also indicated that the youngest bats were gray and that this colour changed to golden before November. Bats from another locality, however, had golden and gray hair in all age classes.

Lucati and López-Baucells (2016: Suppl.) report on five albino and nine piebald (all-white fur/skin patches, eyes always normally coloured) specimens from mines in Tanzania (Howell and Mainoya, 1974: 155; Howell, 1980a).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Jones *et al.* (1993)] mention a wing loading value of 8.0 Pa, aspect ratio 6.6 for a wingspan of 30 cm and a wing area of 139 cm^2 and a body mass of 11 g.

SEXUAL DIMORPHISM:
Muñoz-Romo *et al.* (2021: 169) report that males posses a coiled-lobule type of apocrine gland; whereas females only have a rudimentary gland without any sac.

ECHOLOCATION:
From Irangi (Kivu province, DRC), Heller (1992: 75) reported that *H. ruber* emitted calls with frequencies between 130 and 140 kHz, distinguishing them from *H. caffer*, which emitted calls at a higher frequency.

Fahr and Ebigbo (2003) reported for an individual of *H.* cf. *ruber* from the Simandou Range in southeastern Guinea a CF-component of 146.7 kHz. At Sengwa in Zimbabwe, Jacobs (1996) and Fenton and Bell (1981) reported a highest frequency of 138 kHz. Monadjem *et al.* (2010c: 378) reported from Mozambique that the peak echolocation frequencies ranged between 132 - 136 kHz (ANABAT) and 130.5 kHz (Petterson D240x).

Rainho *et al.* (2010a: 21) and Rainho *et al.* (2022: 605) reported the call parameters from Saõ Tomé Island: F_{min} 139.7 ± 0.2 (139.3 - 139.8) kHz, F_{max}: 141.5 ± 0.4 (140.8 - 141.9) kHz, F_{maxE}: 140.9 ± 0.3 (140.4 - 141.1) kHz, duration: 5.9 ± 0.2 (5.7 -

6.1) ms and interpulse interval: 14.1 ± 4.2 (10.4 - 22.1) ms.

Monadjem *et al.* (2013b: 351) report on two lineages of *H.* cf. *ruber* from Mount Nimba: C1 with a F_{max} of 147.7 ± 1.45 (145 - 150) Khz, and E1 with F_{max} of 127.5 (127 - 128) kHz.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 95 calls of 6 *Hipposideros* cf. *ruber*: F_{peak}: 142.6 ± 3.4 (133.3 - 146.7) kHz, F_{min}: 123.2 ± 2.7 (120.3 - 128.5) kHz, F_{max}: 143.3 ± 4.2 (133.3 - 145.5) kHz, duration: 5.5 ± 1.1 (4.2 - 7.0) ms.

Jones and Siemers (2010: 449 - 450) indicated that males emit pulses with a higher frequency than females, and that the CF-frequency is positively related to the body condition (mass/forearm length).

Trentin and Rovero (2011: 56) describe the call from bats at Uzungwa Scarp Forest Reserve, Tanzania, as having a first modulated component starting at 143.9 kHz, which increases to a maximum frequency of 148.6 kHz, which continues for about 7 ms, and then drops to 121.4 kHz in about 1 ms. The maximum intensity is at 144.8 kHz.

For three Kenyan males and two females, Webala *et al.* (2019b: 15) reported F_{max} between 132.6 and 134.5, and 140.4 and 145.3 kHz, whereas the duration ranged from 7.4 to 8.8 and 7.3 to 7.7 ms respectively.

In Sierra Leone, Weber *et al.* (2019: 21) recorded calls from two types of *H. ruber*: **C1** (n=3): 145.7 ± 4.5 (142.0 - 152.0) kHz and **D** 4 FF: 122.5 ± 2.4 (120.0 - 125.0) kHz and 2 MM: 127.0 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 131.96 kHz and duration: 8.06 ms.

For one call from Zambia Taylor-Boyd *et al.* (2025: 116) report the following values: Interpulse interval: 44.3 ms; F_{max}: 133.4 kHz; Start slope: -0.1 kHz/ms; End slope: -12.7 kHz/ms; Ledge duration: 0.4 ms.

In Benin, the bat's call was categorized as a CF-FMd (Constant frequency - Frequency modulation downward) sonotype by Roemer *et al.* (2021: Suppl.).

Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003661_NHBRVSCXKP.WAV, https://chirovox.elte.hu/sounds/A003662_BNEPDSKABL.WAV, https://chirovox.elte.hu/sounds/A003668_XBPGGGLIBR.WAV

MOLECULAR BIOLOGY:

Karyotype

Koubínová *et al.* (2010b) report on seven females from Senegal, 2*n*= 32, Fna= 60 and FN= 64, they comprised 30 biarmed autosomes, including four metacentric, eight submetacentric and three subtelocentric, eight submetacentric and three subtelocentric pairs, a secondary constriction situated near the centromere was observed in one pair of the medium-sized submetacentric autosomes (approximately the 9th largest pair). The X chromosome was identified as a large metacentric element, the Y chromosome as a medium submetacentric.

Denys *et al.* (2013: 284) report the following karyotype for a male *H.* cf. *ruber* from the Guinean Mount Nimba area: 2*n* = 32, FNa =60, including 15 pairs of meta- and submetacentric chromosomes. The X chromosome is middle-sized submetacentric and the Y chromosome is small subtelocentric.

Genetics

Lim (2007), Vallo *et al.* (2007).

HABITAT:

In Ghana, Nkrumah *et al.* (2016b: 5) reported *H.* aff. *ruber* to prefer foraging in seminatural habitats, followed by mixed farm areas, and, to a much lesser extent, tree farms and savanna grasslands.

In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported that *Hipposideros* cf. *ruber* as only found in undisturbed habitats in the Afromontane forest biome, but this was based on one specimen only.

On Saó Tomé, Araújo-Fernandes *et al.* (2025: 831) found that this species was mainly active in forests, with some minor activity in shaded and oil palm plantations. They also found that 50 out of the 129 recorded passages (39 %) occurred during day time.

On Princípe, Palmeirim *et al.* (2025: 1) found *Hipposideros ruber* exclusively in old-growth and secondary regrowth forests.

HABITS:

Russo *et al.* (2010b: 701) report *H. ruber* to be diurnally active on the island of São Tomé, and indicate that adult males were much more active during the daytime than females, whereas during the night the opposite was true, possibly leading

to a temporal niche partitioning. Russo *et al.* (2010a: 271) indicate that about one fifth of a colony may be out during daytime, also due to the absence of forest-dwelling avian predators.

In Ghana, Nkrumah *et al.* (2016a: 239) found that during the night, males of *H.* aff. *ruber* returned more often to their cave roosts than females. Based on that data for 13 bats, they calculated the bat's homerange as 36 ± 35 (6 - 95) ha. The foraging range covered 50 % of this and the core area 2 %. Nkrumah *et al.* (2016b: 6) found that females had a night activity pattern that peaks between 6 and 8 p.m., with a smaller peak around midnight and another peak between 5 and 6 a.m. In between the flight duration dropped to almost zero. In males, the activity peaked around 8 p.m., midnight and between 4 and 5 a.m. However, their activity in the first part of the night did only decrease by a maximum of 10 minutes. Nkrumah *et al.* (2017: 350) found that activity patters of the bats differed from cave to cave.

ROOST:
Weber and Fahr (2006: 4) indicate that *H. ruber* largely or exclusively depends on the availability of caves as day roosts in Guinea.

In Ghana, Nkrumah *et al.* (2016a: 239) found that caves were used as main roost, but that *H.* aff. *ruber* also used trees as individual night roosts. In the Mframabuom cave, the roost contained some 3,500 individuals (together with *H. abae, H. jonesi* and *Nycteris* cf. *thebaica*).

Happold and Happold (2023: 94) mention that, in the DRC, groups can contain between 5 and 71 individuals, where females outnumber the males by 2-3. In some occasions, the two sexes roost separately, suggesting maternity colonies.

Rainho *et al.* (2022: 606) mention that this species was found roosting in caves and abandoned buildings on Príncipe, and on Sáo Tomé it was also found in these structures, but also in artificial tunnels. Additionally, tree hollows might also be used.

Fedurek *et al.* (2024: 2) reported on *Hipposideros ruber* bats roosting in a *Mildbraediodendron excelsum* tree in the Budongo forest in Uganda. They also observed the bat's guano being eaten by chimpanzees (*Pan troglodytes*), black-and-white colobus (*Colobus guereza occidentalis*), and red duikers (*Cephalophus natalensis*), probably to supplement their mineral intake. These species have been implicated n ebolavirus outbreaks in Central and West Africa (p. 4).

DIET:
Bell and Fenton (1984) [in Fenton, 1986a] found that *H. ruber* depends on flutter to find its prey and varies its hunting pattern by taking both flying prey and gleaning targets from surfaces such as foliage and water. They also found no restriction to a specific prey species or size class.

Nkrumah *et al.* (2017: 353) reports that *H.* cf. *ruber* feeds primarlily on Lepidoptera in Ghana.

PREDATORS:
Based on Fenton *et al.* (1983), Gual-Suárez and Medellín (2021: Suppl.) reported that this species was part of the food items taken by *Nycteris grandis*.

POPULATION:
Structure and Density
This is one of the most common bats in Africa, with some colonies containing up to 500,000 individuals (Mickleburgh *et al.*, 2008ay; IUCN, 2009; Monadjem *et al.*, 2017at).

Trend
2016: Unknown (Monadjem *et al.*, 2017at). 2008: Unknown (Mickleburgh *et al.*, 2008ay; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In Nigeria, Menzies (1973: 937 - 940) reported that that the testes of male "*Hipposideros caffer guineensis*" bats reached a maximum size in November, the only month he was able to find spermatozoa. Female bats reached their maximum weight in April, suggesting this was the end of gestation. Bats collected in March were all pregnant and those collected in May were lactating. Some of the bats were still lactating in July.

Trentin and Rovero (2011: 50) captured nine lactating and two pregnant females in December 2005 at Uzungwa Scarp Forest Reserve, Tanzania.

In Kwamang (Ghana), the bats gave birth from late March to early May (Nkrumah *et al.*, 2017: 348).

In Sierra Leone, Weber *et al.* (2019: 23) reported two pregnant females (type "C1") on 1 and 7 April, and one pregnant (24 March) and one lactating (2 April) female (type "D").

PARASITES:
Peralta-Rodríguez *et al.* (2012: 1006) report on the infection of *H. ruber* by *Spirura hipposiderosi* Khalil, 1975 (Nematode) in Tanzania.

In his review of African chiggers (Acari: Trombiculidae), Stekolnikov (2018a: 49, 50, 72, 117, 119, 121, 123, 173, 179, 184) reported the presence of *Whartonia lepidopteriscuta* Vercammen-Grandjean, 1965, *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957, *Riedlinia willmanni* Vercammen-Grandjean and Minter, 1964, *Trombigastia ascoschoengastoides* Vercammen-Grandjean and Fain, 1958, *Trombigastia berghei* Vercammen-Grandjean and Fain, 1958, *Trombigastia laarmani* Vercammen-Grandjean and Fain, 1958 and *Trombigastia minor* Vercammen-Grandjean and Fain, 1958, *Trombigastia scapularia* Vercammen-Grandjean and Fain, 1958, *Trombigastia vinckei* Vercammen-Grandjean and Fain, 1958, *Afrotrombicula machadoi* (Taufflieb, 1962), *Microtrombicula tanzaniae* Goff, 1982, *Myotrombicula bidentipalpis* Vercammen-Grandjean and Fain, 1958, and *Oudemansidium howelli* (Goff, 1983).

Zajkowska *et al.* (2018: 99) refer to Taufflieb (1965: 22), who mentioned the presence of *Neotrombicula (Neotrombicula) machadoi* Taufflieb, 1962 [=*Afrotrombicula machadoi* (Taufflieb, 1962)] on an Angolan "*Hipposideros caffer centralis*". Zajkowska *et al.* (2018: 118) also mentions *Microtrombicula irangiensis* Vercammen-Grandjean, 1965 from a Congolese specimen originally identified as "*Hipposideros caffer ruber*".

In the CAR, Babyesiza *et al.* (2025: 4) found *Trypanosoma livingstonei* in the single *H. ruber* they examined.

Decher *et al.* (2016: 266) found the bat fly *Penicillida allison* Theodor, 1968 (Nycteribiidae) on a Guinean "*H.* cf. *ruber*".

Ramírez-Martínez *et al.* (2021: Suppl.) reported the presence of streblid bat flies on Ugandan bats. Based on its CO1 sequence, is closest match in GenBank was *Nycterophilia parnelli* Wenzel, 1966, which is a Central American genus/species.

VIRUSES:
Coronaviridae - Coronaviruses
Alphacoronavirus
SARS-CoV (subgenus *Duvinacovirus*)
See also note under "viruses" for the genus as possiblitiy.

Corman *et al.* (2015: 11859) tested 1,611 Ghanese *H.* cf. *ruber* specimens, of which 62 (3.8 %) tested positive for 229E-related coronavirsues.

Anthony *et al.* (2017b: Suppl.) mention the beta-coronavirus Predict_CoV_20.

Willoughby *et al.* (2017: Suppl.) report Human coronavirus 229E.

Nziza *et al.* (2019: 157) found a new coronavirus (PREDICT_CoV-43) in a rectal swap from a Rwandan bat.

Maganga *et al.* (2020: 1) reported viruses belonging to the genus from 13 out of 262 (4.96 %) Gabonese *H.* cf. ruber bats and found them to be significantly present in October and November.

For the two Congos, Kumakamba *et al.* (2021: 7) reported 3 out of 21 bats to test positive for coronaviruses, and all were found in the dry season.

George *et al.* (2022: 6) reported on a *H. ruber* specimen from Ife (Nigeria), where they found RNA from an alpha-coronavirus in a rectal swap and from a beta-coronavirus in both rectal and oral swaps.

Flaviviridae
In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against non-specific Flaviviruses.

Hermida Lorenzo *et al.* (2021: 6) reported Hepacivirus C, D, L and K, Jogalong virus, Bat hepacivirus, Heptatitis GB virus B and Sigmodontinae hepacivirus from Guinean bats.

Hantaviridae (formerly included in Bunyaviridae)
Hantavirus
Witkowski *et al.* (2016: 113) report a new hantavirus from Gabon: Makokou virus (MAKV). Arai *et al.* (2019b: 2) and Arai and Yanagihara (2020: 7) tentatively assigned this virus to the genus *Mobatvirus*.

Hepadnaviridiae
Orthohepadnavirus Hepatitis B virus (HBV)
Drexler *et al.* (2013c: 16152) report on four out of 51 examined *H.* cf. *ruber* specimens from Gabon that were positive for roundleaf bat HBV (RBHBV). Nie *et al.* (2017: 89) refer to this virus as horseshoe bat HBV (HBHBV).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) reported that two of the 117 specimens they identified as belonging to *H.* cf. *ruber* from Ghana tested positive for *Morbillivirus*. Two of the 337 specimens from Gabon, they identified as *H.* cf.

caffer/ruber also tested positive for *Morbillivirus* and one other specimen for *Rubulavirus*.

In their overview table, Maganga *et al.* (2014a: 8) report the following viruses were already found on *H.* cf. *ruber*: Rift Valley Fever virus (RVF), Rubulavirus, Morbillivirus unclassified, Coronavirus.

Retroviridae

Hermida Lorenzo *et al.* (2021: 6) reported an unclassified Gammaretrovirus and Simiam retrovirus 4 from Guinean bats.

Rhabdoviridae

Two *Hipposideros ruber* specimens captured in the Republic of Congo, were found by Cameron *et al.* (2021: 2) to harbour new rhabdoviruses.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mali, Mozambique, Niger, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia.

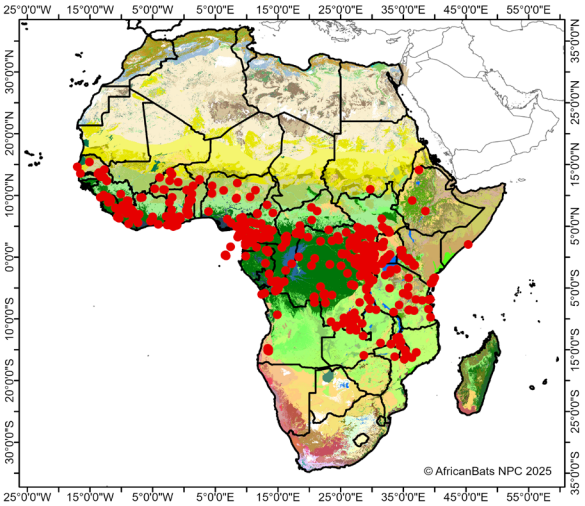

Figure 67. Distribution of *Hipposideros ruber*.

Hipposideros tephrus (Cabrera, 1906)

1861. *Phyllorrhina bicornis* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 7. Publication date: 1861. Type locality: Eritrea: Kérén region [ca. 15 45 N 38 20 E]. [Goto Description]. Lectotype: ZMB 2795: ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: undated. Formerly in SMNS. Lectotype designated by Turni and Kock (2008: 36). - Comments: Meester *et al.* (1986: 43) and Turni and Kock (2008:36) mentioned it as *Phyllorhina bicornis*.

*1906. *Hipposiderus tephrus* Cabrera, Bol. r. Soc. espan. Hist. nat. , 6: 358. Publication date: June 1906. Type locality: Morocco: Mogador [=Essaouira] [31 31 N 09 46 W]. Holotype: MNCN 110: ad ♂. Collected by: Mr. Martínez de la Escalera; collection date: 29 August 1905. See Ibáñez and Fernández (1989: 11). Paratype: MNCN 111: ad ♀. See Ibáñez and Fernández (1989: 11). (Current Combination).

1939. *Hipposideros braima* Monard, Arq. Mus. Bocage, 10: 73, fig 5. Publication date: March 1939. Type locality: Guinea-Bissau: Bagíngarà [12 35 N 14 28 W]. [Goto Description]. Holotype: [Unknown] |TS408|: ad ♀. Original number: 602. See Monard (1939: 73).

1965. *Hipposideros braimah:* Rosevear, Bats of West Africa, 221, 226. - Comments: Lapsus for braima Monard, 1939 (see Kock, 1969a: 130). (Lapsus).

2014. *Hipposideros (caffer) tephrus:* Moores and Brown, Go-South Bull., 11: 19. (Name Combination).

? *Hipposideros caffer tephrus:*

? *Hipposideros caffer:*

? *Hipposideros tephrus:* (Name Combination, Current Spelling).

TAXONOMY:
Hayman and Hill (1971) and Simmons (2005: 376) recognised it as a subspecies of *caffer*. Vallo *et al.* (2009: 200) suggest that this taxon is elevated to species rank based on the genetic distance, the small size and the wide geographical separation from South-African true *Hipposideros caffer*.

Patterson *et al.* (2020: 121) place it in the *ruber* subgroup of the *bicolor* group.

Given the extensive distribition range of this species, Benda *et al.* (2025: 60) question whether *tephrus* is indeed the prior name for this species, or whether this might be one of the other names described from the area, e.g. *Phyllorrhina bicornis* von Heuglin, 1861). However, this needs to be examined in more detail.

COMMON NAMES:
Czech: pavrápenec sahelský. Dutch: Cabrera's rondbladneus. English: Lesser leaf-nosed bat, Lesser (Sundevall's) Leaf-nosed Bat. French: Phyllorine cendrée, Rhinolophe de Cafrerie. German: Marokkanische Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001) in view of its wide distribution, presumed large population, and because it is unlikely to be

declining at the rate required to qualify for listing in a threatened category (Monadjem and Shapiro, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Shapiro, 2017b)

Regional
None known.

MAJOR THREATS:
Human disturbance to roosting sites (caves) could have a negative effect (Monadjem and Shapiro, 2017b).

CONSERVATION ACTIONS:
No specific conservation measures in place. May occur in several protected areas throughout its range (Monadjem and Shapiro, 2017b).

GENERAL DISTRIBUTION:
Morocco to Senegal, and Yemen (Vallo *et al.*, 2009; Benda *et al.*, 2011b: 29). *H. tephrus* is confined to the coastal areas of northern Morocco. Probably Mauritania (Padial and Ibáñez, 2005: 240); Ethiopia (Lavrenchenko *et al.*, 2004b: 133); SW Saudi Arabia. Possibly Gambia (Emms and Barnett, 2005: 50), Guinea (Fahr and Ebigbo, 2003: 128, as "*Hipposideros* cf. *caffer*"), Benin (Capo-Chichi *et al.*, 2004: 162), Liberia (Fahr, 2007a: 104).

Patterson *et al.* (2020: Suppl.) mentioned "*caffer* 1 and 3" [=*tephrus* (see Benda *et al.* (2025: 50)] specimens from Kenya and Uganda.

Native: Burkina Faso (Kangoyé *et al.*, 2015a: 608); Ethiopia (Nyssen *et al.*, 2020: 9); Kenya (Benda *et al.*, 2025: 59), Mauritania (Allegrini *et al.*, 2011: 2); Morocco (Disca *et al.*, 2014: 209; Moores and Brown, 2014: 20; Dbiba *et al.*, 2025: 6); Uganda, Yemen (Benda *et al.*, 2011b: 29).

ECHOLOCATION:
Mayer *et al.* (2007) reported a CF-component of 133 to 137 kHz for Moroccan specimens. See also Jones *et al.* (1993).

Disca *et al.* (2014: 226) indicate that the type of call is FC-FM, with the following parameters: F_{start}: 147.1 ± 1.1 kHz, F_{end}: 128.2 ± 5.4 kHz, F_{peak}: 146.8 ± 1.3 kHz, bandwidth: 19 ± 4.7 kHz, duration: 6.6 ± 1.1 ms. They also mention (p. 213) that the maximum energy is in the FC part of the third harmonic. The start frequency is also at least 10 kHz above the value provided by Dietz et al. (2009).

Moores and Brown (2014: 21) recorded the following values for social calls at Bou Jerif fortress, Morocco: F_{peak}: 46.7 kHz, F_{start}: 55 kHz, F_{end}: 29 kHz, duration: 8 ms.

MOLECULAR BIOLOGY:
Karyotype
Koubínová *et al.* (2010b) report on three females and two males from Senegal, 2*n*= 32, Fna= 60 and FN= 64, they comprised of 30 biarmed autosomes, including four metacentric, eight submetacentric and three subtelocentric pairs. A secondary constriction situated near the centromere was observed in one pair of the medium-sized submetacentric autosomes (approximately the 9th largest pair). The X chromosome was identified as a large metacentric element, the Y chromosome as a medium submetacentric.

Genetics
Vallo *et al.* (2009).

POPULATION:
Has a wide distribution and the population is presumed to be large, but more precise information is not available (Monadjem and Shapiro, 2017b).

Trend:- 2016: Unknown (Monadjem and Shapiro, 2017b).

PARASITES:
Okafor (1988: 11) reported the presence of the cestode *Oochoristica agamae* Baylis, 1919 (Eucestoda, Linstowiidae) from *H. caffer tephrus* specimens from Nsukka, Nigeria.

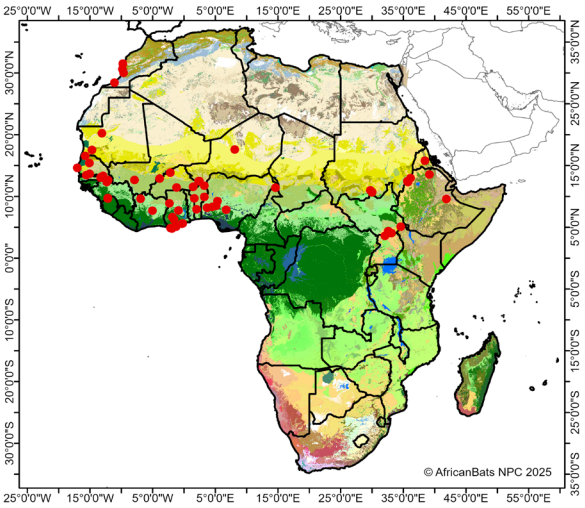

Figure 68. Distribution of *Hipposideros tephrus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Eritrea, Ethiopia, Ghana, Mali, Mauritania,

Morocco, Niger, Nigeria, Senegal, Sierra Leone, South Sudan, Sudan, The Gambia, Uganda.

†*Hipposideros vetus* (Lavocat, 1961)

*1961. *Asellia vetus* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, 155: ?. - Comments: Marandat (1994: 61) mentions that the holotype consists of a left maxillary fragment with P^4-M^3.
1982. *Hipposideros (Syndesmotis) vetus:* Legendre, J. Vert. Paleont., 2 (3): 379. Publication date: December 1982. (Name Combination).
2013. *Asellia/Hipposideros vetus:* Stoetzel, Palaeog., Palaeoclim., Palaeoecol., 392: 363. Publication date: 29 September 2013. (Name Combination).
? *Hipposideros vetus:* (Current Combination).

TAXONOMY:
Originally described in the genus *Asellia*, the generic assignment of this taxon was unclear. Some authors (e.g., Legendre, 1982: 372; Gunnell *et al.*, 2011: 71; Hugueney *et al.*, 2015) assign it to the genus *Hipposideros*, whereas others (e.g., Aulagnier, 2013a: 360) assign it to the genus *Asellia*. Stoetzel, 2013: 363) furthermore mentions it as *Asellia/Hipposideros vetus*.

Legendre (1982: 382) examined the teeth and dental characters and found that although the absence of a P^2 and the degree of reduction of M^2 as well as M^3 are similar to those of other fossil *Asellia*, there are characters that are incompatible with this genus: upper canines with a separate secondary cusp on the distal edge, mandible with a long and slender horizontal ramus; low coronoid process; long and outward deflected angular process. These characters are much more like those of *Hipposideros*. Legendre (1982: 383) assigned *vetus* to the subgenus *Syndesmotis*, together with *H. megalotis*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Miocene - Pliocene (Langhian, Serravallian - Brown *et al.*, 2019: Suppl.).

Genus ***Macronycteris*** J. E. Gray, 1866

*1866. *Macronycteris* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 82. Publication date: May 1866 [Goto Description]. - Comments: Type species: *Rhinolophus gigas* Wagner, 1845, by monotypy (see Decher and Fahr, 2005: 1; Jackson and Groves, 2015: 246). - Etymology: From the Greek "*μακρός*", meaning large and "*νυκτερις*", meaning bat (see Palmer, 1904: 393).

TAXONOMY:
This taxon was longtime considered to be a synonym of *Hipposideros*, but molecular analyses of Cyt-*b* by Foley *et al.* (2017) indicated that its representatives are sufficiently different from that genus to be assigned to a separate genus.

Alumbaugh *et al.* (2021: 34), however, confirm that both modern Malagasy species (*commersoni* and *cryptovalorona*) are currently morphologically indistinguishable.

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Macronycteris*: ***commersoni*** (E. Geoffroy Saint-Hilaire, 1813); ***cryptovalorona*** (Goodman, Schoeman, Rakotoarivelo and Willows-Murno, 2016); ***gigas*** (Wagner, 1845); ***thomensis*** (Bocage, 1891); ***vittata*** (Peters, 1852).

MOLECULAR BIOLOGY:
Karyotype
Foley *et al.* (2017: 11) indicate that the karyotype of the genus *Hipposideros* is very conservative, with almost all species having $2n = 32$. Both *M. commersoni* and *M. gigas*, however, have $2n = 52$.

PREDATORS:
Goodman *et al.* (2022: 1900) indicate that remains of *Macronycteris* sp. have been found in food remains of *Asio madagascariensis* (A. Smith, 1834) (Madagascar Long-eared Owl) and *Galidictis fasciata grandidieri* Wozencraft, 1986 (Broad-striped Vontsira - Eupleridae).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

†*Macronycteris besaoka* (Samonds, 2007)

*2007. *Hipposideros besaoka* Samonds, Acta Chiropt., 9 (1): 49, fig 5A - C, 6A - D. Type locality: Madagascar: Anjohibe cave. Holotype: UA 9478. Right maxialla: see Samonds (2007: 49). - Etymology: The word *besaoka* is derived from the Malagasy and means 'big chin' (see Samonds, 2007). - Phonetics: bay-SOH-ka.
2019. *M[acronycteris] besaoka:* Rakotoarivelo, Goodman, Schoeman and Willows-Munro, PeerJ, 7 (e5866): 15. Publication date: 17 January 2019. (Current Combination).

TAXONOMY:
Goodman *et al.* (2016: 435) examined some *besaoka* skulls and found these to have a more robust mandibula and lower teeth than both other Madagascan "*Hipposideros*" [=*Macronycteris*"] species (*commersoni* and *cryptovalorona*), but further DNA study is required to see whether it is genetically distinct from either of them. However, Alumbaugh *et al.* (2021: 34, 42) indicate that attempts to isolate DNA from specimens had been unsuccessful, which makes it impossible to conclude whether *besaoka* became extinct or was only a more robust morphotype of *commersoni*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 49 - 53) found samples in deposits (TW-10) dated at 10,000 years old or younger within the Anjohibe cave, Madagascar. Michielsen *et al.* (2023: 2) mention that the fossil record is insufficient to determine whether this species' extinction occurred prior or after human arrival.

Timeframe:
Pleistocene (Brown *et al.*, 2019: Suppl.).

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

HABITAT:
Rakotoarivelo *et al.* (2019: 14) presume that *M. besaoka* was ecologically similar to *M. commersoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Macronycteris commersoni (E. Geoffroy St.-Hilaire, 1813)

*1813. *Rhinolophus Commersonii* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 20: 263, pl 5. Publication date: 1813. Type locality: Madagascar: Tuléar province: Fort Dauphin [25 02 S 47 00 E]. [Goto Description]. Neotype: FMNH 175972: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 9 December 2002; original number: SMG 13401. Type locality: Madagascar: Province de Fianarantsoa, Parc National de l'Isalo, along Sahanafa River, near foot of Bevato Mountain, 28 km south-east of Berenty-Betsileo, 22°19.0′S, 45°17.6′E, 550 m a.s.l. (see Goodman *et al.*, 2016: 437). - Etymology: Geoffroy's description was based on drawings and notes found among Mr. Philibert Commerson's papers, in who's honour Geoffroy named this species (see Smithers, 1983: 133; Taylor, 2005).
2017. *M[acronycteris] commersonii:* Foley, Goodman, Whelan, Peuchmaille and Teeling, Acta Chiropt., 19 (1): 10. Publication date: June 2017. (Current Combination).
2017. *Macronycteris commersonii:* Sotero-Caio, Baker and Volleth, Genes, 8 (272): 9. Publication date: 13 October 2017. (Name Combination, Alternate Spelling).
2018. *Macronycteris commersoni:* Reher, Ehlers, Hajatiana and Dausmann, J. Comp. Physiol., B 188 (6): 1015. Publication date: 18 August 2018. (Name Combination).
? *Hipposideros commersoni commersoni:* (Name Combination).
? *Hipposideros commersoni:* (Name Combination).
? *Hipposideros sp. cf. H. commersoni:*

TAXONOMY:
Simmons (2005: 369, 372, 377) restricts "*Hipposideros commersoni*" to Madagascar, and assigns "*H. gigas*", "*M. vittatus*" (including *marugensis*) and "*H. thomensis*" as the mainland forms based on morphology and echolocation differences.

A combined molecular and morphological study by Rakotoarivelo *et al.* (2015: 1) indicates that cryptic species exist in Madagascan *M. commersoni*, but also that a further fine-scale phylogeographic study is needed to fully resolve the systematics of this species (see *M. cryptovalorona*). Rakotoarivelo *et al.* (2019: 1) investigated this further and found several lineages in bats from the western part of Madagascar: the animals from northern Madagascar formed a single monophyletic clade (clade C), whereas the animals from the southwestern part of the island (clade B) showed more phylogeographical partitioning where different mtDNA haplotypes frequencies were detected between populations from different bioclimatic regions.

Goodman *et al.* (2016: 439) point out that the original spelling by Geoffroy (1813) was "*Rhinolophus Commersonii*", but that most of the subsequent authors spelled it with only one "i". They refer to article 33.3.1 of the ICZN code to maintain the usage of the single "i" version.

COMMON NAMES:
Afrikaans: Commerson se bladneusvlermuis, Commerson-bladneusvlermuis, Commersonse Blaarneusvlermuis. Czech: pavrápenec Commersonův. English: Commerson's Leaf-

nosed Bat, Giant Leaf-nosed Bat, Commerson's roundleaf bat, Commerson's Rhinolph. French: Chauve-souris de Commerson à nez feuillu, Phyllorine de Commerson. German: Madagaskar-Rundblattnase, Commerson-Rundblattnase. Portuguese: Morcego de nariz enfolhado de commerson. Ukrainian: Листоніс Коммерсона [= Lystonis Kommersona].

SIMILAR SPECIES:
Grunwald *et al.* (2025: 296) indicate that further research is needed to determine better ways to distinguish *Macronycteris commersoni* from *Macronycteris cryptovalorona*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Sabatier and Legendre (1985: 23) reported the presence of *M. commersoni* (and *Hipposideros* sp.) in the Tsimanampetsotsa deposit.

Samonds (2007: 45 - 46, 58 - 60) found samples in deposit (OLD SE locality) dated at 10,000 yrs old or younger and deposit (SS2) which was collected from the surface near the main cave entrance, the dating attempts revealed that this sample was contaminated, therefore no date is known, these two sites identified specimens belonging to *M.* sp. cf. *commersoni*. Samonds (2007: 54 - 55) also found *M. commersoni* within the deposit (NCC-1 locality) dating at 69,000 to 86,800 years old, from within the Anjohibe cave, Madagascar.

Gunnell *et al.* (2014: 3) refer to Goodman and Junkers (2013), who report on fossil material from the Andrahomana cave in Madagascar.

CONSERVATION STATUS:
Global Justification
This species is listed [as *Hipposideros commersoni*] as Near Threatened (NT ver 3.1 (2001)) in view of the significant threat from hunting in the west, which is likely to have resulted in a decline in the region of 20 - 25 % over the past 15 years. Almost qualifies as threatened under criterion A. However, as this species is generally widespread across Madagascar, occurs both in and outside a number of protected areas, and has an ability to tolerate some degree of habitat modification, it is unlikely to be declining fast enough to warrant listing in a threatened category (Andriafidison *et al.*, 2008d; IUCN, 2009; Monadjem *et al.*, 2019a).

Assessment History
Global
2016: NT ver 3.1 (2001) assessed as *Hipposideros commersoni*. 2008: NT ver 3.1 (2001) (Andriafidison *et al.*, 2008d; IUCN, 2009). 2004: Not assessed (IUCN, 2004).

Regional
None known.

MAJOR THREATS:
Andriafidison *et al.* (2008d) state that besides habitat loss, it is also threatened by hunting and is particularly vulnerable at roosting sites where bats are hunted as they emerge at dusk (Goodman *et al.*, 2008d; Jenkins and Racey, 2008). It can be legally hunted on between the first of February and the first of May (Anonymus, 2007b: 6). In the extreme south-west of Madagascar, there were an estimated 140,000 individuals harvested for food annually between January and March (Goodman, 2006). This hunting is thought to occur throughout western Madagascar in areas where local people live in close proximity to roosting colonies (Jenkins and Racey, 2008).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008d) and Monadjem *et al.* (2019a) report that this species occurs in a number of protected areas as well as other forest areas that are actively managed for conservation (Goodman *et al.*, 2005a; Rakotoarivelo and Randrianandrianina, 2007; Ranivo and Goodman, 2007b).

Due to the existence of several clades within *M. commersoni*, Rakotoarivelo *et al.* (2019: 16) stress the conservation importance of the localities where clade C was found to occur: Analamera, Ankarana, Montagne d'Ambre, and Marovaza.

GENERAL DISTRIBUTION:
Madagascar; adjacent small islands.

GEOGRAPHIC VARIATION:
Ranivo and Goodman (2007b: 48) indicate that there is a clinal variation in *commersoni* on Madagascar, where the individuals from the north are larger than those from the south. In the Isalo region, both sizes were found together, which might indicate that there are two cryptic species.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Goodman *et al.* (2025: 211) reported the presence of a well-developed white crown tuft in the folds of the frontal sac of an adult male in reproductive condition.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Alumbaugh *et al.* (2021: 40) found that mandibles are deeper for *Macronycteris* specimens from the dry bioclimatic zone as compared to those from the subarid zones (although this was only based

on a limited number of specimens). Additionally, males also differ in size between the two zones.

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 56) reported that the baculum of *commersoni* has a bifurcated distal tip, a straight central shaft and a basal portion that is narrower than the distal part; length: 3.73 ± 0.540 (3.00 - 4.52) mm, width: 1.92 ± 0.330 (1.48 - 2.41) mm. In the bat's clades (sensu Rakotoarivelo *et al.*, 2015), they found two morphotypes with some slight differences: Morphotype A/Clade B: distinct bifurcated distal tip, sometimes with an indentation; length: 3.77 ± 0.545 (3.00 - 4.52) mm, width: 1.94 ± 0.325 (1.50 - 2.41) mm; Morphotype B/Clade C: "This same structure is also found in certain animals allocated to Clade C, with the exception of two" (unfortunately, without further details); length: 3.05, 3.37 mm, width: 1.48, 1.69 mm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 15.7 Pa, aspect ratio 7.7 for a wingspan of 65 cm and a wing area of 556 cm^2 and a body mass of 89 g.

SEXUAL DIMORPHISM:
Muñoz-Romo *et al.* (2021: 169) [referring to McWilliam, 1988a)] mention that males have tufted nasal glands, which were observed everted over the nasal region of females during courtship. Males are also larger than females (Goodman *et al.*, 2022: 1900).

ECHOLOCATION:
In Madagascar Russ *et al.* (2001) recorded a constant-frequency of 64 kHz. Kofoky *et al.* (2009: 379) reported the calls of 28 individuals from six different sites in Madagascar, which produced narrowband and long CF calls which terminate with brief FM elements with a high duty cycle (31.2 %) and maximum energy at about 66.6 kHz. The calls consisted of a maximum of three harmonics most energy in the fundamental or second harmonic.

Ramasindrazana *et al.* (2015b: 85) reported a sexual dimorphism in bats from the western half of Madagascar. In males, the average forearm length was 93.1 mm and they emitted calls at 68.6 kHz. In females, the average forearm length was 83.9 mm and their calls were at 72.9 kHz. They also found that females from the far northern part of the island (Ankarana) emitted calls that were much lower than expected from size.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 61 kHz and duration: 12 ms. Hending *et al.* (2023: 372) mentioned F_{peak}: 63.3 ± 0.9 kHz, duration: 15 ± 11 ms, and interpulse interval: 74 ± 50 ms.

For 140 calls from the Sahamalaza-Iles Radama National Park, Hending *et al.* (2021a: 158) reported F_{peak}: 64.0 ± 1.52 (60.0 - 66.0) kHz, F_{min}: 58.3 ± 1.85 (50.0 - 60.0) kHz, F_{max}: 73.8 ± 1.32 (70.0 - 76.0) kHz, duration: 14.2 ± 3.46 (8.4 - 24.5) ms, and interpulse interval: 60.7 ± 31.46 (29.4 - 220.1) ms. In the same area they also found an additional sonotype with a peak frequency of about 78 kHz [F_{peak}: 77.7 ± 2.24 (72.0 - 82.0) kHz, F_{min}: 71.5 ± 1.99 (66.0 - 76.0) kHz, F_{max}: 86.7 ± 1.82 (82.0 - 91.0) kHz, duration: 7.7 ± 2.03 (4.0 - 14.3) ms and interpulse interval: 42.4 ± 18.26 (19.4 - 114.9) ms]. Given the fact that there is a high echolocation divergence among the genetically different populations, and also among male and female *Macronycteris commersoni* individuals, Hending *et al.* (2021a: 159) cannot exclude that this sonotype represents a second phonic type for the species or that these calls were produced by either a yet undescribed species or a species for which the calls have not yet been recorded (e.g., *Macronycteris cryptovalorana*).

MOLECULAR BIOLOGY:
Karyotype
2N = 52 and FN = 60, containing one large metacentric, a medium-sized submetacentric, three pairs of medium-to-small-sized metacentrics. The others are acrocentric. The X chromosome is a large sub-metacentric one and the Y an acrocentric (see Richards *et al.*, 2016d: 187, 191).

HABITAT:
Dammhahn and Goodman (2013: 108) indicate that the lower one-half of forest and perhaps partially open areas form the foraging habitat of this species. The home range of males is 31.8 ± 9.2 ha and of females 41.7 ± 12.9 ha (Razafimanahaka *et al.*, 2016: 423).

Crowley and Goodman (2025: 4) mention that it is widespread in both intact and degraded forests, and in the ecotone between forests and agricultural areas.

HABITS:
Bouchard (2001b: 109) mentions that males scent-mark their territories and mates by rubbing them with their glandular areas.

ROOST:
M. commersoni roosts singly in trees at some sites (Jenkins and Racey, 2008). Razafimanahaka *et al.* (2016: 427) found that these roosts are generally on branches of trees (*Uapaca ferruginea* Baill., *Canarium boivinii* Engl., *Diospyros* sp., *Gaertnera* sp. and *Erythroxylum corymbosum* Boivin ex Baill.) with a diameter at breast height of about 8.2 ± 0.7 cm and at 5.4 ± 0.2 m above the ground. *Aucoumea klaineana* Pierre [angouma, gaboon, or okoumé], an introduced tree in plantations, is hardly used by the bats. The mean distance between the roost and the foraging area was 313.9 ± 15.3 m (max: 1.6 km).

Reher *et al.* (2018: 1024) indicated that the bats chose to roost in the hottest and most humid cave in the region, where the environment was more buffered than in the cooler caves, which were preferred by other bat species.

Occasionally, open roofs of rural buildings are also used as roost (Garbutt, 2022: 81).

MIGRATION:
Reher *et al.* (2019: 121) found that *M. commersoni* was only present in two southwestern Madagascan caves during the wet season, whereas other species such as *Triaenops menamena* and *Miniopterus mahafaliensis* were present in both the dry and wet season. However, Garbutt (2022: 81) (referring to Reher *et al.*, 2018) suggests that they might not migrate during the dry season but remain in the cave in a torpid state for up to two months.

DIET:
Razakarivony *et al.* (2005) examined the stomachs of 11 individuals and found that 90 % of the diet were Coleoptera. Rakotoarivelo *et al.* (2007) found *M. commersoni* mainly to consume Coleoptera, but also included large-bodied taxa such as Cicadidae, Lucanidae, and Passalidae.

In the Tsimanampetsotsa NP, Ramasindrazana *et al.* (2012: 120-121) reported faecal pellets containing 76.2 ± 19.1 volume percent Coleoptera, 20.0 ± 20.0 Blattaria, 2.4 ± 1.0 Homoptera/Hemiptera and 1.4 ± 0.9 Hymenoptera. No Blattaria were found during the wet season, whereas the percentage Coleoptera rose to 93.0 (from 72.0 in the dry season).

Rakotondramanana *et al.* (2015: 78) report the following prey items (mean volume percentages ± 1 SD, mean frequency percentages ± 1 SD): Coleoptera (46.6 ± 38.85, 77.7 ± 36.36); Hymenoptera (6.6 ± 11.49, 26.1 ± 40.70); Lepidoptera (8.2 ± 13.34, 26.1 ± 37.85); Isoptera (37.4 ± 40.53, 49.2 ± 48.41); Homoptera (0.9 ± 3.49, 6.7 ± 19.85); Blattoidea (0.2 ± 0.98, 0.2 ± 0.98); Arachnida (0.04 ± 0.20, 0.77 ± 3.92).

Crowley and Goodman (2025: 4) indicated that this bat is an "entomophage" (which besides insects also includes arachnids and worms), which predominantly eats Coleoptera, but is also suspected of eating small frogs in southeastern Madagascar.

PREDATORS:
Goodman *et al.* (1991: 22) reported an almost intact skull in a pellet from the Madagascar Long-eared Owl *Asio madagascariensis* (A. Smith, 1834). Additionally, Goodman and Griffiths (2006) found that *M. commersoni* comprised 0.6 % of the total biomass predated by the barn owl (*Tyto alba* (Scopoli, 1769)).

Mikula *et al.* (2016: Supplemental data) mention the Madagascan serpent eagle (*Eutriorchis astur* Sharpe, 1875) as avian diurnal predator.

POPULATION:
Structure and Density
There is little information available on population size, but this species can roost in colonies of many
thousand individuals. It is thought to have declined in the region of 20-25% over the past 15 years (Monadjem *et al.*, 2019a).

Trend
2016: Decreasing (Monadjem *et al.*, 2019a).

ACTIVITY AND BEHAVIOUR:
Preliminary observations in Madagascar reveal that foraging behaviour of *M. commersoni* involves short hunting flights from night perches (Russ *et al.*, 2003).

Reher *et al.* (2018: 1015) found that *M. commersoni* can enter in a torpor state to cope with the dry and unpredictable environmental conditions in the dry spiny forest of south-western Madagascar. On average, it took the bats 4.1 ± 1.4 minutes to enter torpor and 12.3 ± 3.3 minutes to arouse (p. 1020). Reher and Dausmann (2021: 3) observed that on warm days, the bats alternated between short micro-torpor bouts lasting between 3 and 53 min (12.4 ± 10.5 minutes; n = 462) and resting metabolic rate. On hot days ($T_{ambient}$ 37.8 ± 1.85°C), however, they extended their torpor bouts over the hottest part of the day ant that their skin temperatures could rise to 42.9°C. These types of torpor are typical for the *M. commersoni* populations in a western Malagasy dry deciduous forest, where

the bats roost solitary in open vegetation (Reher *et al.*, 2021: 2). The populations in a dry spiny forest in southwestern Madagascar roost in a large colony in a hot cave with a stable microclimate. The torpor rates used by these bats was relatively low in the resource-poor and cooler dry season. During that period the bats hardly left the cave and Reher *et al.* (2021: 12) suspected that the bats would hibernate and display prolonged torpor (-> 24 hours). However, it turned out that only 60 % of the bats used extended torpor and 80 % used repetitive micro-torpor bouts.

REPRODUCTION AND ONTOGENY:
Razafimanahaka *et al.* (2016: 429) recorded flying juveniles in early February and March, which suggests that births take probably place in January. They were also unable to catch females in nets in January, possibly because they were not foraging or because they had moved to maternity roosts.

Goodman *et al.* (2023b: 236) reported that - at Antsahabe - of five females captured in early October to late November 2019, three were pregnant (embryos with crown-rump length 16 - 35 mm). Three animals collected in Andatsakala (March 2022) included two non-breeding males and one subadult female. Therefore, it seems that females give birth at the end of the year.

PARASITES:
BACTERIA
Gomard *et al.* (2016: 5) and Esteves *et al.* (2022: 8) reported the presence of *Leptospira* bacteria in 13 out of 27 tested bats (48.1 %).

VIRUSES:
Nieto-Rabiela *et al.* (2019: Suppl.) reported the following viruses from "*Hipposideros commersoni*": African bat icavirus, Bat coronavirus, Bat flavivirus, Bat hepacivirus, Bat paramyxovirus, Bat pegivirus, Bat rhabdovirus, Leopards Hill Virus, Shimoni bat lyssavirus.

Astroviridae
Hoarau *et al.* (2021: Suppl.) reported on the presence of these viruses.

Rhabdoviridae
The serum of one of six bats tested by Mélade *et al.* (2016a: 6) showed a reaction against *Duvenhage lyssavirus*, and one of four against *European bat lyssavirus 1*.

UTILISATION:
Goodman (2006) observed in February 2005, in south-western Madagascar, that local people were extensively hunting *M. commersoni*. This coincided with the onset of famine in the region. Goodman (2006) describes the hunting method used by local inhabitants. In PN d'Ankarafantsika, local people - while collecting forest tubers - occasionally encounter roosting *M. commersoni* which are taken back to the village and eaten (Jenkins and Racey, 2008).

In the villages *M. commersoni* is either roasted over a fire or boiled.

Goodman (2006) concluded that harvest level of *M. commersoni* (ca. 70,000 - 140,000 bats annually) surpasses the likely productivity of the species in the area. Goodman *et al.* (2002) suggested that hunting at the Mitoho Cave in PN de Tsimanampetsotsa may have been the reason *M. commersoni* abandoned the site.

See also Goodman *et al.* (2008d) and Jenkins and Racey (2008).

Tackett *et al.* (2022: 8) [referring to Fernández-Llamazares *et al.* (2018)] report that fluids of *M. commersoni* are used to "treat" baldness and coughs.

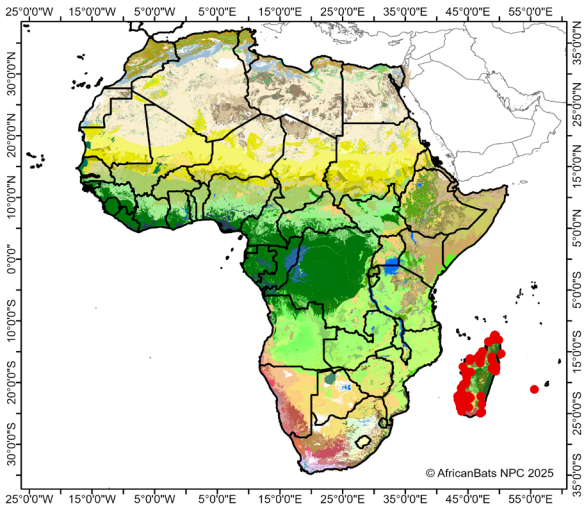

Figure 69. Distribution of *Macronycteris commersoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar, Réunion.

Macronycteris cryptovalorona (Goodman, Schoeman, Rakotoarivelo and Willows-Munro, 2016)

*2016. *Hipposideros cryptovalorona* Goodman, Schoeman, Rakotoarivelo and Willows-Munro, Zool. J. Linn. Soc., 177 (2):428, 443. Publication date: 20 May 2016. Type locality: Madagascar: Fianarantsoa province: Parc National de l'Isalo, along Sahanafa River, near foot of Bevato: Berenty-Betsileo, 28 km SE [22 19.0 S 45 17.6 E, 550 m]. Holotype: FMNH 175970: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 9

December 2002; original number: SMG 13399. Type locality: Madagascar: Province de Fianarantsoa, Parc National de l'Isalo, along Sahanafa River, near foot of Bevato, 28 km south-east of Berenty-Betsileo, 22°19.0′S, 45°17.6′E, 550 m a.s.l. Paratype: FMNH 184173: ♀. Collected by: Steven M. Goodman; collection date: February 2005; original number: SMG 14582. - Etymology: The name is derived from the Greek "kryptos", meaning hidden or concealed, and from the Sakalava dialect of Malagasy "valorona", which is the local vernacular name of *Hipposideros* and refers to its distinct nasal structure, and can be translated as "eight nose", referring to the complicated and multiple layers of the nose structure (see Goodman *et al.* (2016: 444).

2017. *M[acronycteris] cryptovalorona* Foley, Goodman, Whelan, Puechmaille and Teeling, Acta Chiropt., 19 (1): 10. Publication date: June 2017. (Current Combination).

2019. *Macronycteris cryptovalorona:* Monadjem, Handbook Mammals of the World, vol 9 Bats: 232. (Name Combination, Current Combination).

TAXONOMY:
Analysing the cyt *b* sequences of 148 Madagascan *M. commersoni* s.l. specimens, Goodman *et al.* (2016: 428) found three well-supported monophyletic clades: A, B, and C. Clades B and C form a monophyletic lineage, which they were able to refer to *M. commersoni* s.s. Clade A showed a 9 to 11 % sequence variation with *M. commersoni* s.s., enough to warrant a separate species status. This new species is known from two adult females only.

COMMON NAMES:
English: Madagascar cryptic leaf-nosed bat. French: La Phyllorhine cryptique de Madagascar. German: Kryptische Madagaskar-Rundblattnase, Madagaskar-Rundblattnase.

SIMILAR SPECIES:
Grunwald *et al.* (2025: 296) indicate that further research is needed to determine better ways to distinguish *Macronycteris cryptovalorona* from *Macronycteris commersoni*.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Only known from a limited number of localities in southwestern Madagascar (Garbutt, 2022: 82).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

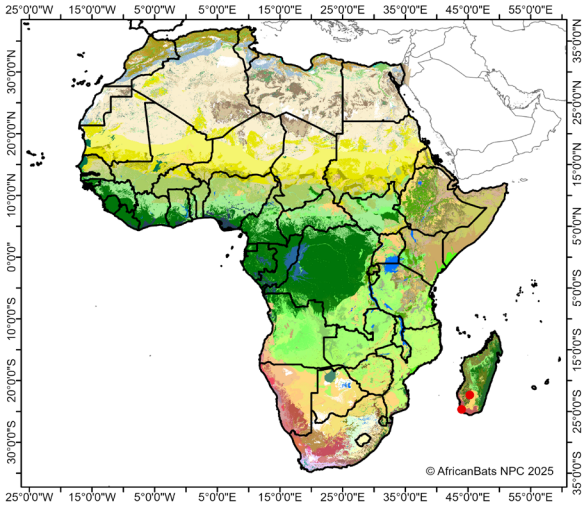

Figure 70. Distribution of *Macronycteris cryptovalorona*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Macronycteris gigas (Wagner, 1845)

*1845. *Rhinolophus Gigas* Wagner, Arch. Naturgesch. Berlin, 11 (1): 148. Publication date: 1845. Type locality: Angola: Benguela [12 34 S 13 24 E, 160 m]. [Goto Description].

1906. *H[ipposiderus]. gigas gambiensis* K. Andersen, Ann. Mag. nat. Hist., ser 7, 17 (97): 42. Publication date: 1 January 1906. Type locality: The Gambia: "Gambia". [Goto Description]. Holotype: NHMUK 1842.9.27.36: ad ♀, alcoholic (skull not removed). Presented/Donated by: 13th Earl of Edward Smith Stanley Derby.

1917. *Hipposideros gigas niangaræ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 438, pl 51, fig 1. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Niangara [03 24 N 27 52 E]. [Goto Description]. Holotype: AMNH 49103: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 2 June 1913; original number: 2069.

1939. *Hipposideros gigas viegasi* Monard, Arq. Mus. Bocage, 10: 70. Publication date: March 1939. Type locality: Guinea-Bissau: Madina Boé [11 45 N 14 13 W]. [Goto Description]. Syntype: [Unknown] |TS483|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 909. Syntype: [Unknown] |TS484|: ♂, skin and skull. Collected by: P. Rigaux; collection date: 9 March 1938; original number: 910. Syntype: [Unknown] |TS485|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March

1938; original number: 911. Syntype: [Unknown] |TS486|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 912. Syntype: [Unknown] |TS487|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 913. Syntype: [Unknown] |TS488|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 914. Syntype: [Unknown] |TS489|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 917. Syntype: [Unknown] |TS490|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 918. Syntype: [Unknown] |TS491|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 919. Syntype: [Unknown] |TS492|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 920. Syntype: [Unknown] |TS493|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 921. Syntype: [Unknown] |TS494|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 922. Syntype: [Unknown] |TS495|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 923. Syntype: [Unknown] |TS496|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 924. Syntype: [Unknown] |TS497|: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 926. Syntype: MHNG 1079.070: skull and alcoholic. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 918. Syntype: MHNG 1489.080: skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 926. Syntype: MHNG 861.043: ♀, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 912. Syntype: MHNG 861.044: ♀, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 913. Syntype: NMBA 5266/9283: ♂. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 915. Syntype: NMBA 5267/9284: ♀. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 908. Syntype: RMCA 15305: ♂, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 925. Syntype: RMCA 15306: ♀, skin and skull. Collected by: Dr. Albert Monard; collection date: 9 March 1938; original number: 916. - Comments: Monard (1939: 70) mentions a series of 19 specimens (nrs 908 to 926 and 14 skulls).

2017. *Macronycteris gigas:* Foley, Goodman, Whelan, Puechmaille and Teeling, Acta Chiropt., 19 (1): 7. Publication date: June 2017. (Current Combination).

? *Hipposideros commersoni gigas:* (Name Combination).

? *Hipposideros commersoni niangarae:*

? *Hipposideros commersoni:* (Name Combination).

? *Hipposideros gigas gigas:* (Name Combination).

? *Hipposideros gigas niangarae:*

? *Hipposideros gigas:* (Name Combination).

? *Hipposideros marungensis marungensis:*

? *Hipposideros marungensis:*

Taxonomy:

McWilliam (1982: 9) found two forms of "*Hipposideros commersoni*" occurring sympatrically in Kenya, which he separated into "*H. commersoni*" and "*H. gigas*", with the latter species being significantly larger and heavier than the prior.

Simmons (2005: 369, 372, 377) restricts "*Hipposideros commersoni*" to Madagascar, and assigns *H. gigas*, *H. vittatus* (including *marugensis*) and *H. thomensis* as the mainland forms based on morphology and echolocation differences. Meester *et al.* (1986) state that Hayman and Hill (1971) note that *marungensis* may be antedated by *vittata* Peters, 1852, from Ibo Island, which is more often regarded as a synonym of the subspecies *gigas* Wagner, 1845 (Allen, 1939a, Ellerman *et al.*, 1953, Hill, 1963a).

The karyotypic studies for the African mainland forms (*M. vittatus* and *M. gigas*) indicate that they share the exact same numbers and forms (Porter *et al.*, 2010); Rautenbach *et al.*, 1993; Koubínová *et al.*, 2010b). Koubínová *et al.* (2010b) suggest that African mainland forms may belong to the same species.

Common Names:

Afrikaans: Commerson se bladneusvlermuis, Commerson-bladneusvlermuis, Commersonse Blaarneusvlermuis. Chinese: 巨蹄蝠. Czech: pavrápenec obrovský. English: Commerson's Leaf-nosed Bat, Giant Leaf-nosed Bat, Commerson's roundleaf bat, Commerson's Rhinolph. French: Chauve-souris de Commerson à nez feuillu, Phyllorine de Commerson. German: Riesen-Rundblattnase. Kinande (DRC): Mulima. Portuguese: Morcego de nariz enfolhado de commerson.

Similar Species:

Grunwald *et al.* (2025: 296) indicate that further research is needed to determine better ways to distinguish *Macronycteris gigas* from *Macronycteris vittata*.

Conservation Status:

Global Justification

Currently not been globally assessed hence no justification.

Assessment History

Global

No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Gambia over Liberia (Monadjem *et al.*, 2016y: 365 as *Hipposideros gigas*), Ghana (Decher and Fahr, 2007: 17 as *Hipposideros gigas*), Benin (Capo-Chichi *et al.*, 2004: 162), Cameroon (Waghiiwimbom *et al.*, 2019b: 6), Central African Republic (Lunde *et al.*, 2001: 537), Republic of the Congo (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 538 as *H. vittatus*; Bates *et al.*, 2013: 335, as *H. commersoni*) to Ethiopia, south to Angola (Crawford-Cabral, 1989: 17, as *H. c. gigas*; Monadjem *et al.*, 2010d: 538, as *H. gigas* and *H. vittatus*), Zambia (Ansell, 1967; Ansell, 1974; Monadjem *et al.*, 2010d: 538 as *H. vittatus*), Zimbabwe (Monadjem *et al.*, 2010d: 538 as *H. vittatus*), Namibia (Monadjem *et al.*, 2010d: 538 as *H. vittatus*), Botswana (Smithers, 1971; Monadjem *et al.*, 2010d: 538 as *H. vittatus*), Transvaal (South Africa (Monadjem *et al.*, 2010d: 538 as *H. vittatus*), Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Monadjem *et al.*, 2010d: 538 as *H. vittatus*) and Mozambique (Monadjem *et al.*, 2010d: 538, Monadjem *et al.*, 2010c: 381 as *H. vittatus*).

Rainho and Ranco (2001: 54) report "*H. commersoni*" from Guinea-Bissau (see also Peters, 1870; Seabra, 1900c; Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992).

Benda *et al.* (2025: 68) indicate that the distribution range for this species (as for *Macronycteris vittata*) is still insufficiently known, but is considered to be mainly West African. In East Africa it is known only from the coastal areas of southeastern Kenya and Tanzania.

DETAILED MORPHOLOGY:
Brain
Kruger *et al.* (2010a) describe - based on three brains from Kenya and using immunohistochemical methods - the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems. Kruger *et al.* (2010b) also describe the distribution of Orexin-A immunoreactive cell bodies and terminal networks.

ECHOLOCATION:
O'Shea and Vaughan (1980) reported an ultrasonic frequency of 155 kHz for Masalani in Kenya. A highest frequency of 62 kHz was recorded at Sengwa in Zimbabwe by Jacobs (1996) and Fenton and Bell (1981), and at Pafuri in South Africa by Aldridge and Rautenbach (1987). Monadjem *et al.* (2010c: 381) reported from Mozambique [as *M. vittatus*] that the peak echolocation frequencies ranged between 64 - 66 kHz (ANABAT). Rainho *et al.* (2010a: 21) report [as *Hipposideros thomensis*] the calls of 10 individuals from Saõ Tomé.

Monadjem *et al.* (2013b: 351) report the F_{max} to be 52.0 ± 0.41 (51 - 53) kHz for four specimens from Mount Nimba.

For two unsexed bats, two females and three males from the Shimoni cave in Kenya, Webala *et al.* (2019b: 15) reported an F_{max} value ranging between 54.8 and 55.3, 53.4 and 54.3, and 53.4 and 54.1 kHz, respectively. The duration of the calls were respectively 12.3 to 14.6, 17.1 to 19.2, and 10.4 to 15.7 ms.

Patterson *et al.* (2020: 137) mention a peak frequency of 53.4 - 54.8 kHz, which distinguishes this species from *M. vittatta*, which has a peak frequency of 64 - 70 kHz.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 115 calls of 4 bats: F_{peak}: 51.9 ± 1.0 (50.7 - 53.6) kHz, F_{min}: 46.2 ± 1.1 (44.5 - 47.9) kHz, F_{max}: 52.7 ± 0.7 (52.2 - 53.9) kHz, duration: 11.9 ± 2.0 (9.1 - 14.6) ms.

For one female from the Boundou cave in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data: F_{pmin}: 51 kHz, F_{pmean}: 54.2 kHz, F_{ppeak}: 54.3 kHz, F_{flat}: 54 kHz, F_{knee}: 54.8 kHz, F_{mean}: 54.3 kHz, Duration: 12.4 ms.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported for female individuals with a diploid number of 2*n* = 52, FN = 60?, and BA = 10?. Porter *et al.* (2010) found the same diploid number described by Rautenbach *et al.* (1993) for a single male Gabonese specimen reported as *Hipposideros gigas*, with six pairs of biarmed and 20 pairs of acrocentric chromosomes (including the sex chromosomes). Koubínová *et al.* (2010b) reported for two females from Senegal [as "*Hipposideros gigas*"] a 2*n*= 52, and FNa= 60, supposing the X chromosomes to be (sub)metacentric. The autosomes would then consist of one pair of large metacentrics, two pairs of medium-sized sub-metacentrics, one pair of small submetacentrics, one pair of small metacentrics, and 20 pairs of acrocentrics, the two smallest acrocentric pairs were of a dot-like appearance.

HABITAT:
Monadjem *et al.* (2016y: 365) recorded this species widely in forested and disturbed habitats in the Mount Nimba area, at altitudes between 460 and 1,060 m. In Angola, it occurs in lowland forest and moist savanna (Beja *et al.*, 2019: 388). In the Yapi Daniel private forest (Côte d'Ivoire), it was found the most abundant in the edge zone (Kadjo *et al.*, 2021: 26).

MIGRATION:
Chidoti *et al.* (2022: 6) mention *Macronycteris gigas* to be a migratory species, which was primariy present at the Magweto cave (Zimbabwe) between October and March.

DIET:
Andreas (2010: 266) indicates that there is some proof from Senegal that *M. gigas* might be carnivorous, as was already suggested by Eger and Mitchell (2003) for *M. commersoni*.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

REPRODUCTION AND ONTOGENY:
Kurta and Kunz (1987: 82) report that, at birth, the young has about 25.2 % of the mother's body mass (28.0 versus 111.0 g).

Kurta and Kunz (1987: 227) indicate that in Gabon, all adult females (of *M. commersoni*) were pregnant between July and October (with implantation occurring in mid June), and generally gave birth in October. The young is being fed with milk until the beginning of May. The males were in full spermiogenesis by mid April.

PARASITES:
DIPTERA
Nycteribiidae
Nycteribia schmidlii scotti Falcoz, 1923, *Eucampsipoda africana* Theodor, 1955, and *Penicilidia fulvida* (Bigot, 1885) (Obame-Nkoghe *et al.*, 2016: 5, Gabon)

Streblidae
Brachytarsina allaudi (Falcoz, 1923) (Obame-Nkoghe *et al.*, 2016: 5, Gabon). Szentiványi *et al.* (2019a: Suppl.) indicated that a similar bat fly from a Gabonese "*Hipposideros gigas*" was carrying an *Arsenophonus* sp. bacteria. *Raymondia huberi* Frauenfeld, 1856 group (Obame-Nkoghe *et al.*, 2016: 5, Gabon).

Júnior *et al.* (2020: Suppl.) reported *Eucampsipoda africana* Theodor, 1955) from "*Hipposideros gigas*".
Decher *et al.* (2021: 271) reported six *Ascodipteron variisetosum* Maa, 1965 specimens being present on one bat.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in "*Hipposideros commersonii*" [as they considered "*H. vittatus*" to be a separate species, the bats probably represent *M. gigas*]: Astroviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 to 1999, for antibodies for SARS-CoV in sera of 16 individuals from the Oriental Province, DRC. None tested positive (0/16). Tong *et al.* (2009) found coronavirus RNA in this bat, collected in 2006 in Kenya. In Nigeria, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs.

Maganga *et al.* (2020: 1) reported viruses belonging to the genera *Alphacoronavirus* and *Betacoronavirus* from bats in Gabon. These were significantly present in July and October.

38.9% of the bats collected by Chidoti *et al.* (2022: 7) in Zimbabwe tested positive for coronaviruses, with a peak of 56.4% in the October 2020 gestation period.

Meyer *et al.* (2024: 4) reported that one Ghanaian bat [possibly not the same] was infected by CoV 2b, Cov 2bBasal and Cov 2c viruses.

Filoviridae - Filoviruses
Marburgvirus
Towner *et al.* (2007) reported on one individual [as *Hipposideros gigas*] from Gabon, which they tested for Marburg virus RNA by conventional and real-time RT-PCR and for anti-Marburg virus IgG antibodies by ELISA. The results were negative.

Ebolavirus
Fiorillo *et al.* (2018: 7) included "*Hipposideros gigas*" in their Ebola distribution model, indicating that there is evidence that suggests their relation with filoviruses infection cases, although they provide no details on this.

Flaviviridae
Maganga *et al.* (2014a: 5) tested 227 bats from Gabon of which only one tested positive for a *Flavivurus*. This is probably the Bat Flavivirus

Belinga virus mentioned by Shchelkanov *et al.* (2020a: 18).

Pegivirus (BPgV)
1 out of 5 Nigerian specimens examined by Quan *et al.* (2013: Table S5) was infected by clade K type *Pegivirus*.

Nairoviridae
Orthonairovirus
Ishii *et al.* (2014: 2) isolated a new Nairovirus (tentatively called Leopards Hill Virus - LPHV) from a *H. gigas* specimen collected in the Leopards Hill cave in Lusaka, Zambia. In a test on 129 specimens from Gabon, Müller *et al.* (2016: 3) found 32 of them positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that two of the 20 specimens they examined from Ghana tested positive for *Morbillivirus*, and one for *Rubulavirus*.

In their overview table, Maganga *et al.* (2014a: 8) report that the following viruses were already found on "*Hipposideros gigas*": Rubulavirus, Morbillivirus unclassified, Flavivirus, Shimoni bat virus, SARS-like CoV.

Picornaviridae:
Mischivirus
This virus was reported by Zeghbib *et al.* (2019: Suppl.) from a Congolese bat.

African bat Icavirus
This virus was reported by Gonzalez and Banerjee (2022: 17).

Reoviridae
Rotavirus
Simsek *et al.* (2021: 4) found *Rotavirus A* in *M. gigas* specimens from Gabon.

Rhabdoviridae:
Lyssavirus - Rabies related viruses
In Nigeria, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluroescent anitbody testing.
Shimoni
Kuzmin *et al.* (2010a) detected a new lyssavirus, Shimoni bat lyssavirus from the brain of a dead "*H. commersoni*" bat found in the coastal region of Kenya. Genetic distances demonstrated that this may be a new lyssavirus species.

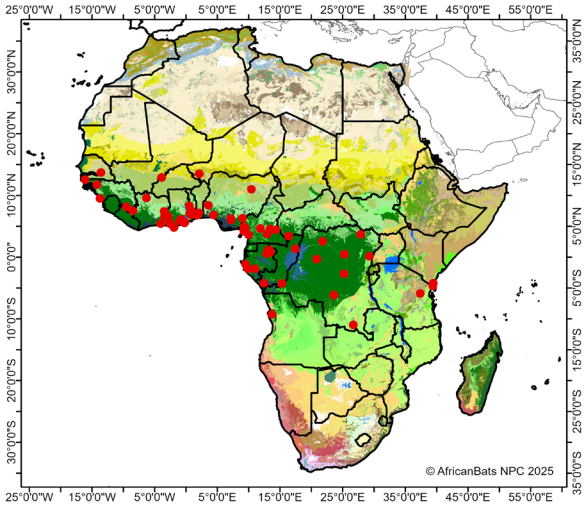

Figure 71. Distribution of *Macronycteris gigas*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Niger, Nigeria, São Tomé and Príncipe, Senegal, Tanzania, The Gambia, Togo.

Macronycteris thomensis (Bocage, 1891)

*1891. *Phyllorhina commersoni var. thomensis* Bocage, J. Sci. mat. phys. nat., ser 2, 2 (6): 88. Publication date: September 1891. Type locality: São Tomé and Príncipe: São Tomé Island. [Goto Description]. - Comments: Bocage (1891: 88) mentions one male and one female specimen.
2005. *Hipposideros thomensis:* Simmons, Mammal Species of the World. Order Chiroptera, 377. (Name Combination).
2017. *M[acronycteris] thomensis* Foley, Goodman, Whelan, Puechmaille and Teeling, Acta Chiropt., 19 (1): 10. Publication date: June 2017. (Current Combination).

TAXONOMY:
Considered a valid species by Simmons (2005: 377), Matthiessen (1985: 565), Simmons and Cirranello (2023a: 11).

COMMON NAMES:
English: São Tomé Leaf-nosed Bat. German: Sâo-Tomé-Rundblattnase.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Saõ Tomé (Rainho *et al.*, 2010a: 26 as *H. thomensis*)

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Rainho *et al.* (2022: 606) described this species as a dwarf form of *Macronycteris gigas*.

ECHOLOCATION:
Rainho *et al.* (2022: 605) mention the following characteristics for 10 calls: F_{min}: 66.0 ± 0.8 (64.3 - 66.8) kHz, F_{max}: 68.0 ± 1.0 (66.8 - 70.2) kHz, F_{maxE}: 67.2 ± 0.4 (66.4 - 68.0) kHz, duration: 20.7 ± 4.0 (15.6 - 28.6) ms and Interpulse interval: 66.8 ± 17.4 (43.2 - 106.4) ms.

HABITAT:
On São Tomé, Castro-Fernandes *et al.* (2024: 1) reported this species as being most active in forests and shaded plantations.

ROOST:
Rainho *et al.* (2022: 606) mentioned an underground colony of several hundred animals, but also a single individual roosting under the leaves of a palm tree.

ACTIVITY AND BEHAVIOUR:
Araújo-Fernandes *et al.* (2025: 831) reported that *Macronycteris thomensis* is active throughout the night, with a peak around the middle of the night.

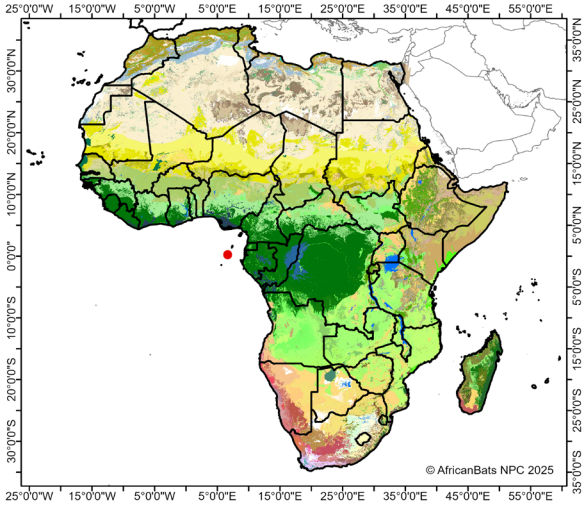

Figure 72. Distribution of *Macronycteris thomensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
São Tomé and Príncipe.

Macronycteris vittata (Peters, 1852)

*1852. *Phyllorrhina vittata* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 32, pl 6; pl 13, fig 7 - 13. Publication date: 1852. Type locality: Mozambique: Cap Delgado group [=Querimba islands]: Ibo Island [ca. 12 20 S]. [Goto Description]. Syntype: ZMB 363: ♀, alcoholic, skull and skeleton. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 37150: ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. Legs and wings missing, see Turni and Kock (2008: 40). - Etymology: From the feminine Latin adjective *vittàta* meaning "striped", referring to the occurrence of dorsal light bands in this species (Lanza *et al.*, 2015 149).

1879. *Phyllorhina commersoni:* Dobson, Proc. zool. Soc. Lond., 1878, IV: 879. Publication date: April 1879.

1887. *Phyllorhina commersonii var. marungensis* Noack, Zool. Jb. Syst., 2 (2): 272, pl 10, fig 31 - 33. Publication date: 7 May 1887. Type locality: Congo (Democratic Republic of the): W Shore Lake Tanganyika, Marungu: Qua Mpala [=Mpala / Pala] [06 43 S 29 31 E]. [Goto Description]. Syntype: ZMB 6312: ♂, skin and skull. Collected by: Richard Böhm; collection date: 12 July 1883. See Turni and Kock (2008). Syntype: ZMB 86257: skin and skull. Collected by: Richard Böhm; collection date: 12 July 1883. Old number A4269; see Turni and Kock (2008). Syntype: ZMB 86258: skull only. Collected by: Richard Böhm; collection date: 12 July 1883. Old number A4268; see Turni and Kock (2008). Syntype: ZMB 86259: skull only. Collected by: Richard Böhm; collection date: 12 July 1883; original number: A4270. See Turni and Kock (2008). - Comments: Actually, in Noack (1887: 272), the name is mentioned as "*Phyllor hinacommersonii Peters, var. marungensis N.*". Noack (1887: 272) also mentions five specimens, including one female, collected in July-August.
Ansell and Dowsett (1988: 34) refer to Hayman and Hill (1971: 28) who indicate that *marungensis* may be antedated by *vittata* Peters, 1852.

1904. *Hipposideros Commersoni mostellum* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (77): 385. Publication date: 1 May 1904. Type locality: Kenya: Tana River [ca. 02 33 S 40 31 E, 700 ft]. [Goto Description]. Holotype: NHMUK 1889.3.8.3: ad ♂, skin and skull. Presented/Donated by: H.C.V. Hunter Esq.

1993. *Hipposideros commersoni matungensis:* Koneval, Honors Projects - Illinois Wesleyan University: 1. Publication date: 11 May 1993. (Lapsus).

2017. *M[acronycteris] vittatus:* Foley, Goodman, Whelan, Puechmaille and Teeling, Acta Chiropt., 19 (1): 10. Publication date: June 2017. (Current Combination).

2017. *Macronycteris vittata:* Musila, Prokop and Gichuki, Anthrozoös, 31 (2): 249. Publication date: 6 March 2018. (Current Combination).

2020. *Macronycteris vitattus:* Weier, Keith, Neef, Parker and Taylor, Diversity, 12 (188): 5. Publication date: 11 May 2020. (Lapsus).
? *Hipposideros commersoni marungensis:*
? *Hipposideros commersoni:* (Name Combination).
? *Hipposideros vittatus:* (Name Combination).
? *Macronycteris vittatus:* (Alternate Spelling).

TAXONOMY:
Simmons (2005: 369, 372, 377) restricts "*Hippposideros commersoni*" to Madagascar, and assigns *H. gigas*, *H. vittatus* (including *marugensis*) and *H. thomensis* as the mainland forms based on morphology and echolocation differences. Meester *et al.* (1986) state that Hayman and Hill (1971) noted that *marungensis* may be antedated by *vittata* Peters, 1852, from Ibo Island, which is more often regarded as a synonym of the subspecies *gigas* Wagner, 1845 (Allen, 1939a, Ellerman *et al.*, 1953, Hill, 1963a).

The karyotypic studies for the African mainland forms (*M. vittatus* and *M. gigas*) indicate that they share the exact same numbers and forms (Porter *et al.*, 2010); Rautenbach *et al.*, 1993; Koubínová *et al.*, 2010b). Koubínová *et al.* (2010b) suggests that African mainland forms may belong to the same species.

Foley *et al.* (2017: 3) indicate that the morphological characters used to distinguish *M. gigas* from *M. vittatus* are not straightforward and that these are generally used in combination with habitat and distribution data, which is complicated by the fact that their distributions partially overlap. They also indicate that the differences between the forms *gambensis* [sic], *marungensis, niangarae* and *viegasi* have been based on non-molecular characters, and as such the assignment of these synonyms is not yet definitive.

COMMON NAMES:
Chinese: 大白纹蹄蝠. Czech: pavrápenec pruhovaný. English: Striped Leaf-nosed Bat. German: Streifen-Rundblattnasen, Gestreifte Rundblattnase. Italian: Ipposìdero vittàto. Malawian: Mleme.

SIMILAR SPECIES:
Grunwald *et al.* (2025: 296) indicate that further research is needed to determine better ways to distinguish *Macronycteris vittata* from *Macronycteris gigas*.

CONSERVATION STATUS:
Global Justification
Assessed by Mickleburgh *et al.* (2020a) as Near Threatened (nearly meets criterion A4cd) as its global population is suspected to have declined by 25-30% over the past 10 years (two generations) and will continue to decline over next 5 years due to habitat loss and harvest, making it close to qualifying as Vulnerable under A4c. Although the species is still widely distributed, a large proportion of the global population of this species is found in a few very large cave roosting colonies that are threatened by forest loss and degradation and cave/mine loss, disturbance, and over harvest.

Assessment History
Global
2019: NT A4cd ver 3.1 (2001) (Mickleburgh *et al.*, 2020a). 2008: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2008z; Mickleburgh *et al.*, 2008z).

Bioko: Conenna *et al.* (2017: Suppl.) mentioned the status of "*Hipposideros thomensis*" as Least Concern (LC).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016v). 2004: considered a vagrant not assessed, single locality (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
Mickleburgh *et al.* (2020a) report that the species is still widely distributed, a large proportion of the global population of this species is found in a few very large cave roosting colonies that are threatened by forest loss and degradation and cave/mine loss, disturbance, and over harvest. A number of the major colonies are threatened by the mining of limestone caves, disturbance by tourists, and subsistence overhunting, particular for the use of their fat for making candles.

CONSERVATION ACTIONS:
This species is present in several protected areas in East Africa, it has been recorded from Tsavo National Park in Kenya. In southern Africa it has been recorded from the Kruger National Park in Limpopo Province, South Africa and from Gorongosa National Park, Mozambique (Monadjem *et al.*, 2010d). The Gorongosa site also includes a large roost in a natural cave network. Mickleburgh *et al.* (2020a) recommended that there is a need to protect important roosting sites of this species, and to limit collection of animals to sustainable levels. Additional studies are needed into the identity of populations currently allocated to *Hipposideros vittatus*.

GENERAL DISTRIBUTION:
Gambia over Benin (Capo-Chichi *et al.*, 2004: 162), Ghana (Decher and Fahr, 2007: 17 as *H. gigas*), Burkina Faso (Kangoyé *et al.*, 2015a: 608); Central African Republic (Lunde *et al.*, 2001: 537), Republic of the Congo (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 538) to Ethiopia, south to Angola (Crawford-Cabral, 1989: 17, as *H. c. gigas*; Monadjem *et al.*, 2010d: 538, as *H. gigas* and *H. vittatus*; Taylor *et al.*, 2018b: 62), Zambia (Ansell, 1967; Ansell, 1974; Monadjem *et al.*, 2010d: 538), Zimbabwe (Monadjem *et al.*, 2010d: 538), Namibia (Monadjem *et al.*, 2010d: 538), Botswana (Smithers, 1971; Monadjem *et al.*, 2010d: 538), Transvaal (South Africa (Monadjem *et al.*, 2010d: 538)), Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Monadjem *et al.*, 2010d: 538) and Mozambique (Monadjem *et al.*, 2010d: 538, Monadjem *et al.*, 2010c: 381); Madagascar; adjacent small islands..

Benda *et al.* (2023a: 67) indicate that *Macronycteris vittata* is primarily a southern and central African species, and therefore consider its presence in West Africa as doubtful. These records should probably be assigned to *Macronycteris gigas*.

Reported from the Tanzanian island of Pemba by O'Brien (2011: 287).

Rainho and Ranco (2001: 54) report "*H. commersoni*" from Guinea-Bissau (see also Peters, 1870; Seabra, 1900c; Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,043,916 km^2.

DETAILED MORPHOLOGY:
Brain
Using immunohistochemical methods, Kruger *et al.* (2010a) describe the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems based on three brains from Kenya. Kruger *et al.* (2010b) also describe the distribution of Orexin-A immunoreactive cell bodies and terminal networks.

Other
Koneval (1993) described several significant differences in the hyoid morphology of "*Hipposideros commersoni matungensis*" (from Kenya) and other bats of the family Rhinolophidae (including Hipposideridae): a modified stylohyal, fused to the auditory bulla; loss of the stylohyoid; addition of a new muscle, possibly from the stylopharyngeus; a modified mylohyoid profundus; and insertion of the ceratohyoid onto only the stylohyal. She found this morphology to be closest related to this of the east Asian *H. armiger*.

SEXUAL DIMORPHISM:
Muñoz-Romo *et al.* (2021: 169) mention that males have a frontal gland that presumably can be everted.

ECHOLOCATION:
O'Shea and Vaughan (1980) reported an ultrasonic frequency of 155 kHz for Masalani in Kenya. A highest frequency of 62 kHz was recorded at Sengwa in Zimbabwe by Jacobs (1996) and Fenton and Bell (1981), and at Pafuri in South Africa by Aldridge and Rautenbach (1987). From Mozambique, Monadjem *et al.* (2010c: 381) reported that the peak echolocation frequencies ranged between 64 - 66 kHz (ANABAT). Rainho *et al.* (2010a: 21) reports [as *H. thomensis*] the calls of 10 individuals from São Tomé.

Musila *et al.* (2018c: 44) [referring to Monadjem *et al.* (2010d: 162]) mention a high-duty, constant frequency call with a peak frequency of 61 kHz.

Two males and 7 females from three localities in Kenya had F_{max} values between respectively 67.9 and 70.1, and 64.3 and 69.7 kHz, whereas the duration was 14.3 to 17.9 ms for the males and 10.6 to 17.8 for the females.

In Sierra Leone, Weber *et al.* (2019: 21) recorded calls from a male and a female with a CF value of 62.5 (62.0 - 63.0) kHz.

Weier *et al.* (2020: Suppl.) reported on four calls from the Okavango River Basin with the following characteristics: F_{max}: 60.23 ± 6.07 kHz, F_{min}: 58.34 ± 6.08 kHz, F_{knee}: 59.52 ± 6.12 kHz, F_{char}: 59.17 ± 6.21 kHz, slope: 3.49 ± 9.39 OPS, duration: 3.84 ± 1.36 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 7 *Hipposideros vittatus* calls from the Kruger Park (RSA): F_{min}: 58.3 ± 1.5 (56.4 60.4) kHz, Duration: 8.8 ± 2.2 (5.9 11.7) ms, F_{max}: 64.4 ± 1.6 (61.5 66.3) kHz, F_{knee}: 63.6 ± 1.4 (61.1 65.2) kHz, F_{char}: 63.3 ± 1.4 (60.9 64.9) kHz,

Patterson *et al.* (2020: 137) mention a peak frequency of 64 - 70 kHz, which distinguishes this species from *M. gigas*, which has a peak frequency of 53.4 - 54.8 kHz.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 63.3 ± 1.40 kHz, F_{max}: 64.40 ± 1.60 kHz and F_{min}: 58.30 ± 1.50 kHz.

From Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 19 calls: Interpulse interval: 66.1 ± 21.3 (37.9 - 101.0) ms; F_{max}: 64.4 ± 1.9 (60.5 - 66.8) kHz; Start slope: -0.1 ± 0.0 (-0.1 - -0.2) kHz/ms; End slope: -1.7 ± 1.1 (-0.6 - -4.7) kHz/ms; Ledge duration: 1.3 ± 0.9 (0.3 - 3.3) ms.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported for female individuals with a diploid number of 2*n* = 52, FN = 60?, and BA = 10?. Porter *et al.* (2010) found the same diploid described by Rautenbach *et al.* (1993) for a single male Gabonese specimen reported as "*Hipposideros gigas*", with six pairs of biarmed and 20 pairs of acrocentric chromosomes. While, Koubínová *et al.* (2010b) reported for two females from Senegal [as *H. gigas*] a 2*n*= 52, and FNa= 60, including a pair of large metacentrics, three pairs of medium-sized sub-metacentrics, one pair of small submetacentrics, one pair of small metacentrics, and 20 pairs of acrocentrics, the two smallest acrocentric pairs were of a dot-like appearance.

HABITAT:
Tanshi *et al.* (2022a: 331) indicate that "*M. vittatus*" is savanna species, whereas *M. gigas* is primarily found in rainforests.

HABITS:
Happold and Happold (2023: 97) mention that - in Kenya - alternate hours of intense foraging (1 - 2 flights per minute) with periods of one hour or longer, where they took on the wing only three times an hour.

ROOST:
In Angola, *M. vittata* roosts in very large colonies in cave, mainly in the southern part of the country (Beja *et al.*, 2019: 388).

PREDATORS:
Messana *et al.* (1985: 337) shows a photo, taken in a cave in Somalia, on which a dead body of "*Hipposideros commersoni*" is being fed on by *Phaeophilacris* sp. (Insecta: Orthoptera: Phalangopsidae) and *Tura mesopotamica* Taiti and Ferrara, 1985 (Isopoda: Porcellionidae).

POPULATION:
Structure and Density
The global population is estimated to have declined in the past and will continue to decline in the future; it is suspected that the population will undergo a reduction of 25-30% over the three-generation period from 2009 to 2024. This species is historically known to exist in a few large roosts, containing tens of thousands of individuals, which seasonally migrate considerable distances. Some roosts that have been continuously used over decades, and perhaps much longer, appear to have been lost. In some areas the species roosts in smaller colonies (Mickleburgh *et al.*, 2020a).

Trend
2019: Decreasing (Mickleburgh *et al.*, 2020a).

REPRODUCTION AND ONTOGENY:
A pregnant female was recorded on 26 March by Weber *et al.* (2019: 23) in Sierra Leone.

Benda *et al.* (2022: 306) found no signs of reproduction in a female bat collected in December in Zambia.

PARASITES:
BACTERIA
Bartonellae
McKee *et al.* (2021: Suppl.) reported GenBank numbers for *Bartonella* sp. from Kenyan "*Hipposideros vittatus*". A verys similar *Bartonella* sp. was also reported from Zambian bats by Qiu *et al.* (2020: 1).

HAEMOSPORIDA
Blood samples from Zambian *M. vittata* examined by Qiu *et al.* (2019: 236) revealed the presence of two *Trypanosoma* sp., very similar to *T. conorhini* and *T. dionisii* clades.

DIPTERA
Streblidae
Ascodipteron variisetosum Maa, 1965 from Robertspoort, Liberia and Ghana, where the cysts were found under the upper arm (Haeselbarth *et al.*, 1966: 107, hosts identified as *H. commersoni*). *Raymondia huberi huberi* Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254).

Nycteribiidae
Dick *et al.* (2023: 71) mentioned the nycteribiid fly *Cyclopodia greeffi greeffi* Karsch, 1884 has been found from *Macronycteris vittatus*, but they also point out that this might have been an erroneous record.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in "*Hipposideros vittatus*": Paramyxovirus.

Coronaviridae - Coronaviruses
Alphacoronavirus
SARS-CoV (subgenus *Duvinacovirus*)
Müller *et al.* (2007b) tested between 1986 to 1999, for antibodies for SARS-CoV in sera of 16 individuals from the Oriental Province, DRC. None tested positive (0/16). Tong *et al.* (2009) found coronavirus RNA (Kenya-bat-coronavirus [BtKY07]) from faecal material in 2006 in Kenya, and was similar to *Rousettus sp.* coronaviruses from China. In Nigeria, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs.

One out of 123 (0.8 %) Kenyan bats tested by Tao *et al.* (2017: Suppl.) was positive for CoV.

Shchelkanov *et al.* (2020a: 16) reported the virus found in Kenyan bats as the Human Coronavirus 229E.

Filoviridae - Filoviruses
Marburgvirus
Towner *et al.* (2007) as *H. gigas*, tested 1 individual from Gabon for Marburg virus RNA by conventional and real-time RT-PCR and for anti-Marburg virus IgG antibodies by ELISA; the results were negative.

Flaviviridae
Hepacivirus (BHV)
Quan *et al.* (2013: Table S5) report 2 with clade A infected Kenyan specimens on a total of 75 tested (2.7 %), and 4 specimens (5.3 %) that were infected with clade D virus. Shchelkanov *et al.* (2020a: 18) assigned the virus to Hepaciviruses K. and L.

Pegivirus (BPgV)
Quan *et al.* (2013: Table S5) also indicated that 2 of the 75 specimens were infected with a clade K type *Pegivirus*.

Herpesviridae
Percavirus genus
Harima *et al.* (2023: 3) isolated a new virus from Zambian bats, tentatively named Macronycteris gammaherpesvirus 1 (MaGHV1).

Harima *et al.* (2023: 7) also reported the presence of Betaherpesvirinae.

Polyomaviridae
Polyomavirus
Conrardy *et al.* (2014: 259) examined nine "*Hipposideros commersoni*" specimens from the Shimoni cave (Kenya), and found one of them testing positive for this virus.

Rhabdoviridae
Lyssavirus - Rabies related viruses
In Nigeria, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluorescent antibody testing.

Shimoni
Kuzmin *et al.* (2010a) detected a new lyssavirus, Shimoni bat lyssavirus (SHIBV) from the brain of a dead "*H. commersoni*" bat found in the coastal region of Kenya. Genetic distances demonstrated that this may be a new lyssavirus species. Kuzmin and Rupprecht (2015: 73) indicate that this bat is more likely to be the reservoir for this species than any fruit bat.

Fikirini rhabdovirus (FKRV)
Kading *et al.* (2013) report on this new rhabdovirus from a *M. vittata* specimen collected at Three Caves, Shimoni cave in Southern Kenya.

Horton *et al.* (2014: Table S1) tested 77 Kenyan "*H. commersoni*" specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

ANTHROPOPHILOUS:
Dandurand *et al.* (2018: 284) studied the influence of condensation-corrosion processes caused by urine and droppings on the walls of Drotsky's cave (Botswana) and their consequences on archaeological remains and cave art.

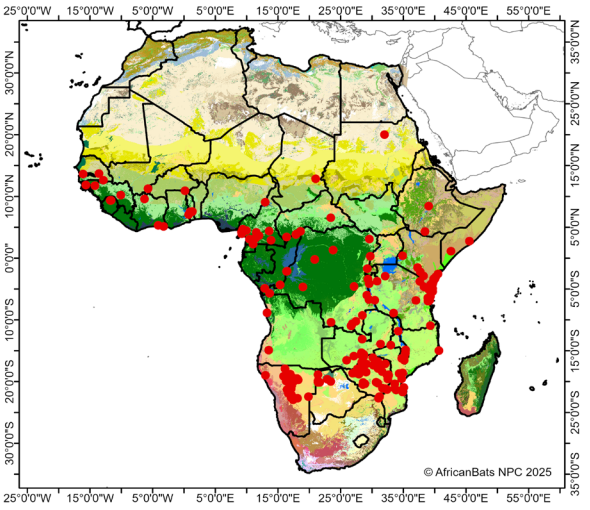

Figure 73. Distribution of *Macronycteris vittata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Burundi, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Guinea, Guinea-Bissau, Kenya, Madagascar, Malawi, Mali, Mozambique, Namibia, Niger, Rwanda, Senegal, Sierra Leone,

Somalia, South Africa, Sudan, Tanzania, The Gambia, Togo, Zambia, Zimbabwe.

†Genus ***Madanycteris*** Samonds, Simmons, Goodman, Alumbaugh, Hand, Irwin, Rasolofomanana and Gunnell, 2025

*2025. *Madanycteris* Samonds, Simmons, Goodman, Alumbaugh, Hand, Irwin, Rasolofomanana and Gunnell, J. Vert. Paleont., 44 (5) e2488447: 1, 3. Publication date: 6 May 2025. - Etymology: "Mada" refers to the country where the genus was found and "nycteris" to the Greek word “nykteros” meaning “nocturnal”..

†***Madanycteris razana*** Samonds, Simmons, Goodman, Alumbaugh, Hand, Irwin, Rasolofomanana and Gunnell, 2025

*2025. *Madanycteris razana* Samonds, Simmons, Goodman, Alumbaugh, Hand, Irwin, Rasolofomanana and Gunnell, J. Vert. Paleont., 44 (5) e2488447: 1, 3, figs 2, 3D. Publication date: 6 May 2025. Holotype: UA M-011. Right maxilla with P4, M1–3 and alveoli for C1 and P2 (Samonds *et al.* (2025: 3).. - Etymology: “razana” (RA-za-nah), refers to the Malagasy word meaning “ancestor”..

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Miocene (Early Tortonian - 10 mya - Samonds *et al.*, 2025: 6)

†Genus ***Palaeophyllophora*** Revilliod, 1917

1917. *Palaeophyllophora* Revilliod, Abh. Grossherz.-hess. Geol. Landesanst, 7: 1??.

†***Palaeophyllophora tunisiensis*** (Ravel, 2016)

*2016. *?Palaeophyllophora tunisiensis* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 368, figs 6, 7. Publication date: 30 September 2016. Type locality: Tunisia: Kassérine province: Dejbel Chambi National Park: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: The species name refers to the country from which uit was described: Tunisia.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

Family MEGADERMATIDAE H. Allen, 1864

*1864. *Megadermatidae* H. Allen, Monograph of North American Bats, xxiii, 1. - Comments: Type genus: *Megaderma* Geoffroy, 1810. See Handley (1980: 10) for the correct formation of the family name. (Current Combination).
1866. *Megadermata* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 256. - Comments: In Part (see Taylor, 1934). Originally included the genera *Rhinopoma* É. Geoffroy, 1818; *Megaderma* É. Geoffroy, 1810; *Nycteris* É. Geoffroy & G. Cuvier, 1795; and *Nyctophilus* Leach, 1821 (see Jackson and Groves, 2015: 241).
1866. *Megadermina* J. E. Gray, Proc. zool. Soc. Lond., 1866, I: 83. Publication date: May 1866.
1872. *Megadermidae* Gill, Arr. Families of Mammalia, p 17. - Comments: Originally included the subfamilies Vampyrinae Peters, 1865 [= Family Phyllostomidae Gray, 1825], Glossophaginae Bonaparte, 1845 and Stenoderminae Gill, 1872 (see Jackson and Groves, 2015: 241).
1893. *Megadermatini* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 24. - Comments: Proposed as tribe (?) and originally included the genera *Nycteris* É. Geoffroy and G. Cuvier, 1795 and *Megaderma* É. Geoffroy, 1810 (see Jackson and Groves, 2015: 241).

TAXONOMY:
Based on morphological data, the Family Megadermatidae was placed in the superfamily Rhinolophoidea with the families Nycteridae, Rhinolophidae and Hipposideridae (Simmons, 1998; Simmons and Geisler, 1998), but more recent molecular studies have contradicted many groupings based on morphological data. Hand (1985, 1996) and Griffiths *et al.* (1992) have provided alternative phylogenies for the group.

See Handley (1980) [in Corbet and Hill (1992: 89)] for correct formation of family name.

No subfamilies recognized (Simmons, 2005: 379).

Currently (Simmons and Cirranello, 2024a) recognized genera of the family Megadermatidae: ***Cardioderma*** Peters, 1873; *Eudiscoderma* Soisook, Prajakjitr, Karapan, Francis and Bates, 2015; ***Lavia*** Gray, 1838; *Lyroderma* Peters, 1872; *Macroderma* Miller, 1906; *Megaderma* E. Geoffroy Saint-Hilaire, 1810.
Additionally, there is one extinct genus: †***Saharaderma*** Gunnell, Simons and Seiffert, 2008

COMMON NAMES:
Czech: lyronosovití, kožnatcovití, megadermovití. Dutch: Onechte vampieren. English: False Vampire Bats, Large-winged Bats. Finnish: Valevampyyrit. French: Mégadermatidés, Faux vampire de l'ancien monde. German: Grossblattnasen, Großblattnasen, Falsche Vampire. Italian: Megadermàtidi, Fàlsi vampìri. Norwegian: Storøreflaggermus, falske vampyrer. Russian: Лжевампиры. Vietnamese: Họ dơi ma.

ETYMOLOGY OF COMMON NAME:
The common name of the family, false vampire bats, stems from the old, erroneous belief that they fed on blood, as do the true vampire bats of the New World (Happold, 2013ay: 401). There are no blood-sucking bats in Africa.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The Megadermatidae appear in the late Eocene or early Oligocene of Europe (Butler, 1978). Butler and Hopwood (1957) reported an indetermined species of Megadermatidae from the early Miocene at Rusinga. The locality was corrected by Butler (1984: 185) to Kaswanga, where it was found in the Hiwegi Formation.

Russell and Sigé (1970) suggest that *Afropterus gigas* Lavocat, 1961, is a megadermatid.

Shi and Rabosky (2015: 1532) indicate that the Megadermatidae split off from the Rhinopomatidae some 34 million years ago. They also reported (p. 1537) the family-level stem age to be 53.4 Mya and the crown age 27.2 Mya.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^0/_2$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 26.

Except in one non-African species, which has two upper premolars.

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) indicate that the 2*n* value for the family varies between 38 and 54.

HABITS:
Rainho *et al.* (2023: 7) assigned the *Lavia* and *Megaderma* bats in Meru county (Kenya) to a low-flying guild as they are flying at altitudes less than 3.5 m.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that 50 % of the species belonging to this family are confirmed viral carriers.

Genus ***Cardioderma*** Peters, 1873

*1873. *Cardioderma* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 488. Publication date: 23 June 1873. - Comments: Type species: *Megaderma cor* Peters, 1872. - Etymology: From the Greek "*καρδία*", meaning heart and "*δέρμα*", meaning skin, referring to the "cordiform" base of the central longitudinal crest of the nose-leaf (see Palmer, 1904: 160; Csada, 1996: 3).

TAXONOMY:
Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Cardioderma*: ***cor*** (Peters, 1872).
Additionally, there is the extinct African †***leakeyi*** Gunnell, Butler, Greenwood and Simmons, 2015.

COMMON NAMES:
Czech: srdcoví lyronosi. English: Heart-nosed Bats, African False Vampire Bats. French: Cardiodermes. German: Herznasen-Fledermäuse. Italian: Cardiodèrma.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Cardioderma sp. has been found in the early Pleistocene deposits in Olduvai (Butler and Greenwood, 1965; Butler, 1978).

Cardioderma cor (Peters, 1872)

*1872. *Megaderma cor* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 194. Type locality: Ethiopia: "Ethiopia". Holotype: ZMB 4181: ad ♂, skull and alcoholic. Collection date: undated. Vendor Gerrard; see Turni and Kock (2008: 28). - Etymology: From the neuter Latin substantive *cor* meaning "heart", used as an apposition, referring to the heart-shaped noseleaf (see Lanza *et al.*, 2015: 167).
? *Cardioderma cor:* (Current Combination).

TAXONOMY:
See Csada (1996, Mammalian Species, 519).

COMMON NAMES:
Chinese: 非洲假吸血蝠. Czech: lyronos srdcový, megaderma africká. Dutch: Hartneusvleermuis. English: Heart-nosed Bat, African Heart-nosed Bat, African False Vampire Bat, Heart-nosed Big-eared Bat. French: Cardioderme à nez en cœur, Pseudo-vampire à nez en cœur. German: Herznasen-Fledermaus. Italian: Cardiodèrma nàso a cuòre, Fàlso vampìro dàl nàso a cuòre.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008b; IUCN, 2004; Monadjem *et al.*, 2017i).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017i). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004a; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Mickleburgh *et al.* (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017i) report that there appear to be no major threats to this species, however, further studies are needed into the impact of disturbance on roosting sites.

CONSERVATION ACTIONS:
The species has been recorded from protected areas in Kenya (e.g., Tsavo West National Park (Vaughan, 1976; Aggundey and Schlitter, 1984) and is likely to be present in protected areas in some other East African countries. Additional studies are needed into the impact of disturbance on this species (Mickleburgh *et al.*, 2008b; IUCN; Monadjem *et al.*, 2017i).

GENERAL DISTRIBUTION:
Cardioderma cor is distributed from north-east Sudan (near the Red Sea) south to central Tanzania. The distribution extends from the border area of Uganda and Sudan in the west, to east Somalia (near the tip of the Horn of Africa) in the east.

Native: Djibouti (Pearch *et al.*, 2001: 397); Eritrea; Ethiopia (Glass, 1965: 179); Kenya; Somalia; Sudan; Tanzania; Uganda, Zanzibar.

DETAILED MORPHOLOGY:
Brain
Based on three brains from Kenya, Kruger *et al.* (2010a) describe the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems, using immunohistochemical methods. Kruger *et al.*, 2010b) describe the distribution of Orexin-A immunoreactive cell bodies and terminal networks based on three brains from Kenya.

Vomeronasal complex
The VNC is strongly curved in this species, but does not rise to encapsulate the vomeronasal organ (VNO) (Smith *et al.*, 2024: 8)..

ECHOLOCATION:
See O'Shea and Vaughan (1980) and Taylor *et al.* (2005).

Davies *et al.* (2013b: Table S8) report a peak frequency of 56.7 kHz and a range between 39.6 and 90.9 Khz.
Kaňuch *et al.* (2015: 55) found that the bats emitted relative broadband FM signals with a very sort duration (2 ms). The average peak frequency was 50.4 kHz (49.2 - 51.7 kHz), and the mean inter-signal interval was 186 ms (130 - 286 ms). The signals also had a second (around 65 kHz) and third (around 88 kHz) component, which are probably not true harmonics.

Smarsh and Smotherman (2016: 429) report up to four harmonics, of which the second and third are emphasized and the first suppressed. They also present the following data (p. 435): F_{peak}: 49.13 ± 1.39 kHz, F_{max}: 62.19 ± 2.29 kHz, F_{min}: 40.14 ± 0.73 kHz, bandwidth: 22.04 ± 2.72 kHz, duration: 1.34 ± 0.06 ms, and interpulse interval: 47.53 ± 22.19 ms. Furthermore, males had significantly lower F_{min} values than females.

Luo *et al.* (2019a: Supp.) reported the following data: F_{peak}: 49.13 kHz and duration: 1.34 ms.

HABITAT:
Typically this species has been recorded from lowland savanna, shrubland, and the coastal strip, and in some instances, it may be observed in river valleys (Varty and Hill, 1988; Csada, 1996). Highest altitudinal record is 940 m (Csada, 1996).

Stanley *et al.* (2007c: 58) mention that *C. cor* is a common resident of baobab trees (*Adansonia digitata* L.).

During their study of the bat diversity at the Arabuko-Sokoke Forest and adjacent farmlands, Musila *et al.* (2019b: 8) captured 621 *C. cor* specimens in the farmlands and only two in the forest areas.

HABITS:
McWilliam (1987a: 243) reported that *C. cor* males sing to mark their feeding territories. Contrary to echolocation calls, which are produced nasally, these songs are produced orally (Smarsh and Smotherman, 2017: 2), and are seasonally. Smarsh and Smotherman (2017: 11) also found that *C. cor* reacted to play-back sounds by producing faster, lower-frequency songs.

Smarsh *et al.* (2022: 1, 4) found that males sang from small, largely exclusive areas (avg = 3.48 ± 2.71 ha) and that singing increased hourly during the night. These areas were smaller in size than the areas the bats covered during these nights. Some males used specific trees and sang from these for long periods, whereas others switched trees frequently. The most productive singers were found using more singing perches, but not perches overall. The most prolific singers had smaller testes.

Smarsh and Smotherman (2016: 429) [referring to Bogdanowicz and Owen (1990)] mention that *Cardioderma cor* is a surface gleaner, which sits in perches and scans the environment, rotating its body and pinnae until it detects a prey to pick off the surface in the dense scrub habitat. Vaughan (1976) [in Fenton, 1986a], however, indicated that *C. cor* alternates between prey on the ground and flying prey, either from a perch about 1 m from the ground or from flight.

ROOST:
It roosts alone, or in small numbers (from 5 to up to 100 bats), in caves, hollow trees (e.g., baobab) and abandoned buildings (Kingdon, 1974; Vaughan, 1976; Ryan and Tuttle, 1987; Csada, 1996; Pearch *et al.*, 2001; Altringham, 2011: 143; Smarsh and Smotherman, 2016: 429). When roosting in trees, open sites are preferred, since this species doesn't seem to be very agile in roosting situations (Kunz, 1996: 50). In the Mago National Park (Ethiopia), Kaňuch *et al.* (2015: 55) found that dozens of male and female bats were roosting in two underground cesspits of the toilet, which they entered through waste holes. Roosting in latrine cesspits was also reported by Dorward *et al.* (2021: 1) from the Ruaha National Park in Tanzania, and by Webala *et al.* (2022: 2) in Kenya, where a group of about 10 animals (including young) were using it as a maternity roost.

DIET:
The diet of *C. cor* generally consists of larger (> 25 mm) terrestrial arthropods, although small vertebrates (including frogs and bats) are eaten too (Csada, 1996: 2, 3).

Gual-Suárez and Medellín (2021: 1) found that vertebrates only make up a minor part of the diet of *Cardioderma cor* and concluded that this species should not be considered carnivorous.

Gual-Suárez and Medellín (2021: Suppl.) also mention the following prey items were found for *Cardioderma cor*: Arachnida: Scorpionidae. Insects: Blattodea; Coleoptera: Carabidae, Cerambycidae, Chrysomelidae, Elateridae, Scarabaeidae, Tenebrionidae; Hemiptera: Cicadoidea; Orthoptera: Caelifera, Locustidae, Tettigonididae; Lepidoptera: Heterocera, *Agrius convolvuli, Hippotion celerio*. Furthermore, they reported the frog *Ptychadena anchietae*, the gecko *Hemidactylus mabouia*, and the bat *Neoromicia nanus*.

These bats use a small area (0.1 to 1.01ha) to search for food (Vleut *et al.*, 2019: 11).

PREDATORS:
During their study into singing strategies of these bats in Tanzania, Smarsh *et al.* (2022: 4) had one of the bats killed by a puff adder (*Bitis arietans* Merrem,1820).

POPULATION:
Structure and Density
Although there is little overall information on the abundance of this species, up to 81 bats have been found roosting in a hollow baobab tree (Vaughan, 1976).

Trend
2016: Unknown (Monadjem *et al.*, 2017i). 2008: Unknown (Mickleburgh *et al.*, 2008b; IUCN,

2009). 2004: Unknown (Mickleburgh *et al.*, 2004a; IUCN, 2004).

ACTIVITY AND BEHAVIOUR:
Smotherman *et al.* (2016: 537) refer to Vaughan (1976) and McWilliam (1987a) in describing the song structure for this species as consisting of different syllable types in a basic motif.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 121) mention that both males and females need about 16 months to attain sexual maturity.

Matthews (1941) and Krutzsch (2000: 95) indicate that the central duct of the ampullary gland seems to act as a temporary storage site for spermatozoa. They also mention that *C. cor* is the only polyoestrous species in the Megadermatidae, all others are seasonally monoestrous.

Vaughan (1976) and Kunz and Hood (2000: 418) suggest that paternal recognition of young would occur in monogamous species, such as *C. cor*, where males participate in the care of young. The males also defend the foraging territories in which young bats learn to feed (Kunz and Hood, 2000: 440).

MATING:
Vaughan (1976), McWilliam (1987a), and McCracken and Wilkinson (2000: 351) report this species to be monogamous.

PARASITES:
PROTOZOA
Kassahun *et al.* (2015: 168) tested one *C. cor* specimen from Awash-Methara (Ethiopia) and found it to be infected by *Leishmania tropica* Wright, 1903 (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 4).

ACARI
Trombiculidae
Grandjeana kanuchi Kalúz and Ševčík, 2015 collected and described from *C. cor* in Ethiopia (Kalúz and Ševčík, 2015: 381; Stekolnikov, 2018a: 136; Zajkowska *et al.*, 2018: 108).

Stekolnikov (2022: 419) described a new genus and species of bat chigger (*Minteracarus mombasa*) from a *Cardioderma cor* collected in Kenya.

DIPTERA
Streblidae
Raymondia huberi huberi Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254). *Raymondia planiceps* Jobling, 1930 (Haeselbarth *et al.*, 1966: 102; Kaňuch *et al.*, 2015: 55; Shapiro *et al.*, 2016: 255); *Raymondia seminuda* Jobling, 1954 in Ethiopia (Jobling (1954) in (Haeselbarth *et al.*, 1966: 104).

Nycteribiidae
Basilia daganiae Theodor and Moscona, 1954 from Mombasa, Kenya (Haeselbarth *et al.*, 1966: 110).

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Cardioderma cor*: Adenoviruses and Astroviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Tong *et al.* (2009) found coronavirus RNA in fecal samples collected of one bat collected in Kenya in 2006.

Tao *et al.* (2017: 3) indicate that one (25 %) of the Kenyan *C. cor* they examined tested positive for CoV.

Paramyxoviridae
Conrardy *et al.* (2014: 259) tested 14 individuals from Kenya with the use of an RT-PCR assay. Of the 10 individuals tested from Panga Yambo cave, one individual tested positive for paramyxovirus RNA that grouped phylogenetically to an *Otomops martiensseni*-related paramyxovirus.

Polyomaviridae
Cardioderma PyV KY336
Tao *et al.* (2012) detected polyomavirus DNA in fecal/oral swabs from Kenya in 2006.

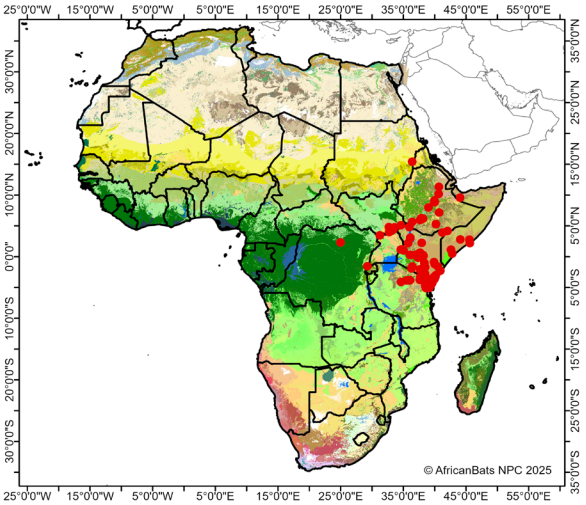

Figure 74. Distribution of *Cardioderma cor*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Congo (Democratic Republic of the), Egypt, Eritrea, Ethiopia, Kenya, Somalia, South Sudan, Sudan, Tanzania, Uganda.

†*Cardioderma leakeyi* Gunnell, Butler, Greenwood and Simmons, 2015

*2015. *Cardioderma leakeyi* Gunnell, Butler, Greenwood and Simmons, Am. Mus. Novit., 3846: 1, 7, figs 4B-D, 5C. Publication date: 16 December 2015. Type locality: Tanzania: Arusha province: Olduvai Gorge: Bed I, FLK NI, Layer 2. - Etymology: Named in honor of Louis S.B. Leakey who was instrumental in initiating and leading the search for vertebrate fossils, especially fossil humans, in East Africa (Gunnell *et al.*, 2015a: 7). (Current Combination).

SIMILAR SPECIES:
The teeth of *C. leakeyi* are on average 18 - 20 % larger than those of *C. cor* (Gunnell *et al.*, 2015a: 8).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pleistocene (Brown *et al.*, 2019: Suppl.).

Genus ***Lavia*** J. E. Gray, 1838

*1838. *Lavia* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 490. Publication date: 1 February 1838. - Comments: Type species: *Megaderma frons* E. Geoffroy Saint-Hilaire, 1810. - Etymology: From "*lavo*" meaning fine, elegant, splendid (see Vonhof and Kalcounis, 1999: 4). Lanza *et al.* (2015: 172), however, indicate that *lavo* is a Latin verb meaning "wash, wash away, wash off, wet, moisten, bathe, soak", while its passive Latin perfect participle *lauta* (corresponding to a feminine verbal adjective) actually means - besides "washed", "clean", and "sumptuous" - "splendid" and "magnificent", referring to the beauty of the animal. (Current Combination).
1846. *Livia:* Agassiz, Nomenclator. Zool., Mamm., addenda 6. (Lapsus).

TAXONOMY:
See Simmons (2005).

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Lavia*: ***frons*** (E. Geoffroy Saint-Hilaire, 1810).

COMMON NAMES:
Czech: žlutokřídlí lyronosi. English: Yellow-winged Bats. French: Mégadermes à ailes orangées. German: Gelbflügel-Fledermäuse. Italian: Fàlsi vampìri dàlle àli giàlle.

Lavia frons (E. Geoffroy St.-Hilaire, 1810)

1799. *Vespertilio megalotis* Bechstein, Thomas Pennant's allgemeine Uebersicht der vierfüssigen Thiere, 615, 622. Publication date: 6 October 1799. Type locality: South Africa: Great Namaqualand: Orange River, 50 mi [=75 km] N. [Goto Description]. - Comments: Nomen oblitum. See Grubb (2004: 91 - 92) for a discussion.
*1810. *Megaderma frons* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 15: 192. Type locality: Senegal: "Senegal". Holotype: MNHN ZM-MO-1997-1824: skin and skull. Collected by: Michel Adanson. Number 175 in Rode (1941: 236). Skull number A6844. Previously mentioned as MNHN 928. Paratype: MNHN ZM-MO-1997-1825: skin only. Collected by: Michel Adanson. Skull removed and lost. Number 175a in Rode (1941: 236). Previously mentioned as MNHN 929. Paratype: MNHN ZM-MO-1997-1826: skull in skin. Collected by: Michel Adanson. Number 175b in Rode (1941: 2436). Previously mentioned as MNHN 929.C. Paratype: MNHN ZM-MO-1997-1827: skull in skin. Collected by: Michel Adanson. Number 175c in Rode (1941: 236). Previously mentioned as MNHN 929.D. - Etymology: From the Latin "*frons*" meaning forehead (see Vonhof and Kalcounis, 1999: 4).
1905. *Lavia rex* Miller, Proc. Biol. Soc. Wash., 18: 227. Publication date: 9 December 1905. Type locality: Kenya: Taveta [03 23 S 37 40 E]. [Goto Description]. Holotype: USNM 18993/38197: ad ♂, skin and skull. Collected by: Dr. William Louis Abbott; collection date: 1889. Skin catalogued 24 June 1890; skull catalogued 18 February 1904: see Miller (1905: 227), Lyon and Osgood (1909: 260), Poole and Schantz (1942: 118).
1907. *Lavia frons affinis* K. Andersen and Wroughton, Ann. Mag. nat. Hist., ser 7, 19 (110): 138, 140. Publication date: 1 February 1907. Type locality: South Sudan: White Nile: Kaka [10 36 00 N 32 11 00 E, 375 m]. [Goto Description]. Holotype: NHMUK 1901.8.8.3: ad ♂, skin only. Collected by: R. McDonald Hawker Esq. - Comments: Not mentioned by Vonhof and Kalcounis (1999: 1).
? *Lavia frons frons:* (Name Combination).
? *Lavia frons rex:* (Name Combination).
? *Lavia frons:* (Name Combination, Current Combination).

TAXONOMY:



Figure 75. *Lavia frons,* Zanzibar Island.

See Vonhof and Kalcounis (1999, Mammalian Species, 614). Grubb (2004: 91) calls *Megaderma frons* a "nomen protectum".

COMMON NAMES:

Azande (DRC): Ndima. Chinese: 黄翼蝠. Czech: lyronos žlutokřídlý, weloblánec lupenatý, megaderma žlutokřídlá. English: Yellow-winged Bat, African Yellow-winged Bat. Finnish: Keltapoimulepakko. French: Feuille de Daubenton, Megaderme à ailes orangées, Lavie à ailes jaunes, Le Megaderme feuille, Megaderme à ailes orangées. German: Gelbflügelige Großblattnase, Gelbflügel-Fledermaus. Italian: Fàlso vampìre dàlle ali giàlle. Kiluba (DRC): Kasusu. Kinande (DRC): Kakoro kombe.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008n; IUCN, 2009; Monadjem *et al.*, 2017j).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017j). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008n; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004y; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

While Vonhof and Kalcounis (1999) state that the effects of human activity on population dynamics of this bat are unknown, there do not appear to be any major threats to the species (Mickleburgh *et al.*, 2008n; IUCN, 2009; Monadjem *et al.*, 2017j).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008n) [in IUCN (2009)] and Monadjem *et al.* (2017j) report that it is present in a number of protected areas (e.g., Garamba National Park, Democratic Republic of the Congo). Other than studies into the possible effects of human activity on population dynamics of this bat, and additional research into the range of this species, no conservation measures are currently needed for this widespread species.

GENERAL DISTRIBUTION:

Lavia frons is broadly distributed south of the Sahara from Gambia and Senegal, through much of West and Central Africa, to southern and central Sudan, Eritrea, Ethiopia and Somalia in the east; ranging southwards as far as northern Zambia and northern Malawi. It is typically a lowland species found below 2,000 m asl.

Native: Benin (Capo-Chichi *et al.*, 2004: 162); Burkina Faso (Kangoyé *et al.*, 2015a: 610); Burundi; Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 539); Côte d'Ivoire; Eritrea; Ethiopia (Yalden *et al.*, 1996; Lavrenchenko *et al.*, 2004b: 132); Gabon; Gambia (Grubb *et al.*, 1998); Ghana; Guinea; Guinea-Bissau (Seabra, 1900a; Monard, 1939; Rainho and Ranco, 2001: 46); Kenya (Aggundey and Schlitter, 1984); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988; Vonhof and Kalcounis, 1999; Monadjem *et al.*, 2010d: 539); Mali; Niger; Nigeria; Rwanda (Baeten *et al.*, 1984; Senegal; Sierra Leone; Somalia (Funaioli and Simonetta, 1966); Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 61); Zambia (Ansell, 1967; Ansell, 1978; Monadjem *et al.*, 2010d: 539).

Presence uncertain: Namibia, Zanzibar.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data: Fa: 59.5 mm, mass: 23 g, wing loading: 7.8 N/m^2, aspect ratio: 5.2.

DENTAL FORMULA:

Dorst (1953a: 83 - 84) indicates that he was unable to find any trace of a milk dentition in a foetus of about 35 mm in size (Fa: 25 mm), but also that the permanent teeth were already

perfectly formed, but were not yet grown above the gum.

DETAILED MORPHOLOGY:
Vomeronasal complex (VNC)
In this species, the VNC is a simple curved rod in cross-section, and no impression can be found on the premaxilla where the VNC articulates. There are also no paraseptal grooves Smith *et al.* (2024: 8)..

FUNCTIONAL MORPHOLOGY:
Altringham (2011: 146) mentions that foliage roosters such as *Lavia frons* have a long, thick fur to better isolate it from the heat.

Rummel *et al.* (2023: 4) studied the distribution of sensory hairs on the wings and found the number of hairs per cm^2 to vary between 11.63 on the cranial distal plagiopatagium and 94.92 on the propatagium. These hairs are likely mechanosensory and have been suggested to help bats sense airflow during flight.

King *et al.* (2025) investigated the olfactory system of this species.

SEXUAL DIMORPHISM:
Krutzsch (2000: 115) mentions the presence of dorsal skin glands in males.

Kangoyé *et al.* (2015a: 610) found no differences in body and cranial measurements between the two sexes.

ECHOLOCATION:
See Taylor *et al.* (2005).

Davies *et al.* (2013b: Table S8) report a peak frequency of 18.5 kHz and a range between 16.9 and 82.9 kHz.

Smarsh and Smotherman (2016: 429) report up to four harmonics of which the second and third are emphasized and the first suppressed, with males having a significantly lower F_{min}. They also provide the following data: F_{peak}: 42.21 ± 2.35 kHz, F_{max}: 48.50 ± 2.08 kHz, F_{min}: 35.08 ± 1.25 kHz, bandwidth: 13.42 ± 3.04 kHz, duration: 3.25 ± 2.98 ms, and interpulse interval: 53.99 ± 32.24 ms.

Luo *et al.* (2019a: Supp.) reported the following data (): F_{peak}: 42.21 kHz and duration: 3.25 ms.

HABITAT:
R.B. Woosnam [in Thomas and Wroughton, 1910: 488] mentions it to be plentiful among the acacia trees on the plains around the south end of Ruwenzori at 3,400 ft (1,000 m), where it was found hanging fully exposed to the sun.

Conenna *et al.* (2019: 1) radio-tracked 22 bats during April - May 2017 (rainy season, n = 13) and January - February 2018 (dry season, n = 9) in a desert in northern Kenya. The bat's home ranges averaged 5.46 ± 11.04 (0.45 - 42.32) ha and they travelled a minimum distance of 99.69 ± 123.42 m/hour. These ranges were larger during the dry season than during the wet season.

HABITS:
Vaughan and Vaughan (1987) [in McCracken and Wilkinson (2000: 353)] found that the single young remains closely associated with both parents at roost sites and on the foraging area for up to 50 days after it becomes volant.

Altringham (2011: 25) indicated that this species frequently flies in daylight. Smarsh and Smotherman (2016: 430) consider *L. frons* to be an aerial-hawker, capturing insects in vegetation gaps.

ROOST:
L. frons roosts in trees but prefers relatively open sites as it seems to be less agile in roosting situations (Kunz, 1996: 50). McCracken and Wilkinson (2000: 351) indicate that male/female pairs roost in the same territory, and that pair-specific roost sites and foraging areas remain stable for at least several months.

Smarsh and Smotherman (2016: 429) indicate that *L. frons* roost in male-female pairs in Acacia trees within a foraging territory.

DIET:
Kohles *et al.* (2022: Suppl.) mention that during the dry season (January to March) *Lavia frons* searches for concentrations of smaller insects near acacia trees, whereas during the rainy season (April to June) larger and more dispersed flying insects near acacia trees are hunted.

Conenna *et al.* (2019: 1) found that home ranges were larger during the dry season than during the wet season, probably to ensure access to sufficient food resources during the latter season.

PREDATORS:
Schätti (1984: 339) refers to Loveridge (in Allen, 1940), who found a specimen in the stomach of a Black Mamba (*Dendroaspis polylepis*).

Mikula *et al.* (2016: Supplemental data) mention the Grey kestrel (*Falco ardosiaceus* Vieillot, 1823), Common kestrel (*Falco tinnunculus* Linnaeus, 1758) and Bat hawk (*Macheiramphus*

alcinus Bonaparte, 1850) as avian diurnal predators.

POPULATION:
Structure and Density
Although there is little information on the abundance of this species, it is probably uncommon (Vonhof and Kalcounis, 1999).

Trend
2016: Stable (Monadjem *et al.*, 2017j). 2008: Stable (Mickleburgh *et al.*, 2008n; IUCN, 2009).

LIFESPAN:
No known studies on life expectancy of this species.

ACTIVITY AND BEHAVIOUR:
Smotherman *et al.* (2016: 537) refer to Wickler and Uhrig (1969) and Vaughan and Vaughan (1986) in describing the song structure for this species as consisting of simple syllable types in a basic motif.

REPRODUCTION AND ONTOGENY:
Vaughan and Vaughan (1987: 217) report that females give birth to one young, which hangs on to its mother for about a week, and then starts flying. The young is weaned about 20 days after its first flight, but remains at least 50 days in close contact with its parents, during which time it learns to become a skilled opportunistic forager.

In Malawi, births were reported at the end of the dry season (October) (Happold and Happold, 1990b: 566).

MATING:
Crichton and Krutzsch (2000: 351) and Altringham (2011: 128) [referring to Vaughan and Vaughan (1986; 1987)] mention that *L. frons* is a monogamous species.

PARASITES:
HAEMOSPORIDA
Austen and Barbosa (2021: 7) and Sato and Mafie (2022: 2) mention *Trypanosoma (Megatrypanum) megadermae* as a parasite.

ACARI
Rosensteiniidae
Fain (1979: 125) reported a *Nycteriglyphus laviae* Fain. 1970 on a Rwandan *Lavia frons*.

SIPHONAPTERA
Pulicidae
Echidnophaga aethiops Jordan and Rothschild, 1906 locality not mentioned (Haeselbarth *et al.*, 1966: 135).

Ischnopsyllidae
Chiropteropsylla brockmani Rothschild, 1915 widespread (Haeselbarth *et al.*, 1966: 192).

Psorergatidae
Cierocka *et al.* (2022: 10) mentioned the presence of *Psorergatoides laviae* Fain, 1959 on the wing membrane of *Lavia frons* specimens from Rwanda.

ANTHROPOPHILOUS:
Jeffreys (1944: 73) [referring to Schweinfurt (1878)] mentions the following "Among the Bongo of the Anglo-Egyptian Sudan much the same superstition lurks - 'Spirits, devils and witches have their general appellation of 'Bitaboh', wood-goblins being specially called 'Ronga'. Comprehended under the same term are all the bats (especially the *Megaderma frons*, which flutters about from tree to tree in broad daylight).'"

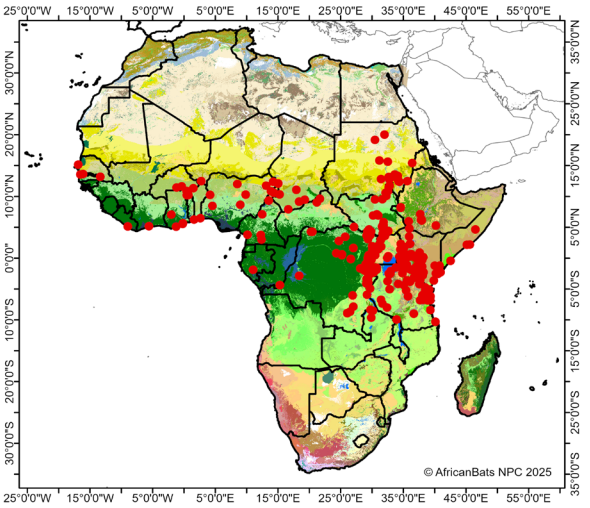

Figure 76. Distribution of *Lavia frons*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia.

Genus ***Megaderma*** E. Geoffroy St.-Hilaire, 1810

*1810. *Megaderma* E. Geoffroy St.-Hillaire, Ann. Mus. Hist. nat. Paris, 15: 197. - Comments: Type species: *Vespertilio spasma* Linnaeus, 1758. - Etymology: From the Greek "*μέγας*", meaning great or large and "*δέρμα*", meaning skin, referring to the large wings and interfemoral membrane (see Palmer, 1904: 403). (Current Combination).
1847. *Eucheira* Hodgson. - Comments: not *Eucheira* Westwood, 1838, an insect.

1866. *Spasma* J. E. Gray.
1872. *Lyroderma* Peters.
1961. *Afropterus* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, 155: ?. - Comments: Mid Miocene-Pliocene in Morocco.

TAXONOMY:
Includes *Lyroderma*, but see Hand (1985).

Two subgenera (*Megaderma* and *Lyroderma*) are recognized by Corbet and Hill (1992) and Simmons (2005: 380).

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Megaderma*: *spasma* (Linnaeus, 1758) – Sri Lanka and India through south east Asia (including Vietnam) to Lesser Sundas, the Philippines and Molucca Isls, various adjacent islands (Simmons, 2005: 380). Additionally there are the extinct †***gigas*** Lavocat, 1961; †***jaegeri*** Sigé, 1976.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
gigas (Lavocat, 1961) fossil bat from the Pliocene.

†*Megaderma gaillardi* (Trouessart, 1898)

*1898. *Miomegaderma gaillardi* Trouessart, Catalogus Mammalium tam viventium quam fossilium. Berlin, 84. Type locality: France: La Grive St. Alban.
1961. *Afropterus gigas* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, xxx. Type locality: Morocco: Beni Mellal.
2013. *Megaderma gaillardia:* Stoetzel, Palaeog., Palaeoclim., Palaeoecol., 392: 363. (Lapsus).
? *Megaderma gaillardi:*

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Middle Miocene (Astaracanian / Langhian, Serravallian - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Europe and Morocco Hugueney *et al.* (2015: 472).

†*Megaderma gigas* (Lavocat, 1961)

*1961. *Afropterus gigas* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, 155: ?. Type locality: Morocco: Beni Mellal. - Comments: Mio-Pliocene. Sigé (1976: 73) mentions "BML (La) 1200, M_3 dr" as type specimen, but it is unclear in which institution this specimen is housed.
? *Megaderma gigas:* (Name Combination, Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea.

†*Megaderma jaegeri* Sigé, 1976

*1976. *Megaderma jaegeri* Sigé, Géol. Médit., 3 (2): 71, 78, figs 8 - 10. Type locality: Morocco: Béni Mellal. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Middle Miocene (Langhian, Serravallian - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Morocco (Hugueney *et al.* (2015: 472).

†Genus ***Saharaderma*** Gunnell, Simons and Seiffert, 2008

*2008. *Saharaderma* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 7. - Comments: Type species - *Saharaderma pseudovampyrus*. - Etymology: For the 'Sahara Desert' in combination with *derma*, Greek for skin, and the common ending for several genera of megadermatids (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

Currently recognized species of the genus *Saharaderma*: †***pseudovampyrus*** Gunnel, Simons and Seiffert, 2008.

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

GENERAL DISTRIBUTION:
Native: Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

†*Saharaderma pseudovampyrus* Gunnell, Simons and Seiffert, 2008

*2008. *Saharaderma pseudovampyrus* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 7, fig 7. Type locality: Egypt: Fayum Depression: Quarry L-41: Lower Sequence, Jebel Qatrani Formation. Holotype: CGM 83672. Right dentary p4-m3: see Gunnell *et al.* (2008: 7). - Comments: latest Eocene, Priabonian. - Etymology: 'Pseudo- and Vampyrus' in reference to the common name of megadermatids (False Vampire Bats), from Slavic, 'wampir', blood-sucking ghost (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Latest Eocene (Priabonian - Brown *et al.*, 2019: Suppl.), Lower Sequence, Jebel Qatrani formation.

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

Family RHINOLOPHIDAE J. E. Gray, 1825

*1825. *Rhinolophidae* J. E. Gray, Zool. Journ., 2 (6): 242. - Comments: Type genus: *Rhinolophus* Lacépède, 1799. Corbet and Hill (1992: 90) mention "Bell, 1836: 599" as author. Jackson and Groves (2015: 242) mention "T. Bell, 1836: 599" as author of this spelling, but attributed the family name to Gray, 1825. (Current Combination).

1825. *Rhinolophina* J. E. Gray, Ann. Philos., 10 (5): 338. - Comments: Proposed as tribe and originally containing the genera *Megaderma* É. Geoffroy, 1810; *Rhinolophus* Lacépède, 1799; *Nycteris* É. Geoffroy & G. Cuvier, 1795; *Mormoops* Leach, 1821 and *Nyctophilus* Leach, 1821. Jackson and Groves (2015: 241, 242) placed this name in the synonymy of both Rhinolophoidea and Rhinolophidae.

1827. *Rhinolophina* Lesson, Mannuel de mammalogie, p 81. - Comments: In Part (see Taylor, 1934).

1854. *Rhinolophides* Gervais, Histoire naturelle des mammifères, p 200. - Comments: In Part (see Taylor, 1934).

1855. *Histiorhina* Van der Hoeven, Handboek Dierkunde, 2nd ed, 2: 1033. - Comments: Proposed as tribe (?), which was not based on a genus name (see Jackson and Groves, 2015: 242).

1866. *Rhinolophi* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 256. - Comments: In Part (see Taylor, 1934). Originally included the genera *Rhinolophus* Lacépède, 1799; *Phyllorrhina* Bonaparte, 1837 [1832–1841] [= *Hipposideros* J. Gray, 1831b]; and *Coelops* Blyth, 1848 (see Jackson and Groves, 2015: 242).

1883. *Phyllorhinidae* de Rochebrune, Act. Soc. Linn. Bordeaux, 37 (4) 7: 94. - Comments: Originally included the genus *Phyllorhina* Leach, 1816 [= *Rhinolophus* Lacépède, 1799]. Howev,er the name is unavailable (see Jackson and Groves, 2015: 242).

1893. *Rhinolophini* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 24. - Comments: Proposed as tribe (?) and originally included the genera *Phyllorhina* [sic] Bonaparte, 1837 [1832–1841] [= *Hipposideros* J. Gray, 1831]; *Anthops* Thomas, 1888: *Rhinonicteris* J. Gray, 1847; *Triaenops* Dobson, 1871; *Coelops* Blyth, 1848; and *Rhinolophus* Lacépède, 1799 (ee Jackson and Groves, 2015: 242).

TAXONOMY:
Koopman and Jones, 1970; Swanepoel *et al.* (1980: 157), Harrison and Bates (1991: 51), Corbet and Hill (1992: 104 - with comment), Pavlinov *et al.* (1995), Peterson *et al.* (1995: 66), Hutson *et al.* (2001: 16) and Simmons (2005: 350) included the Hipposideridae. Hill (1982b) listed Hipposideridae as a distinct family, without comment and Hill and Smith (1984) retained this separation and discussed the question.

Foley *et al.* (2014: 319) state that the Rhinolophidae form a fully supported monophyletic group, but that the intrafamilial relationships are less well resolved than for the Hipposideridae.

Currently (Simmons and Cirranello, 2024a) recognized genus of the family Rhinolophidae: ***Rhinolophus*** Lacépède, 1799.

† Saharaderma

COMMON NAMES:
Czech: vrápencovití, vlastní vrápenci. Dutch: Hoefijzerneusvleermuizen, Hoefijzerneuzen. English: Horseshoe bats. Finnish: Hevosenkenkäyköt, Kaviokuonoyköt. French: Rhinolophidés, Fers-à-cheval, Rhinolophes, Chauve-souris à fer à cheval. German: Hufeisennasen, Hufeisennasen-Fledermäuse. Italian: Rinolòfidi. Norwegian: Hesteskoneser, Ekte hesteskonese. Polish: podkowcowate. Romanian: Lilieci cu pliuri nazale. Russian: Подковоносые. Ukrainian: Підковикові [= Pidkovykovi]. Vietnamese: Họ dơi lá.

ETYMOLOGY OF COMMON NAME:
They are called horseshoe bats because the anterior nose-leaf is shaped like a horseshoe.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The Rhinolophidae, date from the late Eocene or early Oligocene of Europe and have been recorded in Africa only from the Mio-Pliocene of Morocco (Lavocat, 1961) and the late Pliocene of Makapansgat (De Graaf, 1960).

The family-level stem and crown ages were calculated as 49.9 and 49.8 Mya by Shi and Rabosky (2015: 1537). However, Almeida *et al.* (2021: 241) estimate the origin of the crown rhinolophids between 12 and 16 Mya, during the Mid Miocene Climatic Optimum (MMCO).

BIOGEOGRAPHY:
During the Miocene at about 17 Ma, the *Rhinolophus* diversified into distinct clades (Foley *et al.*, 2014: 320).

FUNCTIONAL MORPHOLOGY:
Using micro computed tomography (micro-CT) scans, Curtis A. A. and Simmons N. B. (2016: 310) examined the turbinal morphology in the Rhinolophidae and found strangely formed maxilloturbinal bones within the respiratory airway. These looked distinct in form from the scrolled, branched, or plate shaped turbinals reported in other mammals, including other nasophonating bats, e.g., Hipposideridae, where these maxilloturbinals are either greatly reduced or even lacking (Curtis *et al.*, 2018: 111).

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) indicated that the karyotype for all the members of this family has a 2*n* value varying between 28 and 62.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 38 % of the species belonging to this family are confirmed viral carriers.

Coronaviridae
Morales *et al.* (2025: 450) reported that worldwide 41.6 % of all viruses found in the Rhinolophidae are coronaviruses.

SARS-related coronaviruses
Kumakamba *et al.* (2021: 7) found only one of their 62 rhinolophid bats to test positive for coronaviruses, and this was the only bat collected during the wet season.

SARS (subgenus *Sarbecovirus*)
See Markotter *et al.* (2020: 5) have only been detected in the *Rhinolophus* genus.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Tanzania.

Genus ***Rhinolophus*** Lacépède, 1799

*1799. *Rhinolophus* Lacépède, Tabl. Div. Subd. Orders Genres Mammifères, 15. - Comments: Type species (by monotypy): *Vespertilio ferrum-equinum* Schreber, 1774. Conserved by Opinion 91 (1926) and Direction 24 (1955) (see Corbet and Hill, 1992: 91). - Etymology: From the Greek "*ρις*" or "*ρινός*", meaning nose and "*λόφος*", meaning crest, referring to the complex nose-leaf, consisting of three parts (Palmer, 1904: 606; Taylor, 2005). Lanza *et al.* (2015: 76) translate "*λόφος*" as "comb", which leads to "with a comb on the nose or, more properly, on the snout". - Phonetics: rie'-noh-loh'-fus, rine'-oh-loh-fus. (Current Combination).

1816. *Phyllorhina* Leach, Systematic Catalogue of the species of indigenious Mammals in the British Museum, 5. - Comments: Type species: *Vespertilio minutus* Montagu, 1808. By subsequent designation (see Jackson and Groves, 2015: 243). Not *Phyllorrhina* Bonaparte, 1831 (Mammalia, Chiroptera, Rhinolophidae), a Nomen nudum according to Palmer (1904: 535), nor *Phyllorrhina* Bonaparte, 1837 [1832–1841] (Mammalia, Chiroptera, Hipposideridae) (see Jackson and Groves, 2015: 243).

1836. *Rhinocrepis* Gervais, Dictionnaire Pittoresque d'Histoire naturelle, 4 (2): pt 318, p 617. - Comments: Type species: *Vespertilio ferrum-equinum* Schreber, 1774. By "implication" according to Allen (1939a: 72) or by subsequent designation (Palmer, 1904: 606).

1847. *Aquias* J. E. Gray, Proc. zool. Soc. Lond., 1847, XV (clxix): 15. Publication date: 13 April 1847. - Comments: Type species: *Rhinolophus luctus* Temminck, 1838 / *Rhinolophus trifoliatus* Temminck, 1834. Restricted to *R. luctus* by Ellerman *et al.* (1953): see Meester *et al.* (1986: 36).

1866. *Phyllotis* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 81. Publication date: May 1866. - Comments: Type species (by monotypy): *Rhinolophus philippinensis* Waterhouse, 1843. Preoccupied by *Phyllotis* Waterhouse 1837 (Mammalia, Rodentia, Cricetidae) (see Jackson and Groves, 2015: 243).

1867. *Cœlophyllus* Peters, Proc. zool. Soc. Lond., 1866, III: 427. Publication date: April 1867. - Comments: Type species: *Rhinolophus cœlophyllus* Peters, 1867.
1901. *Euryalus* Matschie, Sber. Ges. naturf. Freunde Berlin, 225. - Comments: Type species (by monotypy): *Rhinolophus mehelyi* Matschie, 1901. Described as a subgenus of *Rhinolophus* (see Meester *et al.*, 1986: 36; Jackson and Groves, 2015: 243). - Etymology: From the specific name *euryale* ("*Ευρυάλη*"), being one of the Gorgons (see Palmer, 1904: 279).
1939. *Coelophyllus* G. M. Allen, Bull. Mus. comp. Zool., 83: 605. Publication date: February 1939. (Alternate Spelling).
1941. *Rhinophyllotis* Troughton, Furred Animals of Australia, 1st edn: 342. - Comments: Type species (by monotypy): *Rhinolophus megaphyllus* Gray, 1834. Redescription for *Rhinophyllotus* Iredale and Troughton, 1934, "nomen nudum" (see Meester *et al.*, 1986: 36).
1951. *Rhinomegalophus* Bourret, Bull. Mus. natn. Hist. nat., Paris, sér 2, 23 (6): 607. - Comments: Type species (by monotypy): *Rhinomegalophus paradoxolophus* Bourret, 1951 (see Jackson and Groves, 2015: 243).
1973. *Rhinomegaphyllus:* Thonglongya, Mammalia, 37: 587. - Comments: Lapsus for *Rhinomegalophus* Bourret, 1951 (see Eger and Fenton, 2003: 1). (Lapsus).
1993. *Rhinilophus:* Amr and Qumsiyeh, Ent. News, 104 (1): 44. (Lapsus).
2003. *Indorhinolophus* Guillén-Servent, Francis and Ricklefs, in: Csorba, Ujhelyi and Thomas, Horseshoe Bats of the World.
2015. *Rhrynolophus:* Thies and Lewis, Occ. Pap. Mus. Texas Tech Univ., 330: 7. Publication date: 10 February 2015. (Lapsus).
2015. *Rhynolophus:* Thies and Lewis, Occ. Pap. Mus. Texas Tech Univ., 330: 7. Publication date: 10 February 2015. (Lapsus).
2018. *Rhinolphus:* Leopardi, Holmes, Gastaldelli, Tassoni, Priori, Scaravelli, Zamperin and De Benedictis, Infec. Gen. Evol., 58: 283. Publication date: 30 January. (Lapsus).
? *Rhinolophus sp. IVK-2011*
? *Rhinolophus sp.:*

TAXONOMY:
The radiation (about 15 million years ago) of Rhinolophidae into five main clades apparently occurred rapidly and the distinct clades could be regarded as different genera (Servent *et al.*, 2003: xvi). Following tradition Servent *et al.* (2003: xvi) split the six subgenera (*Aquias*, *Phyllorhina*, *Rhinolophus*, *Indorhinolophus*, *Coelophyllus*, *Rhinophyllotis*) into groups corresponding to smaller lineages in the phylogeny. A recent analysis by Guo *et al.* (2022) confirmed the monophyletic status of five of these subgenera (the exception being *Coelophyllus*). All African and Palaearctic species are contained within a single clade (Servent *et al.*, 2003: xvii). This confirms the views proposed by Bogdanowicz (1992) and Bogdanowicz and Owen (1992), who suspected that the relationship was monophyletic. Qumsiyeh *et al.* (1988) studied protein electrophoresis of a limited number of African taxa, which grouped together in their phylogeny. All African and Palaeartic Rhinolophid species karyotyped show a diploid number of 58, which differs from all other *Rhinolophus* with the exception of some populations of *R. hipposideros* (Zima *et al.*, 1992b). Servent *et al.* (2003: xvii) note that the geographical distribution of taxa and the phylogeny are strongly congruent.

Uvizl *et al.* (2024: 10) dated the Rhinolophidae divergence at 16.7 million years ago (16.1 - 17.3 Mya) and the Afro-Palaearctic divergence at 10.1 (8.4 - 11.8) Mya for nodes outside the *ferrumequinum* group and 3.8 (3.0 - 4.7) Mya for the *ferrumequinum* lineage. Within the latter, the *clivosus* lineage split off at 2.7 (1.8 - 3.7) Mya ago, and the *acrotis-bocharicus* lineages at 1.7 (0.9 - 2.5) Mya. *acrotis* and *bocharicus* split 1.1 (0.5 - 1.7) Mya. Taylor *et al.* (2024: 7) mention the crown date as 16.8 (14.9 - 18.69) Mya.

Species groups recognized by Servent *et al.* (2003: xvi), for African taxa:
Rhinolophus: ***R. landeri*** - *landeri*, *alcyone*, ?*guineensis*. ***R. euryale*** - *blasii*, *euryale*, *mehelyi*. ***R. capensis*** - ?*capensis*, ?*swinnyi*, ?*denti*, *simulator*. ***R. adami*** - ?*adami*, ?*maendeleo*. ***R. ferrumequinum*** - *ferrumequinum*, *clivosus*, ?*silvestris*, ?*deckenii*. ***R. maclaudi*** - ?*maclaudi*, *ruwenzorii*. ***R. fumigatus*** - *fumigatus*, *eloquens*, *hildebrandtii*, *darlingi*.

Based on cyt *b* analyses, Benda and Uvizl (2025: 297, 300) conclude that the more recently described *R. horaceki* and *R. sakejiensis* do not belong to any of the currently recognized species groups, but form a distinct evolutionary lineage. The two species are relics of an early African radiation of *Rhinolophus*, which was followed by the emergence of the *landeri, capensis* and *euryale* groups, which later gave rise to the *fumigatus* and *ferrumequinum* groups.

Stoffberg *et al.* (2010a: 6 - 7) refer to Guillén-Servent *et al.* (2003), who, based on the complete cytochrome *b* gene, propose that *Rhinolophus* should be divided into six subgenera: *Aquias* (*trifoliatus* group), *Coelophyllus* (*affinis*, *coelophyllus*, *euryotis*, and *pearsonii* groups), *Indorhinolophus* (*rouxi* group), *Phyllorhina* (*hipposideros* group), *Rhinolophus* (*adami*, *capensis*, *euryale*, *ferrumequinum*, *fumigatus*, *landeri*, and *maclaudi* groups), and *Rhinophyllotis* (*acuminatus*, *borneensis*, *macrotis*,

malayanus, *megaphyllus*, and *pusillus* groups), and confirm most of these.

See Csorba *et al.* (2003: 1 - 3) for key to species.

See Taylor *et al.* (2019a: 316) for a discussion on the recent increase in Afro-Madagascan species.

Nesi *et al.* (2015: 1) indicate that the taxonomy and true number of species of African *Rhinolophus* remains unresolved because of the highly convergent morphology observed across taxa, and that the current species delimitation is based on slight variations in morphological measurements and echolocation call frequency. Due to the extensive phenotypic variation, these characters are not always very clearly separable and as such the true diversity of the genus is most probably underestimated, based on these methods alone.

Using mitochondrial cytochrome-*b* and four nuclear introns, Demos *et al.* (2019a) found indications that twelve undescribed cryptic species might be present in Africa, and that two to five of the currently accepted species are invalid. They distinguish the following putative species: *alcyone, blasii* 1, *blasii* 2, *capensis, clivosus* 1, *clivosus* 2, *clivosus* 3, *clivosus* 4, *clivosus* 5, *clivosus* 6, *cohenae, damarensis, darlingi, deckenii, denti*, cf. *denti*, cf. *denti/simulator, euryale, ferrumequinum* 1, *fumigatus/eloquens* 1, *fumigatus/eloquens* 2, *fumigatus/eloquens* 3, *fumigatus/eloquens* 4, *fumigatus/eloquens* 5, *fumigatus/eloquens* 6, *fumigatus/eloquens* 7, *fumigatus/eloquens* 8, *gorongosae, hildebrandtii* 1, *hildebrandtii* 2, *horaceki, kahuzi, landeri*, cf. *landeri, lobatus, mabuensis, mehelyi, mossambicus, rhodesiae, ruwenzorii, simulator* 1, *simulator* 2, *smithersi, swinnyi, willardi*.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Rhinolophus*: *achilles* Thomas, 1900 – Kai islands, N Queensland (Australia); *acuminatus* Peters, 1871 Thailand, Laos, Cambodia, Peninsular Malaysia and Sabah, Borneo, Sumatra (including Nias and Engano Isls), Java, Karkatau, Lombok, and Bali (Indonesia), Palawan, Balabac, Busuanga (Philippines) (Csorba *et al.*, 2003: 98; Simmons, 2005: 350); ***adami*** Aellen and Brosset, 1968; *affinis* Horsfield, 1823 – India and Nepal to south China and Vietnam, through Malaysia to Borneo and Lesser Sunda Isls, Andaman Isls (India) (Csorba *et al.*, 2003: 68; Simmons, 2005: 351); ***alcyone*** Temminck, 1853; ***alticolus*** Sanborn, 1936; *andamanensis* Dobson, 1872 – Andaman Islands (India); *arcuatus* Peters, 1871 – Sumatra to Philippines, New Guinea and South Molucca Isls (Csorba *et al.*, 2003: 20; Simmons, 2005: 351); *beddomei* K. Andersen, 1905 – southern India, Sri Lanka (Csorba *et al.*, 2003: 123; Simmons, 2005: 351); *belligerator* Patrick, McCulloch, and Ruedas, 2013 – Indonesia (Sulawesi); ***blasii*** Peters, 1867; *bocharicus* Kastchenko and Akimov, 1917 – Kyrgyzstan, western Tajikistan, northeastern Iran, Uzbekistan, Turkmenistan, Afghanistan (Csorba *et al.*, 2003: 35; Simmons, 2005: 352); *borneensis* Peters, 1861 – Borneo, Labuan and Banguey Isls (Malaysia), Java, Karimata Isls and South Natuna Isls (Indonesia), Cambodia, Laos and Vietnam (Csorba *et al.*, 2003: 70; Simmons, 2005: 352); *canuti* Thomas and Wroughton, 1909 – Java, Bali, Timor (Indonesia) (Csorba *et al.*, 2003: 22; Simmons, 2005: 352); ***capensis*** Lichtenstein, 1823; *celebensis* K. Andersen, 1905 – Java, Bali, Timor, Sulawesi, Sangihe, Kangean and Talaud Isls (Indonesia) (Csorba *et al.*, 2003: 72; Simmons, 2005: 352); *chaseni* Sanborn, 1939 – Laos, Cambodia, Vietnam, Malaysia; *chiewkweeae* Yoshiyuki and Lim, 2005 – Malaysia; *chutamasae* Soisook and Bates, 2022 – Thailand; ***clivosus*** Cretzschmar, 1828; *coelophyllus* Peters, 1867 – western Malaysia, Thailand, Burma, Laos (Csorba *et al.*, 2003: 24; Simmons, 2005: 353); *cognatus* K. Andersen, 1906 – Andaman Isls (India) (Csorba *et al.*, 2003: 99; Simmons, 2005: 353); ***cohenae*** Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012; *convexus* Csorba, 1997 – Peninsular Malaysia, Laos (Csorba *et al.*, 2003: 100; Simmons, 2005: 353); *cornutus* Temminck, 1834 – Japan (Csorba *et al.*, 2003: 102; Simmons, 2005: 353); *creaghi* Thomas, 1896 – Borneo, Madura Isl, Kalimantan (Indonesia), Sabah, Sarawak (Malaysia) (Csorba *et al.*, 2003: 25; Simmons, 2005: 354); ***damarensis*** Roberts, 1946; ***darlingi*** K. Andersen, 1905; ***deckenii*** Peters, 1868; ***denti*** Thomas, 1904; ***eloquens*** K. Andersen, 1905; *episcopus* G.M. Allen, 1923 – China; ***euryale*** Blasius, 1853; *euryotis* Temminck, 1835 – Aru Isls, Buru, Bacan, Amboina, Seram and Tanimbar Isls, Kai Isls, Halmahera and Sulawesi (Indonesia), New Guinea, Bismarch Arch, adjacent small islands (Csorba *et al.*, 2003: 27; Simmons, 2005: 355); ***ferrumequinum*** (Schreber, 1774); *foetidus* K. Andersen, 1918 – Kalimantan; *formosae* Sanborn, 1939 – Taiwan (Csorba *et al.*, 2003: 124; Simmons, 2005: 355); *francisi* Soisook, Struebig, Bates and Miguez, 2015 – Known from 6 specimens only: two in Sabah, three in Indonesian Borneo, and one in Thailand; ***fumigatus*** Rüppell, 1842; ***guineensis*** Eisentraut, 1960; ***hildebrandtii*** Peters, 1878; ***hilli*** Aellen, 1973; ***hillorum*** Koopman, 1989; ***hipposideros*** (Borkhausen, 1797); *hirsutus* K. Andersen, 1905 – Philippines; ***horaceki*** Benda and Vallo, 2012;

imaizumii Hill and Yoshiyuki, 1980 – Iriomote Island and Yaeyama Island (Japan: Ryukyu Islands) (Csorba *et al.*, 2003: 104; Simmons, 2005: 357); *inops* K. Andersen, 1905 – Philippines except Palawan region (Csorba *et al.*, 2003: 29; Simmons, 2005: 357); *keyensis* Peters, 1871 – Many islands in Indonesia (Simmons, 2005: 357); ***landeri*** Martin, 1838; *lepidus* Blyth, 1844 – Afghanistan, Pakistan, northern India, Nepal, Burma, Thailand, Szechwan and Yunnan (China), Peninsular Malaysia, Sumatra (Indonesia) (Csorba *et al.*, 2003: 106; Simmons, 2005: 358); ***lobatus*** Peters, 1852; *luctoides* Volleth, Loidl, Mayer, Yong, Müller and Heller, 2015 – Peninsular Malaysia; *luctus* Temmink, 1834 – India, Nepal, Burma, Sri Lanka, south China, Vietnam, Cambodia, Laos, Thailand, Peninsular Malaysia, Borneo, Sumatra, Java and Bali (Indonesia) (Csorba *et al.*, 2003: 126; Simmons, 2005: 358); ***mabuensis*** Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012; ***maclaudi*** Pousargues, 1898; *macrotis* Blyth, 1844 – Pakistan, northern India, Nepal to south China, Burma, Thailand, Laos, Vietnam and Peninsular Malaysia, Sumatra (Indonesia), Philippines (Csorba *et al.*, 2003: 87; Simmons, 2005: 358); *madurensis* K. Andersen, 1918 – Madura and Kangean Isls (Indonesia) (Simmons, 2005: 358); ***maendeleo*** Kock, Csorba and Howell, 2000; *malayanus* Bonhote, 1903 – Thailand, Burma, Cambodia, Laos, Vietnam, Peninsular Malaysia (Csorba *et al.*, 2003: 74; Simmons, 2005: 359); *marshalli* Thonglongya, 1973 – Thailand, Burma, Vietnam, Laos, Peninsular Malaysia (Csorba *et al.*, 2003: 89; Simmons, 2005: 359); *mcintyrei* Hill and Schlitter, 1982 – New Guinea; *megaphyllus* Gray, 1834 – eastern New Guinea; Misima Island (Louisiade Archipelago), Goodenough Island (D'Entrecasteaux Islands) and Bismarck Archipelago (Papua New Guinea), Moluccas, Lesser Sundas, eastern Queensland, eastern New South Wales and eastern Victoria (Australia) (Csorba *et al.*, 2003: 76; Simmons, 2005: 359); ***mehelyi*** Matschie, 1901; *microglobosus* Csorba and Jenkins, 1998 – Cambodja, Laos, Thailand (N of Kra isthmus), N + C Vietnam, China (Yunnan); *midas* K. Andersen 1905 – Iraq; E Turkey to Kashmir (Pakistan, India); *mitratus* Blyth, 1844 – India (Csorba *et al.*, 2003: 131; Simmons, 2005: 360); *monoceros* K. Andersen, 1905 – Taiwan (Csorba *et al.*, 2003: 108; Simmons, 2005: 360); *montanus* Goodwin, 1979 – Timor (Indonesia) (Csorba *et al.*, 2003: 91; Simmons, 2005: 360); *morio* Gray, 1842 – Sumatra (part); Peninsular Malaysia; ***mossambicus*** Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012; ***namuli*** Curran, Kopp, Ruedi, and Bayliss, 2022; *nereis* K. Andersen, 1905 – Anamba and North Natuna Islands (Indonesia) (Csorba *et al.*, 2003: 78; Simmons, 2005: 360); *nippon* Temminck, 1835 – Japan; *osgoodi* Sanborn, 1939 – Yunnan (China) (Csorba *et al.*, 2003: 109; Simmons, 2005: 360); *pearsoni* Horsfield, 1851 – Northern India, Nepal, Bhutan, Burma, Tibet, Szechwan, Anhwei and Fukien (China) to Vietnam, Laos, Thailand, Peninsular Malaysia (Csorba *et al.*, 2003: 83; Simmons, 2005: 360); *perditus* K. Andersen, 1918 – Ryukyu Islands, Ishigaki Island (Japan); *perniger* Hodgson, 1843 – Bangladesh, India (including Manipur), Nepal; *philippinensis* G.R. Waterhouse, 1843 – Phillipines, Kai Isls, Sabah, Sarawak and Sulawesi (Indonesia), Borneo, New Guinea, northeastern Queensland (Australia) (Csorba *et al.*, 2003: 94; Simmons, 2005: 361); *proconsulis* Hill, 1959 – Borneo; *pumilus* K. Andersen, 1905 – Ryukyu Islands, Okinawa Island (Japan); *pusillus* Temminck, 1834 – India, Nepal, Thailand, Burma, Laos, south China, Peninsular Malaysia, Mentawai Isls, Java and Lesser Sunda Isls (Indonesia), small adjacent islands (Csorba *et al.*, 2003: 112; Simmons, 2005: 361); *refulgens* K. Andersen, 1905 – Malaysia; *rex* G. M. Allen, 1923 – southwestern China (Csorba *et al.*, 2003: 96; Simmons, 2005: 361); *robinsoni* K. Andersen, 1918 – western Malaysia, Thailand, adjacent small islands (Simmons, 2005: 361); *rouxii* Temminck, 1835 – Sri Lanka, peninsular India to southern Burma and Vietnam (Csorba *et al.*, 2003: 117; Simmons, 2005: 362); *rufus* Eydoux and Gervais, 1836 – Philippines (Csorba *et al.*, 2003: 30; Simmons, 2005: 362); ***ruwenzorii*** J. Eric Hill, 1942; ***sakejiensis*** Cotterill, 2002; *sedulus* K. Andersen, 1905 – Peninsular Malaysia, Sarawak and Sabah (Malaysia), Borneo (Indonesia) (Csorba *et al.*, 2003: 128; Simmons, 2005: 362); *septentrionalis* Sanborn, 1939 – Yunnan province (China); *shameli* Tate, 1943 – Burma, Thailand, Laos, Cambodia, Peninsular Malaysia (Csorba *et al.*, 2003: 31; Simmons, 2005: 363); *shortridgei* K. Andersen, 1918 – northern India, Burma (Csorba *et al.*, 2003: 114; Simmons, 2005: 363); *siamensis* Gyldenstolpe, 1917 – Thailand, Laos, Vietnam (Simmons, 2005: 363); ***silvestris*** Aellen, 1959; ***simulator*** K. Andersen, 1904; *sinicus* K. Andersen, 1905 – southern China, Nepal, northern India, Vietnam (Csorba *et al.*, 2003: 119; Simmons, 2005: 363); ***smithersi*** Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012; *stheno* K. Andersen, 1905 – Vietnam, Thailand, Laos, Peninsular Malaysia, Sumatra and Java (Indonesia) (Csorba *et al.*, 2003: 80; Simmons, 2005: 363); *subbadius* Blyth, 1844 – northeastern India, Nepal, Vietnam, Burma (Csorba *et al.*, 2003: 115; Simmons, 2005: 364); *subrufus* K. Andersen, 1905 – Philippines except Palawan region (Csorba *et al.*, 2003: 33; Simmons, 2005: 364); ***swinnyi*** Gough, 1908;

tatar Bergmans and Rozendaal, 1982 – Central part of Sulawesi (Indonesia); *thailandensis* Wu, Harada and Motokawa, 2009 – N Thailand (Chiang Mai); *thomasi* K. Andersen, 1905 – Burma, Vietnam, Thailand, Laos (Csorba *et al.*, 2003: 121; Simmons, 2005: 364); *trifoliatus* Temminck, 1834 – northeastern India, southwestern Thailand and Burma, Peninsular Malaysia, Sarawak and Sabah (Malaysia), Singapore, Borneo, Sumatra, Riau Archipelago, Banguey Isl, Java, Banka Isl and Nias Isl (Indonesia) (Csorba *et al.*, 2003: 130; Simmons, 2005: 364); *virgo* K. Andersen, 1905 – Philippines (Csorba *et al.*, 2003: 81; Simmons, 2005: 364); ***willardi*** Kerbis Peterhans and Fahr, 2013; *xinanzhongguoensis* Zhou, Guillén-Servent, Lim, Eger, Wang and Jiang, 2009 Yunnan Province (China); *yunanensis* Dobson, 1872 – Yunnan (China), Burma, Thailand, northeastern India (Csorba *et al.*, 2003: 85; Simmons, 2005: 365); ***ziama*** Fahr, Vierhaus, Hutterer and Kock, 2002.

Additionally, in Africa there is also the extinct ***†maghrebensis*** Gunnell, Eiting, and Geraads, 2011.

COMMON NAMES:
Czech: vrápenci, wrápenecové, vrápníkové, vrápeníkové, podkováčkové, vrápenec. Dutch: Hoefijzerneuzen. English: Horseshoe bats. French: Rhinolophes, Fers-à-cheval. German: Hufeisennasen, Hufeisennasen-Fledermäuse. Italian: Fèrri di cavàllo, Rinòlofi. Kiluba (DRC): Kasusu. Korean: Gwan-bak-jwi-sok (

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The approximate fossil date for the crown *Rhinolophus* is placed at about 37.2 MYA by Shi and Rabosky (2015: 1532). Guo *et al.* (2022: 173) found that the genus originated in Asia and that the two major clades (African and Oriental) within the genus arose during the Oligocene, with ancestors of the extant African species being present at about 25.59 MYA. Diversification in the African clade occurred in the late Oligocene and early Miocene.

Three or four *Rhinolophus* species were reported by Avery (2007: 619) from Pleistocene deposits at Wonderwerk Cave, South Africa.

Geraads *et al.* (2010: 279) reported the presence of *Rhinolophus* in Late Cenozoic (ca. 2.5 MYA) deposits in Ahl al Oughlam, Morocco.

BIOGEOGRAPHY:
See Servent *et al.* (2003: xii - xxiv) for discussion on phylogeny and biogeography of the horseshoe bats.

During the Miocene at about 17 Mya, *Rhinolophus* diversified into three distinct clades, two of these clades showed distinct geographical origins (Foley *et al.*, 2014: 320). In Eastern/South Eastern Asia represented by *R. trifoliatus* and *R. luctus* and East Asia represented by *R. pearsoni*, *R. sinicus*, *R. creaghi*, *R. shameli* and *R. pusillus*. While the clade that contains *R. hipposideros*, *R. ferrumequinum* and *R. euryale* is less clear indicating a widespread geographical origin including Europe, East Asia, Middle East and Africa.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Schmieder *et al.* (2015) studied the wing morphology of five species of European Rhinolophid bats, which also occur in northern Africa: *R. blasii, R. euryale, R. ferrumequinum, R. hipposideros*, and *R. mehelyi*, and they provide a table of geometric differences (p. 8).

DENTAL FORMULA:
The permanent dental formula is variable, usually $I^1/_2$, $C^1/_1$, $PM^2/_3$, $M^3/_3$ = 32.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Santana and Lofgren (2013: 2521) investigated the evolution of skull morphology and modularity in the recent radiation of rhinolophid bats and predict that nasal echolocation has resulted in the evolution of a third cranial module (the 'nasal dome'), in addition to the two cranial modules conserved across mammals.

FUNCTIONAL MORPHOLOGY:
Jacobs *et al.* (2007a) found that in Africa the peak echolocation frequency was inversely correlated with size in the Rhinolophidae, while for rhinolophids from around the world, peak frequency was inversely correlated with forearm length. Similarly, there was an inverse correlation between mass and peak frequency, between forearm and peak frequency and between wing loading and peak frequency in the African Rhinolophidae (Jacobs *et al.*, 2007a).

SEXUAL DIMORPHISM:
Wu *et al.* (2018: 7) found that sexual dimorphism in rhinolophids is larger in species inhabiting open habitats compared to those occurring in forested habitats.

ECHOLOCATION:
Jacobs *et al.* (2014: 2829) found that echolocation frequency was positively correlated with bite force, which suggests that its evolution is influenced by a trade-off between the masticatory and sensory functions of the skull. In support of this, variation in skull shape was explained by

both echolocation frequency (80 %) and bite force (20 %). They also found that selection has acted on the nasal capsules, which have a frequency-specific impedance matching function during vocalization.

In the Mapungubwe National Park (RSA), Parker and Bernard (2018: 56, 57) recorded a *Rhinolophus* species with a F_{char} = 100.72 ± 0.52 kHz, F_{max}: 100.93 ± 0.77 kHz, F_{min}: 91.34 ± 6.08 kHz, F_{knee}: 100.72 ± 0.52 kHz, duration: 34.89 ± 14.42 ms, with 8.32 ± 3.39 calls/sec. This type of call was also recorded by Taylor *et al.* (2013b: 14) from the Soutpansberg area, and probably is produced by an undescribed species.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the following diurnal avian predators: African fish eagle (*Haliaeetus vocifer* (Daudin, 1800)), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) [on either *landeri* or *fumigatus* or *hildebrandti*].

PARASITES:
BACTERIA
Bartonellae
Kamani *et al.* (2014: 628) tested 12 Nigerian "*Rhinolophus*" sp. and found at least 8 of them testing positive for *Bartonella* DNA. Of the six Nigerian bats, examined by Di Cataldo *et al.* (2020: 2), 2 were found to be infected by hemoplasma bacteria.

HAEMOSPORIDA
Schaer *et al.* (2015a: 381) found *Nycteria* sp. parasites in *Rhinolophus* sp. 1 from South Sudan, which were also reported by Arnuphapprasert *et al.* (2020: Suppl.). The same bat species was also infected by *Nycteria* cf. *gabonensis*. Landau *et al.* (2012: 142) and Perkins and Schaer (2016: Suppl.) also reported *Nycteria krampitzi* Rosin, Landau and Hugot, 1978 from the Republic of Congo and Gabon.

Wünschmann *et al.* (2010: 178) refer to Boulard (1975), who reported the first case of renal coccidiosis in a bat (on *H. caffer* and *Rhinolophus* sp.) from Sierra Leone and the Congo and caused by *Klossiella killicki*.

Garnham (1973: 236) refers to Anciaux de Faveaux for a *Polychromophilus ? murinus* from "Africa".

Bochkov and Fain (2003) reported on *Neomyobia chiroptealis camerounensis* Fain, 1974 and *Neomyobia (Neomyobia) jacksoni* (Radford, 1940) from non-specified specimens.

HEMIPTERA
Cimicidae
Haeselbarth *et al.* (1966: 10) records that only three males of *Loxaspis setipes* Ferris and Usinger, 1957 are known from unknown *Rhinolophus*, from Lukolela, Congo.

Szentiványi *et al.* (2022: 4) reported *Adroctenes horvathi* Jordan, 1912 from Kenyan *Rhinolophus* sp.

DIPTERA
Streblidae
Brachytarsina africana (Walker, 1849) is a typical ectoparasite of the genus *Rhinolophus* in sub-Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Ascodipteron brevior* Maa, 1965 from Sudan (Haeselbarth *et al.*, 1966: 106). *Ascodipteron lophotes* Monticelli, 1898 from Yemen (Haeselbarth *et al.*, 1966: 106). *Raymondia alulata* Speiser, 1908 (Shapiro *et al.*, 2016: 253). *Raymondia aspera* Maa, 1968 (Shapiro *et al.*, 2016: 253). *Raymondia boquieni* Vermeil, 1965 from Congo and the DRC (Shapiro *et al.*, 2016: 254). *Raymondia huberi huberi* Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254). *Raymondia intermedia* Jobling, 1936 (Shapiro *et al.*, 2016: 255). *Raymondia seminuda* Jobling, 1954 (Shapiro *et al.*, 2016: 255). *Raymondia setiloba* (Jobling, 1954) (Shapiro *et al.*, 2016: 256). *Raymondia waterstoni* Jobling, 1931 (Shapiro *et al.*, 2016: 256). *Raymondia* sp. B (Shapiro *et al.*, 2016: 257).

Nycteribiidae
Nycteribia integra Theodor and Moscona, 1954 common in Egypt (Haeselbarth *et al.*, 1966: 109). *Nycteribia ovalis* Theodor, 1957 from Tanzania (Haeselbarth *et al.*, 1966: 110). *Nycteribia tecta* Theodor, 1957 (Haeselbarth *et al.*, 1966: 110). *Dipseliopoda biannulate* (Oldroyd, 1953) from the Sudan (Haeselbarth *et al.*, 1966: 116). Kamani *et al.* (2014: 628) and Stuckey *et al.* (2017: 22) reported the presence of *Cyclopodia greefi* Karsch, 1884 on bats from Nigeria.

Dick *et al.* (2023) mentioned the nycteribiid flies *Penicillidia (Penicillidia) fulvida* (Bigot, 1885), *Phthiridium hoogstraali* (Theodor, 1957) and *Phthiridium tectum* (Theodor, 1957) have been found on *Rhinolophus* sp. *Penicillidia (Penicillidia) pachymela* Speiser, 1901 was reported from *Rhinolophus eloquens/lobatus*, and *Dipseliopoda biannulata* (Oldroyd, 1953) from *Rhinolophus eloquens/landeri*, although this might have been an erroneous record.

SIPHONAPTERA
Ischnopsyllidae
Members of the genus *Rhinolophopsylla* Oudemans, 1909 are known to be parasites of *Miniopterus* and *Rhinolophus* (Haeselbarth *et al.*, 1966: 191).

ACARI
Myobiidae
Fain (1994: 1280) indicates that only two endemic genera are found on *Rhinolophus* species: *Neomyobia* with 13 species and three subspecies, and *Rhinomyobia* with one species. Another genus/species - *Calcarmyobia rhinolophi* - was described from *Rhinolophus lobatus*, but this probably should be from *Miniopterus natalensis arenarius* (Uchikawa, 1985a: 15).

VIRUSES:
Adenoviridae
These viruses were found by Waruhiu *et al.* (2017) in bats from Kenya.

Coronaviridae
Tao *et al.* (2017: 3) found 28.9 % (13 out of 45) of the Kenyan *Rhinolophus* sp. specimens they tested to be positive for CoV. In Guinea, two out of five specimens tested by Lacroix *et al.* (2020: 7) was positive. Tao and Tong (2019: 1) report the complete genomic sequence of a strain of *Betacoronavirus* (BtKY72/*Rhinolophus* sp./Kenya/2007 - BtKY72 - subgenus *Sarbecovirus*).

Meta Djomsi *et al.* (2023: 1) tested 899 *Rhinolophus* specimens from the DRC, Cameroon and Guinea and found 306 (34.1 %) of them to be positive for coronaviruses, primarily Betacoronaviruses of the subgenus Sarbecovirus.

Sánchez *et al.* (2024: 4) indicate that European and African *Rhinolophus* species roost in lower densities and with less species than Asiatic species and therefore there is less risk of viral recombination and adaptation to new hosts.

Rhinolophus 'incertae-sedis'

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Flaviviridae
Hermida Lorenzo *et al.* (2021: 6) reported Pestivirus from Guinean rhinolophids.

Raulino *et al.* (2022: 256) found antibodies against West Nile virus.

Herpesviridae
Hermida Lorenzo *et al.* (2021: 6) reported Bat betaherpesvirus from Guinean bats.

Paramyxoviridae
1 out of nine tested *Rhinolophus* sp. from Cameroon was found to test positive for *Paramyxovirus* sequences by Mortlock *et al.* (2015: 1841).

Parvoviridae
Hermida Lorenzo *et al.* (2021: 6) reported the presence of unidentified Densovirinae in Guinean bats.

Retroviridae
Squirrel monkey retrovirus was reported from Guinean bats by Hermida Lorenzo *et al.* (2021: 6).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 16 Kenyan *Rhinolophus* sp. specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Angola, Benin, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Equatorial Guinea, Eritrea, Eswatini, Ethiopia, Gabon, Kenya, Madagascar, Malawi, Morocco, Mozambique, Namibia, Senegal, Somalia, South Africa, South Sudan, Tanzania, Togo, Tunisia, Uganda, Zambia, Zimbabwe.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

Rhinolophus acrotis Heuglin, 1861

*1861. *Rhinolophus acrotis* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 10. Publication date: 1861. Type locality: Eritrea: Kérén [ca. 15 45 N 38 20 E]. [Goto Description]. Holotype: SMNS 986a: ad ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. Paratype: SMNS 986b: juv ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. Dieterlen *et al.* (2013: 293) mention this specimen as a possible paratype, although they do indicate that Heuglin based his description on one single specimen (probably SMNH 986a). They also indicate that this specimen was marked as "Cotype" by Krauss. - Etymology: From the two neuter Greek substantives "*ἄκρον*" (akron), meaning "extremity" and "*οὖς*", meaning "ear" (see Lanza *et al.*, 2015: 80).

TAXONOMY:
Considered a valid species by Lanza *et al.* (2015: 78 - 81) [referring to a personal communication of Petr Benda]: "I still did not publish the paper with the revision of the current species *clivosus*; however, the situation is more or less clear for me. The species *clivosus* does not deserve a species position any more and should be regarded a subspecies of *R. ferrumequinum* (or a separate species with very limited range in NE Africa and SW Asia and very close positioned to *R. ferrumequinum* species). The "*clivosus*" populations from S Arabia, Ethiopia, Sudan, Eritrea and Somalia are separated from *ferrumequinum/clivosus* and the name for this species is *R. acrotis* (new subspecies of this form will be described from Socotra). The East and South African populations formerly assigned to *clivosus* are also separate form named *R. augur*, probably without subspecific division. Another form, formerly considered under *clivosus* should be described from Cyrenaica. The Saharan forms *brachygnathus, schwartzi* and *andersoni* are synonyms of *clivosus* s. str."

Uvizl *et al.* (2024: 1) and Benda *et al.* (2024: 2) consider *acrotis* to be a valid species, with two subspecies: *R. acrotis acrotis* (a small-sized form endemic to the Ethiopian Highlands) and *R. acrotis augur* (a larger form from open habitats between Kenya and South Africa).

COMMON NAMES:
English: Eritrea Horseshoe Bat, Heuglin's Horseshoe Bat. Italian: Rinólofo di Heuglin, Fèrro di cavàllo di Hèuglin.

GENERAL DISTRIBUTION:
This pecies is found in the Ethiopian highlands, Eritrea and eastern Sudan. In East Africa, it ranges from Sudan in the north, through all East African countries to Malawi in the south; in southern Africa, it is present in Mozambique and Zambia in the north, ranging southwards into South Africa, Namibia and southern Angola. In addition, there are several records from southern and eastern parts of the Democratic Republic of the Congo.

ECHOLOCATION:
For KwaZulu-Natal, Howard *et al.* (2022: 192) mention F_{char}: 88 - 96 kHz, F_{knee}: 88 - 96 kHz, F_{max}: 79 - 96, F_{mean}: 72 - 95 kHz.

In South Africa, Rowland *et al.* (2024: Suppl.) mention F_{peak}: 91.7 ± 1 kHz and a duration of 37.4 ± 6.2 msec.

DIET:
From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 46 faecal pellets from 5 bats (in volume percent): Lepidoptera (62.6 ± 30.8), Coleoptera (29.4 ± 24.8), Hemiptera (2.0 ± 4.5), Hymenoptera (1.4 ± 3.1), and unknown (4.6 ± 6.4).

Jacobs *et al.* (2007a) at De Hoop, South Africa, found that the diet mainly consisted of Lepidoptera and Coleoptera with lesser amounts of Neuroptera, Hemiptera and Diptera. The mean size of measurable prey taken by *R. clivosus* was larger than that taken by *R. capensis*, although the range of prey sizes taken by the two species overlapped (Jacobs *et al.*, 2007a).

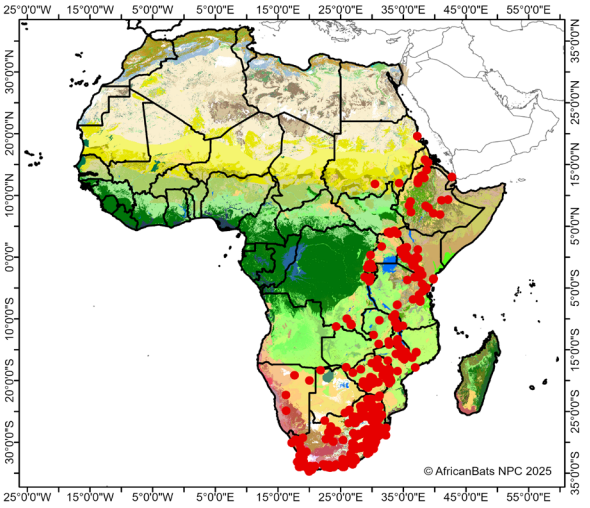

Figure 77. Distribution of *Rhinolophus acrotis*.

Rhinolophus acrotis acrotis Heuglin, 1861

Holotype: SMNS 986a: ad ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. Paratype: SMNS 986b: juv ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. Dieterlen *et al.* (2013: 293) mention this specimen as a possible paratype, although they do indicate that Heuglin based his description on one single specimen (probably SMNH 986a). They also indicate that this specimen was marked as "Cotype" by Krauss.2019. *R[hinolophus] clivosus 6:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 10. Publication date: 22 August 2019. (Name Combination).

? *Rhinolophus clivosus acrotis:* (Current Combination).

GENERAL DISTRIBUTION:
This subspecies is restricted to the Ethiopian highlands, Eritrea and eastern Sudan(?).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Eritrea, Ethiopia, South Sudan, Sudan.

Rhinolophus acrotis augur K. Andersen, 1904

1829. *Rhinolophus Geoffroyii* A. Smith, Zool. Journ., 4 (16): 433. Publication date: May 1829. Type locality: South Africa: "South Africa". [Goto Description]. - Comments: Roberts (1951: 61) nominated Cape Town as type locality; see Meester *et al.* (1986: 38). Allen (1939a: 75) mentioned *geoffroyii* as a separate species. Meester *et al.* (1986: 38) follow Ellerman *et al.* (1953: 57) in considering *geoffroyii* as unidentifiable.

*1904. *Rhinolophus augur* K. Andersen, Ann. Mag. nat. Hist., ser 7, 14 (83): 380. Publication date: 1 November 1904. Type locality: South Africa: Northern Cape province: [formerly Bechuanaland]: Kuruman [26 28 S 22 27 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1904.10.1.1: ad ♂, skin and skull. Collected by: Mr. Richard Bowen Woosnam; collection date: 19 April 1904; original number: 26.

1904. *Rhinolophus augur zambesiensis* K. Andersen, Ann. Mag. nat. Hist., ser 7, 14 (83): 383. Publication date: 1 November 1904. Type locality: Malawi: Fort Hill [=Chitipa] [09 42 S 33 16 E, 1 300 m]. [Goto Description]. Holotype: NHMUK 1897.10.1.18: ad ♂, skin and skull. Collected by: Alexander ("Alex") Whyte (F.Z.S); collection date: July 1896; original number: 136. Presented/Donated by: Sir Harry Hamilton Johnston. - Comments: Considered a synonym of *zuluensis* by Ansell and Dowsett (1988: 32).

1904. *Rhinolophus augur zuluensis* K. Andersen, Ann. Mag. nat. Hist., ser 7, 14 (83): 383. Publication date: 1 November 1904. Type locality: South Africa: KwaZulu-Natal: 20 mi [=32 km] NW Eshowe: Jususie valley [=Insuzi valley] [28 53 S 31 03 E, 1 000 ft]. [Goto Description]. Holotype: NHMUK 1904.5.1.8: ad ♀, skin and skull. Collected by: Captain Claude Henry Baxter Grant; collection date: 17 November 1903; original number: 602. Presented/Donated by: C.D. Rudd Esq. - Comments: Considered a valid subspecies by Ansell and Dowsett (1988: 32), Taylor (1998: 35).

1916. *Rhinolophus keniensis* Hollister, Smiths. Misc. Coll., 66 (1) (2406): 2. Publication date: 10 February 1916. Type locality: Kenya: W side Mount Kenya [ca. 00 10 S 37 19 E, 7 000 ft]. [Goto Description]. Holotype: USNM 166352: ad ♂, skull and alcoholic. Collected by: Edmund Heller; collection date: 27 August 1909; original number: 1154. Fisher and Ludwig (2015: 54) indicate that the Field Catalog mentions that this specimen was collected at the Base Camp on the West side of Mount Kenya.

1932. *Rhinolophus geoffroyi zuluensis:* Ortlepp, 18th Report of the Director of Veterinary Sciences and Animal Industry. Union of South Africa. (Name Combination).

1959. *Rhinolophus ferrum-equinum keniensis:* Harrison, Occ. Pap. Nat. Mus. S. Rhod., 23B: 228. (Name Combination).

1980. *Rhinolophus ferrumequinum keniensis:* Blackwell, Mycologia, 72 (1): 145. (Name Combination).

1993. *angur:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 164. (Lapsus).

2019. *R[hinolophus] clivosus 1:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 10. Publication date: 22 August 2019. (Name Combination).

2019. *R[hinolophus] clivosus 2:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 10. Publication date: 22 August 2019. (Name Combination).

2019. *R[hinolophus] clivosus 3:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 40. Publication date: 22 August 2019.

? *Rhinolophus clivosus augur:* (Current Combination).

? *Rhinolophus clivosus keniensis:* (Name Combination).

? *Rhinolophus clivosus zuluensis:* (Name Combination).

? *Rhinolophus ferrum-equinum zuluensis:* (Name Combination).

? *Rhinolophus geoffroyi augur:* (Name Combination).

? *Rhinolophus geoffroyi geoffroyi:* (Name Combination).

? *Rhinolophus geoffroyi:* (Name Combination, Alternate Spelling).

TAXONOMY:



Figure 78. *Rhinolophus acrotis augur*.

Roberts (1919: 112) points out that *geoffroyii* Smith, 1829 antedates *augur* Andersen, 1904, and later (Roberts, 1951) regards *augur* as a subspecies of *geoffroyii*. Allen (1939a) follows Roberts in regarding *geoffroyii* as the prior name, but Ellerman *et al.* (1953) reject this, pointing out that the description does not identify *geoffroyii* and that the type is apparently lost, and therefore propose that the name be discarded as unidentifiable. The next available name would be *Rhinolophus augur* Andersen, 1904.

Stoffberg *et al.* (2012: 1) indicate that southern African representatives of *R. clivosus* s.l. are as distinct from more northern African samples as they are from *R. ferrumequinum*. In southern Africa, they (p. 5) distinguish five geographic groups: Western Cape clade, Knysna region clade, Northern Cape clade, a predominantly KwaZulu-Natal/Mpumalanga mixed group and a Mpumalanga/Limpopo Province clade. About 3.7 Mya, these groups were separated from more northern groups (Kenya, Tanzania and Mozambique) and all of these were separated from the Egyptian populations at about 4.26 Mya. Stoffberg *et al.* (2012: 2; fig. 1) show the distribution area for four subspecies: *geoffroyi* in the Western Cape province and the coastal part of the Northern Cape province; *zuluensis* in the Eastern Cape province, KwaZulu-Natal province, Mpumalange province, southern Limpopo province and Swaziland and Lesotho; *augur* in eastern Northern Cape province and central Botswana; and *zambesiensis* in Mozambique, Zambia, Zimbabwe and the extreme southeastern DRC. On the other hand, Benda and Vallo (2012: 83) suggest that all populations occurring in the savanna belt from the Cape to Kenya belong to one taxon (subspecies): *augur*. Unfortunately, neither Stoffberg *et al.* (2012) nor Benda and Vallo (2012) provide any information on the validity of the name "*geoffroyii*". Therefore, pending further investigation in the taxonomy of this complex, we retain the usage of the name *R. acrotis augur*.

Benda *et al.* (2025: 31, 50) found that the population from Mount Elgon (Kenya) is rather small-sized, but this seems to be a local montane ecomorph, with no taxonomic value. Their dimensions are somewhat in the overlap zone of the two recognized subspecies, but their nucDNA and mtDNA haplotypes do assign these specimens to the Eastern African *Rhinolophus acrotis augur*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
R. acrotis augur has been recovered (as *R. clivosus*) from both the upper Pleistocene and very late Holocene at Border Cave and is possibly present in the late Holocene at Nkupe, South Africa (Avery, 1991: 6). Avery and Avery (2011: 17) report additional Holocene (Blinkklipkop and Wonderwerk), and Pleistocene (Wonderwerk) remains from the Northern Cape province (South Africa).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough globally to qualify for listing in a more threatened category (IUCN, 2009; Monadjem *et al.*, 2017cy). [Assessed as *Rhinolophus clivosus*, but applicable on *augur* as this is the most widely distributed African form]

Assessment History
Global
[as *R. clivosus*] 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cy). 2008: LC ver 3.1 (2001) (Kock *et al.*, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004an; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa [as *R. clivosus*]: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016d). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
Although there are generally considered to be no major threats to the species as a whole, some populations are locally threatened by disturbance of their roosting sites, and indirect poisoning resulting from the use of insecticides, pesticides and similar chemicals (Kock *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017cy).

CONSERVATION ACTIONS:
Monadjem *et al.* (2017cy) reported [as *Rhinolophus clivosus*] that in view of the species'

wide range it seems likely that it is present in several protected areas.

GENERAL DISTRIBUTION:
Rhinolophus acrotis augur is widely distributed in eastern and southern Africa, from Kenya to South Africa (Benda *et al.*, 2024: 2).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area (for "*Rhinolophus clivosus*") of 1,120,944 km^2.

In South Africa, its distribution is strongly associated with annual precipitation (Babiker Salata, 2012: 49).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
For 5 specimens from the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following wing parameters: Fa: 53.4 ± 1.5 mm, Wing area: 175.9 ± 5.8 cm^2, Wing span: 33.8 ± 1.1 cm, Wing loading: 9.2 ± 0.8 N/m^2, and aspect ratio: 6.5 ± 0.3.

DETAILED MORPHOLOGY:
Jacobs *et al.* (2013b: 76) found that "*R. clivosus*" has a smaller nasal capsule volume than predicted from its size.

FUNCTIONAL MORPHOLOGY:
Jacobs *et al.* (2007a), at De Hoop, South Africa, found "*Rhinolophus clivosus*" to have a higher mean wing loading and aspect ratio than *R. capensis*, but no differences in their mean shape indices. Amador *et al.* (2019: Suppl.) [referring to the previous publication (Jacobs *et al.*, 2007a)] mention a wing loading value of 8.9 Pa, aspect ratio 5.6 for a wingspan of 33 cm and a wing area of 198 cm^2 and a body mass of 18 g.

SEXUAL DIMORPHISM:
At De Hoop, South Africa, Jacobs *et al.* (2007a) found that females were heavier than males, but there were no differences in forearm length, or wingspan.

ECHOLOCATION:
Finger *et al.* (2017: 144) found that echolocation signals enables "*R. clivosus*" to distinguish the sex of the caller (probably linked with the initial and terminal FM components of the signal) and even its identity (probably linked with resting frequency). Raw *et al.* (2018: 1) furthermore found that "*R. clivosus*" could discriminate readily between species using echolocation pulses with discrete frequencies. To discriminate between species with overlapping frequencies, additional parameters such as sweep rate of the FM and duty cycle were used.

For individuals in South Africa, Taylor (1999b), using a Pettersson D980 detector at a locality in Dundee, reported a F_{max}: 94.3± 0.2 kHz, while Jacobs *et al.* (2007a) (detector type and locality not reported) reported a F_{peak} 92.1 ± 0.7 kHz. Monadjem *et al.* (2007a), using an Anabat detector at several different localities in Swaziland, reported a F_{max}: 91.9 ± 0.65 kHz. From the same country, Monadjem *et al.* (2017c: 179) reported F_{min}: 75.7 ± 3.15 (70.4 - 80.3) kHz, F_{knee}: 91.5 ± 0.70 (90.0 - 92.3) kHz, F_c: 91.3 ± 1.06 (88.9 - 92.5) kHz and duration: 32.9 ± 5.35 (23.3 - 40.1) ms. Taylor (2000) indicates a constant frequency component of 94 kHz. Monadjem *et al.* (2010c: 378) reported from Mozambique that the peak echolocation frequencies ranged between 79.8 - 81.0 kHz (ANABAT, Petterson D240x).

From Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the type of calls to be high duty echolocation dominated by constant frequency calls, with a F_{peak}: 92.7 ± 0.5 kHz.

Monadjem *et al.* (2007a) also reported sexual dimorphism in the call with females emitting a higher frequency call than males (females 92.5 ± 0.04 kHz, males 91.6 ± 0.61 kHz).

Taylor *et al.* (2013b: 19) recorded the following parameters for 10 calls from Soutpansberg, South Africa: F_{max}: 92.1 ± 0.51 (91.5 - 92.8) kHz, F_{min}: 86.7 ± 3.21 (89.6 - 90.9) kHz, F_{knee}: 90.3 ± 0.42 (89.6 - 90.9) kHz, F_{char}: 90.7 ± 0.40 (90.1 - 91.4) kHz, duration: 14.3 ± 3.63 (8.6 - 19.4) ms.
Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg area (RSA): F_{min}: 79 - 90 kHz, F_{char}: 90 - 91 kHz, F_{knee}: 91 - 91 kHz, slope: 280 - 606 OPS, duration: 9 - 19 ms.
335 calls from 15 bats from southern KwaZulu-Natal and Eastern Cape (RSA) were reported by Moir (2020: 29) and Moir *et al.* (2021a: 371) with: F_{max}: 94.39 ± 0.74 (93.34 - 96) kHz, F_{min}: 84.99 ± 3.54 (76.30 - 88.77) kHz, F_{char}: 92.76 ± 0.8 (91.73 - 94.66) kHz, F_{knee}: 92.61 ± 0.7 (91.27 - 93.86) kHz, and duration: 16.66 ± 4.09 (10.42 - 25.11) ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 47 "*Rhinolophus clivosus*" calls from the Kruger Park (RSA): F_{min}: 75 ± 3.2 (67.6 - 81.9) kHz, Duration: 18.7 ± 7.0 (7.7 - 32.0) ms, F_{max}: 92.6 ± 0.6 (91.4 - 93.5) kHz, F_{knee}: 108.1 ± 119.7 (89.4 - 91.1) kHz, F_{char}: 90.4 ± 0.6 (89.1 - 91.4) kHz,

Jacobs (2016: 133) and Jacobs *et al.* (2017b: 3) indicated that the call frequency of about 92 kHz

in South Africa is much higher than expected for an animal of that size (which would be something around 66 kHz). They found that climatic factors, especially temperature, play an important role.

Eisenring *et al.* (2016: SI 2) reported the following for 28 calls from the Aberdares Range in Kenya: F_{peak}: 84.9 ± 5.0 (66.9 - 88.3), F_{max}: 86.8 ± 4.3 (69.7 - 89.7), F_{min}: 68.4 ± 6.4 (56.4 - 81.8), DT: 0.4 ± 0.2 (0.0 - 0.6), DF: 18.4 ± 7.3 (4.9 - 32.5), IPI: 0.7 ± 0.7 (0.1 - 3.8).

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 31 calls of 6 bats: F_{max}: 91.66 ± 1.12 kHz, F_{min}: 85.46 ± 13.29 kHz, F_{knee}: 90.21 ± 1.52 kHz, F_{char}: 90.28 ± 1.74 kHz, slope: -1708.34 ± 10,903.27 OPS, duration: 13.58 ± 12.83 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 85.18 kHz, F_{start}: 78.92 kHz, F_{end}: 78.81 kHz, and duration: 54.48 ms.

13 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 79 - 90 kHz, F_{max}: 91 - 93 kHz, F_{char}: 90 - 92 kHz, F_{knee}: 89 - 91 kHz and duration 8 - 19 ms.

Molecular Biology:

Karyotype

Rautenbach *et al.* (1993) reported 2*n* = 58, FN = 60, BA = 4, and submetacentric X and Y chromosomes. Richards *et al.* (2016d: 187, 192) mentioned 2*n* = 58 and FN = 60, with primarily acrocentric chromosomes and two small metacentric pairs.

Erasmus and Rautenbach (1984: 94) mention 50 acrocentric and six bi-armed autosomal chromosomes, resulting in 62 autosomal arms.

Habitat:

Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that "*R. clivosus*" activity was not significantly, nor positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *R. clivosus* preferentially near trees, orchards surrounding wetlands and over these wetlands (Sirami *et al.*, 2013: 35).

Habits:

Jacobs *et al.* (2007a) at De Hoop, South Africa found that the average estimated flying height above ground 0.84 ± 0.20 m, *n*= 6. At the same locality, Thomas and Jacobs (2013: 124) found that "*R. clivosus*" emerged earlier than the other species in the area (in order of emergence): *Miniopterus natalensis, Rhinolophus capensis, Nycteris thebaica, Myotis tricolor, Neoromicia capensis* and *Tadarida aegyptiaca*.

Petersen *et al.* (2019: 439) studied the behaviour and social calls of captive bats and found four acoustically distinct call types: 1) cascading/rising frequency-modulated (FM) calls, 2) oscillatory FM calls, 3) noisy screech calls and 4) whistle calls. These call types showed only weak associations with specific behaviours, situational categories or functional contexts.

Roost:

Avery *et al.* (1990: 7) indicate that cool and moist caves or cave-like structures are used as daytime roosts. Taylor *et al.* (1999: 70) reported a roost containing 20 animals in the Shongweni Dam tunnel (RSA). They can also move up to 10 km between roosts (Happold and Happold, 2023: 80).

Diet:

From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 46 faecal pellets from 5 bats (in volume percent): Lepidoptera (62.6 ± 30.8), Coleoptera (29.4 ± 24.8), Hemiptera (2.0 ± 4.5), Hymenoptera (1.4 ± 3.1), and unknown (4.6 ± 6.4).

Jacobs *et al.* (2007a) at De Hoop, South Africa, found that the diet mainly consisted of Lepidoptera and Coleoptera with lesser amounts of Neuroptera, Hemiptera and Diptera. The mean size of measurable prey taken by *R. clivosus* was larger than that taken by *R. capensis*, although the range of prey sizes taken by the two species overlapped (Jacobs *et al.*, 2007a).

Predators:

Avery *et al.* (2005: 1054) found this species to be present in pellets from the barn owl (*Tyto alba* (Scopoli, 1769)) in South Africa.

Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Population:

Rhinolophus acrotis augur is common in some parts of its range, including South Africa, but is uncommon to rare in other areas, such as in Zimbabwe (Kock *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017cy). In Swaziland, three separate populations contained over a thousand individuals.

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 116) indicates that spermatogenesis occurs in late spring/summer/early fall. Copulation occurs in fall and is followed by sperm storage in the female until arousal and conception in the following spring.

Stanley and Goodman (2011: 41) reported on four females collected in East Usambara (Tanzania), of which two (collected on 17 August 1992) had small teats and two (collected in the first half of August 1991 and 1993) had large, non-lactating teats. Six males collected in the first half of August included three animals with scrotal testes and three with abdominal testes. Four males collected between July and September 1991 to 1993 in West Usambara had scrotal testes too.

PARASITES:
HAEMOSPORIDA
Lutz *et al.* (2021: Suppl.) found two Kenyan *Rhinnolophus clivosus* specimens to be infected by *Nycteria* parasites.

ARACHNIDA
Argasidae
Sándor *et al.* (2021a: 4) reported *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) as a primary tick species and *Carios vespertilionis* Latreille, 1802 as a secondary.

Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides nycteris* Fain, 1959 on the wing membrane, nasal membrane or auricle of bats from the DRC.

Sarcoptidae
Fain (1959b: 340) mentions a paratype of *Nycteridocoptes eyndhoveni* Fain, 1959, collected from a "*R. clivosus zuluensis*" from Lubudi, DRC. Fain (1959d: 237) reported *Psorergates (Psorergatoides) rhinolophi* Fain from "*R. clivosus zuluensis*" from Uvira, Kivu, DRC.

Trombiculidae
Trombicula (Grandjeana) reticulata (Vercammen-Grandjean & Nadchatram, 1963) collected from "*R. geoffroyi zuluensis* [= *R. clivosus zuluensis*]" from South Africa (Vercammen-Grandjean and Nadchatram, 1963; Stekolnikov, 2018a: 136; Zajkowska *et al.*, 2018; 108). Stekolnikov (2018a: 189) also mentioned *Willmannium natalense* (Lawrence, 1949).

Myobiidae
Bochkov and Fain (2003: 41) reported *Neomyobia (Neomyobia) jacksoni* (Radford, 1940) from bats from the DRC and RSA.

DIPTERA
Calliphoridae
Zumpt (1950: 88) reported a calyptrate larva of *Calliphora croceipalpis* Jaennicke, 1867, which was found in decomposing bats ("*Rhinolophus geoffroyi*") on the bottom of the Sterkfontein caves (RSA). Other maggots developed into an unidentified Borboridae and a Phoridae.

Nycteribiidae
Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108; Bendjeddou *et al.*, 2017: 15). *Nycteribia scissa scissa* Speiser, 1901 the nominate form found exclusively on *R. clivosus* from South Africa and Namibia (Haeselbarth *et al.*, 1966: 108). *Nycteribia ovalis* Theodor, 1957 from Pietermaritzburg, South Africa (Haeselbarth *et al.*, 1966: 110). *Penicillidia fulvida* (Bigot 1885) (Zumpt, 1950: 97 - on "*R. geoffroyi*"; Haeselbarth *et al.*, 1966: 114). *Nycteribia integra* Theodor and Moscona, 1954 (Haeselbarth *et al.*, 1966: 109, host referred to as *Rhinolophus acrotis*). *Nycteribia scissa* Speiser, 1901 (Zumpt, 1950: 97 - on "*R. geoffroyi*") .

Szentiványi *et al.* (2019a: Suppl.) also mentions *Penicillidia fulvida* bat flies from Kenyan "*Rhinolophus ferrumequinum keniensis*" which were carrying *Arthrorhynchus nycteribiae* fungi (see also de Groot *et al.*, 2020: Suppl.).

Lutz *et al.* (2021: Suppl.) found "*Phthiridium tecta*" bat flies on 14 bats from Uganda and Kenya.

Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub-Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Nycteribosca africana* Walker, 1849 (Zumpt, 1950: 96 - on "*R. geoffroyi*". *Raymondia hardyi* Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254).

Brachytarsina sp. flies were also reported by Lutz *et al.* (2021: Suppl.)

Verrett *et al.* (2022: 8) reported *Penicillidia fulvida* (Bigot, 1885) from Kenyan *R. clivosus* 2 bats.

Dick *et al.* (2023) mentioned that *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) and *Phthiridium scissum* (Speiser, 1900) have been found on *Rhinolophus clivosus* and *Nycteribia schmidlii scotti* Falcoz, 1923 on "*Rhinolophus clivosus augur*". Additionally, *Penicillidia (Penicillidia)*

fulvida (Bigot, 1885), *Phthiridium scissum* (Speiser, 1900) and a new, undescribed *Phthiridium* on Kenyan "*Rhinolophus clivosus* clade 2" individuals.

SIPHONAPTERA
Ischnopsyllidae
Rhinolophopsylla ashworthi (Waterston, 1913) known only from a few specimens from the Cape Province (King William's Town, Willowmore and Oudtshoorn) (Haeselbarth *et al.*, 1966: 191). *Rhinolophopsylla capensis* Jordan and Rothschild, 1921 (Zumpt, 1950: 97 - on "*R. geoffroyi*"; Haeselbarth *et al.*, 1966: 191, Beaucournu and Kock, 1996).

ACARI
Spinturnicidae
Spinturnix viduus and *Periglischrus africanus* were described by Zumpt (1950: 92, 93) from "*Rhinolophus geoffroyi*" from the Sterkfontein caves (RSA).

Ixodidae
?*Ixodes simplex* Neumann, 1906 (see Zumpt, 1950: 96); *Ixodes pilosus howardi* Neumann (on "*Rhinolophus augur*", see Howard, 1908: 168).

Trombiculidae
Trombicula natalensis Lawrence, 1949 (see Zumpt, 1950: 96).

Listrophoridae
Alabidocarpus nasicolus Lawrence, 1938 (see Zumpt, 1950: 96).

VIRUSES:
Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)
Oelofsen and Van der Ryst (1999) tested 40 individuals from eight localities in the Free State Province, South Africa for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Coronaviridae
Anthony *et al.* (2017b: Suppl.) mention the following *Alphacoronavirus*es: Predict_CoV_70, Human_CoV_229E, Predict_CoV_65, and the *Betacoronavirus*: Predict_CoV_43 (subgenus *Sarbecovirus*; see Markotter *et al.*, 2020: 6).

Nziza *et al.* (2019: 157) found three new Coronaviruses in oral and rectal swaps from Rwandan bats: PREDICT_CoV-42, PREDICT_CoV-43 and PREDICT_CoV-44.

Markotter *et al.* (2019: 5) also reported a new *Betacoronavirus* from Rwandan bats, closely related to BtCoVKY72 from Kenya.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 85 individual brains, from 14 localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Burundi, Congo (Democratic Republic of the), Eswatini, Kenya, Malawi, Mozambique, Namibia, Rwanda, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Rhinolophus adami Aellen and Brosset, 1968

*1968. *Rhinolophus adami* Aellen and Brosset, Rev. suisse Zool., 75 (14): 443. Type locality: Congo: Kouilou [ca. 04 00 N 12 00 E]. [Goto Description]. Holotype: MNHN ZM-MO-1968-408: ad ♀, alcoholic (skull not removed). Collected by: Jean-Paul Adam; collection date: 9 January 1967; original number: 12/8G. 3 paratypes see Aellen and Brosset (1968: 443). Paratype: MHNG 1129.084: ad ♂, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 26 July 1963. Paratype: MNHN ZM-MO-1968-409: sad ♀, alcoholic (skull not removed). Collected by: Jean-Paul Adam; collection date: 9 January 1967. 3 paratypes see Aellen and Brosset (1968: 443). Paratype: MNHN ZM-MO-1968-410: sad ♀, alcoholic (skull not removed). Collected by: Jean-Paul Adam; collection date: 9 January 1967. 3 paratypes see Aellen and Brosset (1968: 443). - Etymology: In honour of J.-P. Adam, the collector of the type specimen. (Current Combination).

TAXONOMY:
Kock *et al.* (2000) place it in the *adami* species group, followed by Csorba *et al.* (2003: xvi, 4 - 5) and Simmons (2005: 351). Species group reviewed by Kock *et al.* (2000). See Csorba *et al.* (2003: 5) for taxonomic background.

COMMON NAMES:
Czech: vrápenec Adamův. English: Adam's Horseshoe Bat, Congo Horseshoe Bat. French: Rhinolophe du Congo. German: Adams Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Jacobs *et al.*, 2008x; IUCN, 2009; Jacobs *et al.*, 2019d).

Assessment History
Global
2018: DD ver 3.1 (2001). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008x; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004ab; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are currently unknown. It is possible that it is threatened by cave disturbance, however, this needs to be confirmed (Jacobs *et al.*, 2008x; IUCN, 2009; Jacobs *et al.*, 2019d).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008x) [in IUCN (2009)] and Jacobs *et al.* (2019d) report that it is not known if the species is present in any protected areas. Further studies are needed into the distribution, abundance, natural history, and threats to this species.

GENERAL DISTRIBUTION:
Rhinolophus adami is known only from the type series collected in Kimanika cave, Kouilou, in the Republic of Congo.

Native: Congo (Aellen and Brosset, 1968; Csorba *et al.*, 2003: 5; Simmons, 2005:351).

DETAILED MORPHOLOGY:
Baculum
See Csorba *et al.* (2003: 4).

POPULATION:
Structure and Density
It is known only from ten specimens held in the Paris and Geneva museums (Aellen and Brosset, 1968), and may be naturally rare, however, this requires confirmation (Jacobs *et al.*, 2008x; IUCN, 2009; Jacobs *et al.*, 2019d).

Trend
2018: Unknown (Jacobs *et al.*, 2019d). 2008: Unknown (Jacobs *et al.*, 2008x; IUCN, 2009).

PARASITES:
Adam and Landau (1973a: 5) report on the presence of a protozoan parasite of the genus *Polychromophilus* (Haemoproteidae) in *R. adami* from the Republic of Congo. About 50 % of the specimens they examined were found to be infected. Gametocytes were found year-round. The bats were also infested (in low numbers) by the nycteribiid flies *Penicillidia fulvida* Bigot, 1885 and *Nycteribia schmidlii scotti* Falcoz, 1923, of which the prior was a major carrier of *Polychromophilus* sporozoites.

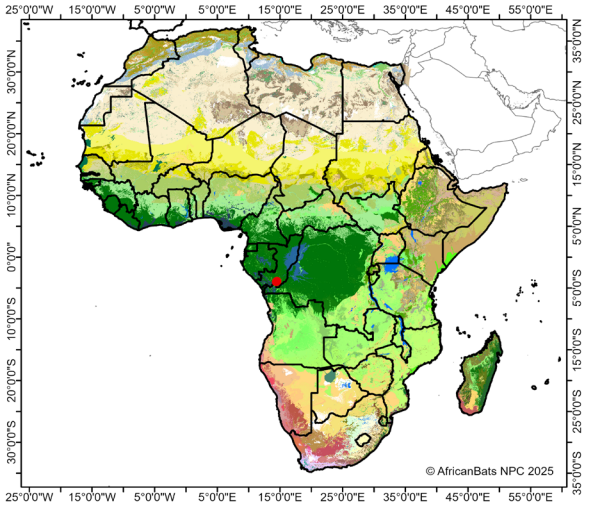

Figure 79. Distribution of *Rhinolophus adami*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo.

Rhinolophus alcyone Temminck, 1853

*1853. *Rhinolophus alcyone* Temminck, Esquisses zoologiques sur la Côte de Guiné. 1e partie, les Mammifères, 80. Type locality: Ghana: Boutry River [=Butre river] [ca. 04 49 N 01 55 W]. [Goto Description]. Holotype: RMNH MAM.35892: ad ♀, skin and skull. Collected by: Hendrik Severinus Pel. Allen (1939a: 73) notes: 'Type in Leiden Mus., but description has not "one single word of any value for identifying the species or determining its affinities" - K. Andersen'. The RMNH catalogue mentions two number 35892.a (for the mounted skin) and 35892.b (for the skull + loose bones). - Comments: Allen (1939a: 73), Kock (1969a: 121), Grubb *et al.* (1998: 77) mention 1852 as year of publication. - Etymology: alcyone: "[=Alkuone] mythological name for the kingfisher" and this is sometimes written as "Halcyon". Alkuone herself is the "daughter of Aiolos, who threw herself in the sea, where her husband Keüks (or Ceyx) was drowned. Thetis changed her in a kingfisher and her husband in a seagull". (Current Combination).

TAXONOMY:
Forms part of the *landeri* species group (Csorba *et al.*, 2003: 55 - 57; Simmons, 2005: 351). See Csorba *et al.* (2003: 56) for remarks on taxonomy.

COMMON NAMES:
Castilian (Spain): Murciélago de Herradura. Czech: vrápenec Alcyone. English: Halcyon Horseshoe Bat. French: Rhinolophe Alcyon, Rhinolophe d'Halcyon. German: Temmincks Hufeisennase, Rothen Kamnase, Halcyon Rundblattnase.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008y; IUCN, 2009; Monadjem *et al.*, 2017cu).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cu). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008y; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004y; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This widespread species is threatened in parts of its range by habitat loss, largely resulting from logging and conversion of land to agricultural use. In some areas the species is hunted for food, although it is unclear whether this represents a major threat (Jacobs *et al.*, 2008y; IUCN, 2009; Monadjem *et al.*, 2017cu).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008y) [in IUCN (2009)] and Monadjem *et al.* (2017cu) reported that it is not known if the species is present in any protected areas. Further studies are needed into the taxonomy and distribution of this species.

GENERAL DISTRIBUTION:
Rhinolophus alcyone ranges through much of West and Central Africa. It has been recorded from Senegal in the west through to Togo, and then from Nigeria to southern Sudan and western Uganda, with patchy records from the Congo basin (although it likely occurs throughout the Congo). It ranges as far south as central Democratic Republic of the Congo.

The record of this species from Gabon needs to be re-examined as it may represent a misidentified specimen of *Rhinolophus sylvestris* (Dowsett *et al.*, 1991).

Amori *et al.* (2016: 219) pointed out that several localities, originally situated in Togo, are currently in Ghana.

Native: Bioko, Burkina Faso (Kangoyé *et al.*, 2012: 6025; 2015a: 610); Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Congo (Dowsett *et al.*, 1991: 259); Congo (The Democratic Republic of the) (Monadjem *et al.*, 2010d: 555); Côte d'Ivoire; Equatorial Guinea; Gabon (?); Ghana; Guinea (Ziegler *et al.*, 2002: 75; Fahr and Ebigbo, 2003: 128); Guinea-Bissau (Rainho and Ranco, 2001: 47); Kenya; Liberia (Monadjem and Fahr, 2007: 50); Nigeria; Senegal; Sierra Leone; Sudan; Togo (?); Uganda. Presence uncertain: Gabon.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Young (1975: 76) indicates that two distinct colour phases can be found: rufous (orange) and grey.

SEXUAL DIMORPHISM:
Muñoz-Romo *et al.* (2021: 170) mention the presence of tufts of long hairs in the armpits forming axillary tuft glands of orange red colour, which probably are involved in seasonal sexual interactions.

ECHOLOCATION:
In Guinea, Fahr and Ebigbo (2003) reported the frequency of the CF-component at 67.4 kHz.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 52 calls of 2 bats: F_{peak}: 63.6 ± 0.4 (63.3 - 64.1) kHz, F_{min}: 57.7 ± 2.1 (55.4 - 60.9) kHz, F_{max}: 64.2 ± 0.3 (64.0 - 64.7) kHz, duration: 68.0 ± 11.7 (23.0 - 83.3) ms.

For two caves in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data for *Rhinolophus* cf. *landeri/alcyone*: Boundou cave: 1 F: F_{pmin}: 49.5 kHz, F_{pmax}: 58.5 kHz, F_{pmean}: 54.3 kHz, F_{ppeak}: 54.3 kHz, F_{flat}: 54.4 kHz, F_{knee}: 54.2 kHz, F_{mean}: 54.3 kHz, Duration: 9.2 ms; 29 FF: F_{pmin}: 46.4 ± 4.6 kHz, F_{pmax}: 60.6 ± 1.9 kHz, F_{pmean}: 54.7 ± 0.7 kHz, F_{ppeak}: 55 ± 0.6 kHz, F_{flat}: 55 ± 0.5 kHz, F_{knee}: 54.7 ± 0.6 kHz, F_{mean}: 54.8 ± 0.6 kHz, Duration: 23 ± 10.2 ms. Mont Belo cave: 14 MM: F_{pmin}: 45 ± 4.8 kHz, F_{pmax}: 61.9 ± 2.2 kHz, F_{pmean}: 54.4 ± 2.7 kHz, F_{ppeak}: 55.4 ± 0.5 kHz, F_{flat}: 55.3 ± 0.6 kHz, F_{knee}: 55.3 ± 0.4 kHz, F_{mean}: 55.1 ± 0.5 kHz, Duration: 19.5 ± 8.9 ms.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003) and Lim (2007).

POPULATION:
Structure and Density
This species is easily found in colonies of up to 20 animals (Jacobs *et al.*, 2008y; IUCN, 2009; Monadjem *et al.*, 2017cu).

Trend
2016: Unknown (Monadjem *et al.*, 2017cu).
2008: Unknown (Jacobs *et al.*, 2008y; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Csorba *et al.* (2003: 57) refer to Kingdon (1984), who indicated that three females from western Uganda were pregnant in mid-June, whereas a fourth one was lactating. One birth was reported in September.

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2013a: 17416; 2015a: 381) report the presence of hemosporidian parasites of the genus *Nycteria* in one investigated bat from Côte d'Ivoire. In the DRC, Karadjian *et al.* (2016: 9835) found *R. alcyone* specimens infected with *Nycteria gabonensis* Rosin, Landay & Hugot 1978. The GenBank data for these parasites were also referred to by Arnuphapprasert *et al.* (2020; Suppl.).

PROTOZOA
Thiombiano *et al.* (2023: 4) reported *Trypanosoma* cf. *livingstonei* in four out of 11 bats from Burkina Faso.

DIPTERA
Streblidae
Raymondia allisoni Theodor, 1968 from Ghana (Shapiro *et al.*, 2016: 253).

Nycteribiidae
Nycteribia inopinata Theodor, 1957 from Ebolowa, Cameroon (Haeselbarth *et al.*, 1966: 109) (see also Dick *et al.*, 2023: 79).

VIRUSES:
Hepadnaviridiae
Hepatitis B virus (HBV)
Drexler *et al.* (2013c: 16152) report on one *R. alcyone* on 16 examined specimens from Gabon that was positive for horseshoe bat HBV (HBHBV).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that none of the 15 specimens they examined from Gabon tested positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

Rhabdoviridae
Lyssavirus - Rabies related viruses
2006 in Nigeria, Dzikwi *et al.* (2010: 269) tested 43 brains by direct fluorescent antibody (DFA) and mouse inoculation test (MIT) which tested negative for lyssavirus antigens.

Lagos bat virus (LBV)
In 2006, 2 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), none tested positive for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

Mokola virus (MOKV)
In 2006, 2 individuals from Nigeria were serum tested by a modified rapid fluorescent focus inhibition test (RFFIT), none tested positive for neutralizing antibodies (Dzikwi *et al.*, 2010: 269).

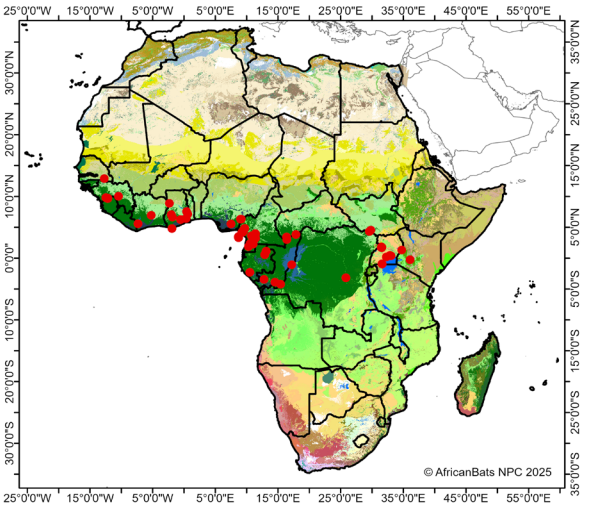

Figure 80. Distribution of *Rhinolophus alcyone*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Nigeria, Senegal, Sierra Leone, Uganda.

Rhinolophus alticolus Sanborn, 1936

*1936. *Rhinolophus alcyone alticolus* Sanborn, Field Mus. Nat. Hist., Zool. Ser., (362) 20 (14): 108. Publication date: 15 August 1936. Type locality: Cameroon: Mount Cameroon [04 13 N 09 11 E, 5 800 ft]. [Goto Description].

Holotype: FMNH 42596: ad ♀. Collected by: Rudyerd Boulton and Laura Boulton; collection date: 2 July 1934; original number: 53.

1956. *Rhinolophus alticolus:* Eisentraut, Zool. Jb. Syst., 84 (3): 519, 523. (Current Combination).

1985. *Rhinolophus simulator alticolus:* Brosset, Mammalia, 48 (4): 546. (Name Combination).

TAXONOMY:

Monadjem *et al.* (2016y: 366) refer to Csorba *et al.* (2003), who indicated that *alticolus* might represent a separate species, as their specimens from the Mount Nimba area are about 2,000 km from the nearest records in Nigeria and Cameroon, which, in turn, are again thousands of kilometres from the main distribution area. However, they still retain *alticolus* as a subspecies of *simulator*.

Simmons and Cirranello (2023b) recognized *alticolus* as a separate species.

COMMON NAMES:

English: Cameroun Horseshoe Bat. German: Kamerun-Hufeisennase.

CONSERVATION STATUS:

Global Justification

Currently not been globally assessed hence no justification.

Assessment History

Global

No assessment known, hence no history of assessment to report.

Regional

None known.

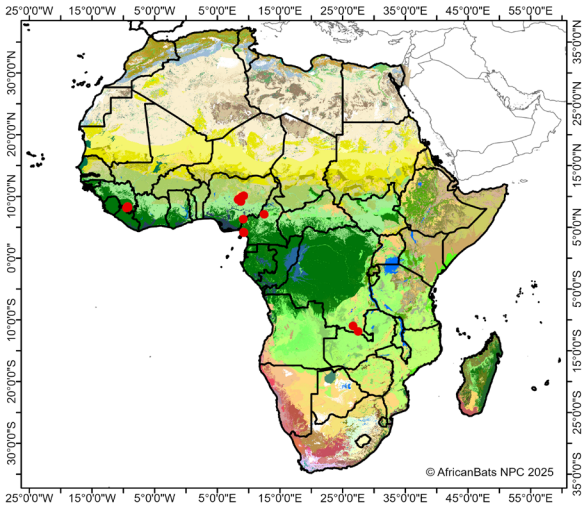

Figure 81. Distribution of *Rhinolophus alticolus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Cameroon, Congo (Democratic Republic of the), Guinea, Liberia, Nigeria.

Rhinolophus axillaris J.A. Allen, 1917

1917. *Rhinolophus axillaris* Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 429. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 49175: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 17 December 1911; original number: 1807. The museum labels indicate it as a female.

TAXONOMY:

Based on the large value for the greatest length of skull (average 20 mm) and the size and position of the second lower premolar (large and in line with the other cheek teeth and therefore separating the first and last premolars), Patterson *et al.* (2024: 12) rejected *axillaris* as a synonym of *Rhinolophus landeri*. They tentatively consider it a valid species of the *landeri* group, more closely related to *Rhinolophus alcyone* and *Rhinolophus guineensis*.

COMMON NAMES:

English: Tufted Horseshoe Bat. German: Allen-Hufeisennase

GENERAL DISTRIBUTION:

Rhinolophus axillaris is only known from the type locality: Aba (DRC).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Congo (Democratic Republic of the).

Rhinolophus blasii Peters, 1867

1857. *Rhinolophus clivosus:* Blasius, Säugethiere Deutschlands, 33, figs 10, 11. Type locality: Italy: "Italy". - Comments: Preoccupied by *clivosus* Cretzschmar, 1828 (see Corbet and Hill, 1992: 100 and Pavlinov *et al.*, 1995: 81).

*1867. *Rhinolophus blasii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 17 (for 1866). Publication date: 1867. Type locality: Italy: "Italy". Holotype: ZMB 557: ♂, alcoholic (skull not removed). Collected by: Johan Heinrich Blasius. See Turni and Kock (2008). - Comments: Type locality originally SE Europe, but restricted to Italy by

Ellerman *et al.* (1953: 59), and Trieste (see Turni and Kock (2008). - Etymology: In honour of the German naturalist Johann Heinrich Blasius (1809 - 1870) (see Kozhurina, 2002: 14). (Current Combination).

1904. *Rhinolophus empusa* K. Andersen, Ann. Mag. nat. Hist., ser 7, 14 (83): 378. Publication date: 1 Novmber 1904. Type locality: Malawi: Zomba [15 23 S 35 19 E,, 800 - 900 m]. [Goto Description]. Holotype: NHMUK 1893.7.9.33: ad ♀. Collected by: Alexander ("Alex") Whyte (F.Z.S); collection date: January 1893. - Comments: Considered a valid subspecies by Ansell and Dowsett (1988: 33), Taylor (1998: 37).

1905. *Rhinolophus andreinii* Senna, Arch. Zool. ital., 2: 256, pl 16, f 1; pl 18, f 7 - 16. Publication date: 30 September 1905. Type locality: Eritrea: Adi Ugri [14 53 N 38 49 E, 1 900 m].

1910. *Rhinolophus blasiusi* Trouessart, Fauna des Mammifères d'Europe, 9.

1910. *Rhinolophus brockmani* Thomas, Ann. Mag. nat. Hist., ser 8, 5 (26): 192. Publication date: 1 February 1910. Type locality: Somalia: Upper Sheikh. [Goto Description]. Holotype: NHMUK 1909.12.17.4: ad ♀. Collected by: Dr. Ralph Evelyn Drake-Brockman; collection date: 13 November 1909; original number: 237. Thomas (1910a: 193) mentions two specimens. - Etymology: In honour of Dr. R.E. Drake-Browkman, the collector of the type specimen.

2019. *R[hinolophus] blasii 1:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).

2019. *R[hinolophus] blasii 2:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 10. Publication date: 22 August 2019. (Name Combination).

2019. *Rhinolophus basii:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

? *Rhinolophus blasii andreinii:* (Name Combination).

? *Rhinolophus blasii complex sp. 1 TD-2019*

? *Rhinolophus blasii empusa:* (Name Combination).

Taxonomy:



Figure 82. *Rhinolophus blasii*.

Includes *brockmani*; see Koopman (1975: 383). Replacement for *clivosus* Blasius, 1857, which was preoccupied (see Ansell and Dowsett, 1988: 33). Part of the *landeri* species group (Csorba *et al.*, 2003: 57 - 59; Simmons (2005: 351 - 352). See Csorba *et al.* (2003: 58 - 59) for remarks on taxonomy.

Herkt *et al.* (2017: Appendix S9) indicate that three subspecies are recognized in continental Africa which are relatively isolated geographically: *blasii* in Northwest Africa, *andreinii* in Ethiopia and *empusa* in southern Africa. No genetic tests have been performed yet to check the validity of these taxa. The analyses carried out by Herkt *et al.* (2017), however, indicate substantial ecological niche differences as well as major geographic gaps in suitable habitat areas between them.

Common Names:

Afrikaans: Spitssaalneusvlermuis. Albanian: Lakuriq nate hundëpatkua i Blasius-it. Arabian: Khaffash. Armenian: Բլագիի կամ, միջերկրածովային պայտաքիթ. Azerbaijani: Blazius nalburunu. Basque: Blasius ferra-saguzar. Belarusian: Падкаванос Блазіўса. Bosnian: Blazijev potkovasti šišmiš. Breton: Frigribell Blasius. Bulgarian: Средиземноморски подковонос. Castilian (Spain): Murciélago de herradura de Blasius, Rinolofo de Blasius, Murciélago dalmata de herradura. Catalan (Spain): Ratpenat de ferradura de Blasius. Croatian: Blazijev potkovnjak. Czech: Vrápenec Blasiův, vrapenec pahrbeční. Danish: Blasius' hestekonæse. Dutch: Blasius' hoefijzerneus, Blasius-hoefijzerneus. English: Peters's Horseshoe Bat, Blasius's Horseshoe Bat, Peak-saddle Horseshoe Bat. Estonian: Hele-sagarnina. Finnish: Vaaleaherkko. French: Rhinolophe de Blasius, Rhinolophe à selle pointue. Frisian: Blasius' hoefizernoas. Galician (Spain): Morcego de ferradura de Blasius. Georgian: ბლაზიის ცხვირნალა. German: Blasius-Hufeisennase. Greek: Μεσορινόλοφος, Ρινόλοφος του Blasius. Hebrew: פרסף מצוי, parsaf matzuy, Parsaf Matsui. Hungarian: Csúcsosnyergű patkósdenevér. Irish Gaelic: Crú-ialtóg Blasius. Italian: Rinolofo di Blàsius, Ferro di cavallo di Blàsius. Latvian: Blāzija pakavdegunis. Lithuanian: Blazijaus pasagnosis. Luxembourgish: Blasius-Huffeisennues. Macedonian: Бласиев потковичар [= Blasiev Potkovichar]. Malawian: Liputiputi, Ndemiya, Namzeze. Maltese: Rinolofu ta' Blasius. Montenegrin: Sredozemni potkovičar. Norwegian: Balkanhesteskonese. Polish: Podkowiec Blasiusa. Portuguese: Morcego-de-ferradura de Blasius, Morcego ferradura de nariz de sela. Rhaeto-Romance: Rinolof da Blasius. Romanian: Liliacul cu potcoavă a lui Blasius, Liliacul-lui-Blasius. Russian: Подковонос средиземноморский. Serbian: Јужни потковичар [= Južni potkovičar]. Scottish Gaelic:

Crudh-ialtag Blasii. Slovak: Podkovár Blasiov. Slovenian: Blasijev podkovnjak. Swedish: Balkanhästskonäsa. Turkish: Blasius Nalburunlu Yarasa. Ukrainian: Підковик (Підковоніс) Блазіуса. Welsh: Ystlum pedol Blasius.

CONSERVATION STATUS:

Global Justification

Assessed as Least Concern (LC ver 3.1 (2001)). Widespread, although patchily distributed. There are some large colonies, and the global population is likely to considerably exceed 10,000. Although the population is declining in some areas (e.g., western Balkans), it is stable in others (Jacobs *et al.*, 2008ag; IUCN, 2009; Taylor, 2016f).

Assessment History

Global

2016: LC ver 3.1 (2001) (Taylor, 2016f). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008ag; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004x; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: NT D1 ver 3.1 (2001) (Jacobs *et al.*, 2016b). 2004: VU D2 ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:

Threats to the species include loss of Mediterranean woodlands, disturbance and loss of underground habitats, and destruction of roost sites (Kryštufek, 1999). In a number of range states, the species is disturbed by tourist visits to caves and by use of the caves as shelters for livestock (Jacobs *et al.*, 2008ag; IUCN, 2009; Taylor, 2016f).

The most important risk factors related to climatic change were identified by Sherwin *et al.* (2012: 174) as being their roosting in caves/trees, the aerial feeding style and its long-distance dispersal. Bilgin *et al.* (2012: 434) predict that *R. blasii* will have a major range contraction as a result of climatic change.

CONSERVATION ACTIONS:

Taylor (2016f) supports Jacobs *et al.* (2008ag) [in IUCN (2009)] who reported that *Rhinolophus blasii* is protected by national legislation in some range states. There are international legal obligations for the protection of this species through the Bonn Convention (Eurobats) and Bern Convention in areas to which these apply. It is included in Annex II (and Annex IV) of the EU Habitats and Species Directive, and hence requires specific conservation measures in some range states, including the designation of Special Areas for Conservation. It occurs in some protected areas. Taxonomic research is needed to clarify the status of the African populations. Monitoring and protection of caves is also required.

GENERAL DISTRIBUTION:

Rhinolophus blasii has a large range in the Palaearctic and the Afrotropics, throughout which it is widely but patchily distributed. Its range extends marginally into the Indomalayan region.

In Africa, it occurs from northeastern South Africa and the Democratic Republic of Congo, through south Malawi, to East African, Ethiopia and Somalia, and in North Africa. Follow Taylor (2000) for southern African distribution. In North African it is only present in Morocco and Algeria (it may occur in Tunisia but there are no confirmed records yet, and likewise for Egypt). Altitude range is from sea level to 1,400 m.

The specimens from the Mount Nimba area (DNSM 12593 and DNSM 12622) might need re-identification. Previous issues of the ACR had these as *Rhinolophus landeri* (as does Taylor *et al.* (2018a: 1267), but Demos *et al.* (2019a) found the sequence data of these two specimens to nest deeply in *R. blasii*.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 602,154 km^2. In South Africa, its distribution is strongly associated with the amount of precipitation in the warmest quarter of the year (Babiker Salata, 2012: 49).

In Asia, it has a patchy distribution extending from Turkey in the west to Pakistan in the east, and from the Caucasus in the north to Yemen in the south (Simmons, 2005). It was confirmed in Georgia in 2006 (Z. Nagy *pers. obs.*). In Europe, it is extinct in northeastern Italy and has not been recorded in Slovenia during the last 50 years (Kryštufek, 2001). Also recorded from western Anatolia and from the Levant (Syria, Lebanon, Jordan, Palestine and Israel). It is now restricted to the Balkan peninsula and to some Mediterranean islands including Crete and Cyprus. There are no recent records in Romania and northern Bulgaria despite intensive work by Christian Dietz (Z. Nagy *pers. comm.,* 2006). Past records from this area are disputed: no specimen has been found in museums in Romania, and the presence of *R. euryale* in the same area might have caused confusion (Z. Nagy *pers. comm.,* 2006).

It occurs from sea level to 2,215 m in Yemen.

Native: Afghanistan; Albania; Algeria; Armenia; Austria; Azerbaijan; Bosnia and Herzegovina; Botswana; Bulgaria; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 555); Croatia; Cyprus; Eritrea; Eswatini (Monadjem, 2005: 5; Monadjem *et al.*, 2010d: 555, Monadjem *et al.*, 2021: 5); Ethiopia; Greece (Kriti); Iran, Islamic Republic of; Israel; Italy; Jordan; Libyan Arab Jamahiriya; Malawi (Ansell, 1978; Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Monadjem *et al.*, 2010d: 555); Montenegro; Morocco (Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 359; Dbiba *et al.*, 2025: 6); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 555; Monadjem *et al.*, 2010c: 377); Oman; Pakistan; Palestinian Territory, occupied; Serbia; Somalia; South Africa (Monadjem *et al.*, 2010d: 555); Syrian Arab Republic; Tanzania; Tunisia (Aellen and Strinati, 1970; Cockrum, 1996; Dalhoumi *et al.*, 2011; 2014: 53); Turkey; Turkmenistan; Yemen; Yugoslavia; Zambia (Ansell, 1969; Ansell, 1978; Monadjem *et al.*, 2010d: 555); Zimbabwe (Monadjem *et al.*, 2010d: 555).
Possibly extinct: Slovenia.

Detailed morphology:

Baculum
See Csorba *et al.* (2003: 4).

Functional morphology:

In a study of flight-initiating jumps, Gardiner and Nudds (2011: 2187) found that the ground gleaning *R. blasii* did not outperform the fast-flying hawker (*Miniopterus schreibersii*) nor the trawling (*Myotis capaccinii*), although it spends a major part of its time foraging on the ground.

In their study on take-off performance, Gardiner *et al.* (2014: 1059) determined a wing beat frequency of 12.96 ± 0.27 Hz.

Amador *et al.* (2019: Suppl.) [referring to Jacobs *et al.* (2007a)] mention a wing loading value of 7.5 Pa, aspect ratio 5.6 for a wingspan of 27 cm and a wing area of 130 cm^2 and a body mass of 10 g.

Echolocation:

Jacobs *et al.* (2007a) reported for individuals from South Africa a F_{peak} 86.6 ± 0.7 kHz (detector type not reported), while Monadjem *et al.* (2007a), using an Anabat detector, reported the same peak frequency albeit a different standard deviation (± 0.23) for an individual from Swaziland. Also from Swaziland, Monadjem *et al.* (2017c: 179) reported F_{min}: 79.4 ± 1.86 (77.9 - 81.5) kHz, F_{knee}: 86.3 ± 0.24 (86.1 - 86.6) kHz, F_c: 86.2 ± 0.21 (86.0 - 86.4) kHz, duration: 20.8 ± 0.72 (19.9 - 21.3) ms. Monadjem *et al.* (2010c: 377) reported for Mozambique that peak echolocation frequencies ranged between 93.2 - 95.4 kHz (ANABAT, Petterson D240x).

Jones and Siemers (2010: 449 - 450) indicated that females emit pulses with a higher frequency than males, and that juveniles emit lower frequencies than adults.

Papadatou *et al.* (2008b: 132) report the following data for 37 Greek specimens: F_{start}: 90.3 ± 4.85 kHz, F_{end}: 78.1 ± 4.48 kHz, F_{peak}: 94.0 ± 0.92 kHz, bandwidth: 4.0 ± 1.65 kHz, duration 44.1 ± 12.14 ms and interpulse interval: 71.8 ± 23.10 ms.

The following data for 10 Iranian calls were reported by Benda *et al.* (2012a: 182): F_{start}: 94.0 ± 0.1 (94.2 - 94.4) kHz, F_{end}: 92.0 ± 0.1 (91.8 - 92.1) kHz, F_{peak}: 93.1 ± 0.1 (93.0 - 93.3) kHz, duration: 48.6 ± 9.4 (40.1 - 68.3) ms and interpulse interval: 109.3 ± 5.6 (103.1 - 117.1) ms.

Walters *et al.* (2012: suppl.) report the following figures for 26 calls (4 sequences) from bats from Algeria and Greece: duration: 44.90 ± 8.52 ms, F_{max}: 95.51 ± 1.34 kHz, F_{min}: 80.58 ± 3.52 kHz, bandwidth: 14.93 ± 3.82 kHz, F_{peak}: 95.41 ± 1.33 kHz.

Luo *et al.* (2019a: Supp.) reported the following data: F_{peak}: 94 kHz, F_{start}: 80.3 kHz, F_{end}: 78.1 kHz, and duration: 44.1 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 7 calls of 1 bat: F_{max}: 89.17 kHz, F_{min}: 84.55 kHz, F_{knee}: 87.25 kHz, F_{char}: 87. 92 kHz, slope: 31.81 OPS, duration: 12.22 ms.

Disca *et al.* (2014: 226) indicate that in Morocco the type of call is FM-FC-FM, with F_{peak}: 96.7 ± 0.3 kHz and duration: 20.7 ± 4.9 ms.

Molecular Biology:

Genetics
Shahabi *et al.* (2019) studied the variation in the mitochondrial control region (D loop) of Iranian bats, but also commented (p. 498) on African representatives, where they found one haplotype (from Algeria) nesting within the west/northwestern Iranian clade. Two other lineages (from southern Africa) might possibly be raised to species level.

Karyotype
Đulić (1967) reported $2n$ = 58, FN = 60, BA = 4, a submetacentric X and an acrocentric Y for specimens from Croatia. Qumsiyeh *et al.* (1986)

and Rautenbach (1986) also reported 2*n* = 58, FN = 60, BA = 4, but differed in the X chromosome being reported in the respective publications as metacentric and submetacentric, and the Y chromosome as acrocentric and metacentric. Arslan and Zima (2014: 9) report that the autosomal complement consists of two medium-size bi-armed pairs and 26 acrocentric pairs, with one of the acrocentrics having a secondary constriction.

HABITS:
Siemers and Ivanova (2004: 470) report that *R. blasii* uses aerial and foliage-gleaning in flight, as well as ground-gleaning (including landing) to detect and capture their prey. Happold and Happold (2023: 78) mention that these bats can hover briefly, and that - in Malawi - they often forage in groups of up to six animals, which can vary in composition.

DIET:
In northern Algeria, Ahmim and Moali (2013: 46) found that *R. blasii* droppings contained 96.87 % Insecta and 3.13 % Chilopoda. The most frequent insect preys were Diptera (37.50 %), specifically Chironomidae/Ceratopogonidae (9.38 %), Culicidae, Anisopodidae and Sphaeroceridae (6.25 %). Trichoptera also were frequently present (15.63 %), followed by Lepidoptera and Hemiptera (both 12.50 %).

Gardiner *et al.* (2014: 1058) assessed its foraging strategy as "low altitude slow aerial hawking", sometimes with gleaning.

POPULATION:
Structure and Density
Africa: Not very common (Jacobs *et al.*, 2008ag; Taylor, 2016f).
Asia: This species has a widespread distribution and the populations in Pakistan and Afghanistan seem to be stable and doing well (Molur *et al.*, 2002). Europe: A rare or infrequent species, probably the rarest horseshoe bat in Europe (Kryštufek, 1999). Summer colonies of ca. 20 - 30 are typical, although up to 400 females may be found in a single colony. In winter, it congregates in mixed-species clusters with other *Rhinolophus* species (up to 2,000 animals in Serbia). There are large colonies in Serbia, Bulgaria and Greece. It is suspected to be declining because of loss of Mediterranean woodlands and cave disturbance, and is considered vulnerable in many range states (e.g., the western Balkans); however, the populations in the eastern Balkans are stable (Mediterranean Workshop, 2007) (Jacobs *et al.*, 2008ag; IUCN, 2009; Taylor, 2016f).

Trend
2016: Decreasing (Taylor, 2016f). 2008: Decreasing (Jacobs *et al.*, 2008ag; IUCN, 2009). *R. blasii* populations within the Asia Minor and Levant region are predicted to have a declining population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

REPRODUCTION AND ONTOGENY:
In Malawi, single young are born from mid-November to early January (beginning of the wet season) and these are lactated for about a month (Happold and Happold, 1990b: 566). The females are also not in close reproductive synchrony.

PARASITES:
Clément *et al.* (2019a: 5) reported on 10 European or southern African *R. blasii* specimens of which one was infected by *Trypanosoma livingstonei*_A.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ixodidae: *Ixodes vespertilionis* Koch, 1844; Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Eyndhovenia euryalis euryalis* (Canestrini, 1884); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851.

ACARI
Ixodidae
Khelfaoui *et al.* (2018: 67) reported *Ixodes vespertilionis* Koch, 1844 from Tunisian bats.

Myobiidae
Bochkov and Fain (2003: 41) reported *Neomyobia africanoides* Kellmann, 1964 from bats in South Africa.

Sarcoptidae
Nycteridocoptes eyndhoveni Fain, 1959 was reported from "*R. blasii empusa*" from Tanganika Moba, DCR by Fain (1959b: 341).

Spinturnicidae
Khelfaoui *et al.* (2018: 67) also reported *Eyndhovenia euryalis* (Canestrini, 1884) from Tunisian bats.

DIPTERA
Ševčík *et al.* (2012: 35) report on the presence of the bat flies *Phthiridium biarticulatum* Hermann, 1804 (Nycteribiidae) and *Brachytarsina flavipennis* Macquart, 1851 (Streblidae) on bats

from Cyprus. The same parasites were found by Benda *et al.* (2010b: 243) in Jordan. *B. flavipennis* was also reported from Iran by Benda *et al.* (2012a: 255). Benda *et al.* (2010b) also refer to previous records of *Penicillidia conspicua* Speiser, 1901 and *P. dufourii* (Westwood, 1835) from Palestine, *Phthiridium integrum* (Theodor and Moscona, 1954) and *Penicillidia fulvida* (Bigot, 1885) from Yemen (all Nycteribiidae); a streblid *Ascodipteron africanum rhinolophi* Jobling, 1958 from Yemen; and an ischnopsillid *Rhinolophopsylla unipectinata* (Taschenberg, 1880) from Yemen.

Dick *et al.* (2023: 77) mentioned the nycteribiid fly *Penicillidia (Penicillidia) fulvida* (Bigot, 1885)

Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Brachytarsina flavipennis* Masquart, 1851 (Júnior *et al.*, 2020: Suppl.; Khelfaoui *et al.*, 2018: 68). *Raymondia alulata* Speiser, 1908 (Shapiro *et al.*, 2016: 253). *Raymondia hardyi* Fiedler, 1954 (Shapiro *et al.*, 2016: 254). *Raymondia waterstoni* Jobling, 1931 (Haeselbarth *et al.*, 1966: 104). *Ascodipteron lophotes* Monticelli, 1898 (Haeselbarth *et al.*, 1966: 106, but Maa (1965) suggests that these records need verification).

Nycteribiidae
Nycteribia integra Theodor and Moscona, 1954 (Haeselbarth *et al.*, 1966: 109). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114).

Júnior *et al.* (2020: Suppl.) mentioned the following species (not specifically from Africa): *Basilia italica* Theodor, 1954, *Basilia nana* Theodor, 1954, *Basilia nattereri* (Kolenati, 1857), *Nycteribia kolenati* Theodor and Moscona, 1954, *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* (Latreille, 1805), *Nycteribia vexata* Westwood, 1835, *Phthiridium biarticulatum* Hermann, 1804.

Bendjeddou *et al.* (2017: 15), Bendjoudi *et al.* (2019) and Khelfaoui *et al.* (2018: 68) reported the following ectoparasites from Algerian bats: Nycteribiidae: *Nycteribia (Nycteribia) latreillii* (Leach, 1817), *Penicillidia (Penicillidia) dufourii* Westwood, 1835 and *Phthiridium biarticulatum* Hermann, 1804, *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii* Schiner, 1853; Streblidae: *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851 and Arachnida: *Eyndhovenia euryalis* (G. Canestrini, 1885); Ixodidae: *Ixodes vespertilionis* Koch, 1844; Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856)

HEMIPTERA
Polyctenidae
Adroctenes horvathi Jordan, 1912 was mentioned by Kock *et al.* (1998b: 237) and Szentiványi *et al.* (2022: 5) from Malawi.

VIRUSES:
Coronaviridae - Coronaviruses
Luis *et al.* (2013: suppl.) mention the presence of BatCoV BB98-15 and a SARS coronavirus-related virus.

Alphacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from German bats.

Betacoronavirus
Reported from bats from Bulgaria and Germany by Kohl and Kurth (2014: 3112).

Picornaviridae
Nieto-Rabiela *et al.* (2019: Suppl.) mentioned the presence of Picornavirus.

Polyomaviridae
Carr *et al.* (2017) reported two new viruses from *R. blasii* from Zambia: *Rhinolophus blasii polyomavirus 1* and *Rhinolophus blasii polyomavirus 2*.

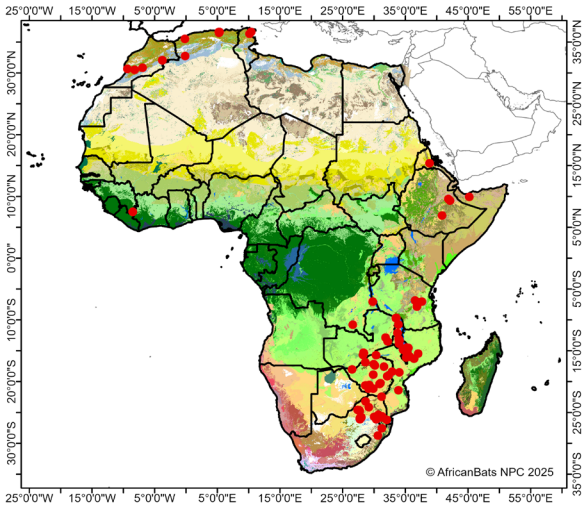

Figure 83. Distribution of *Rhinolophus blasii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Congo (Democratic Republic of the), Eritrea, Eswatini, Ethiopia, Italy, Liberia, Malawi, Morocco, Mozambique, Somalia, South Africa, Tanzania, Tunisia, Zambia, Zimbabwe.

Rhinolophus capensis Lichtenstein, 1823

*1823. *Rhinolophus capensis* Lichtenstein, Verzeichniss der Doubletten des Zool. Mus. K. Univ. Berlin, 4. Type locality: South Africa: Cape province: Cape of Good Hope [ca. 33 56 S 18 28 E]. Lectotype: ZMB 377: juv, skin and skull. Collected by: Krebs; collection date: 1822. Skull damaged. Lectotype designated by Turni and Kock (2008: 32). - Comments: Turni and Kock (2008: 32) also indicate that originally there were two additional specimens, which might have been sold to an unknown collection. Furthermore, Turni and Kock (2008: 32) mention that ZMB 376 and 378, which were longtime considered syntypes of *capensis*, were re-identified by Karl Koopman as belonging to *Rhinolophus clivosus* Cretzschmar, 1828. - Etymology: Referring to Cape of Good Hope or the Cape province, from where the type specimen was obtained. (Current Combination).

1860. *Rhinolophus auritus* Sundevall, Kongl. Svenska Vet.-Akad. Hand., ser 2, 2: no 10, p 13, footnote. Type locality: South Africa: Southern Cape province: Cape of Good Hope, near Knysna: Belvedere [ca. 33 53 S 22 59 E]. [Goto Description]. Holotype: NRM 611907: ♂. Collection date: 3 April 1854. Victorin; Grill 1859; Mam. Ex. No. 1907: see Andersen (1904c: 456).

TAXONOMY:

Part of the *capensis* species group (Csorba *et al.*, 2003: 7 - 8; Simmons, 2005: 352). See Csorba *et al.* (2003: 8) for remarks on taxonomy. Reviewed by Stoffberg (2008).

COMMON NAMES:

Afrikaans: Kaapse saalneusvlermuis, Kaapse Vlermuis. Czech: vrápenec jihoafrický. English: Cape Horseshoe Bat, Southern Africa horseshoe bat. French: Rhinolophe d'Afrique du Sud, Rhinolophe du Cap. German: Kap-Hufeisennase, Capischen Kamnase, Russbraunen Kamnase. Portuguese: Morcego ferradura de cabo.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

De Graaf (1960) identified material as *R* cf. *capensis* from the Late Pliocene, at Makapansgat, South Africa. Avery and Avery (2011: 16) reported Holocene remains from Blinkklipkop, Powerhouse Cave, Wonderwerk (Northern Cape province, South Africa), as well as Pleistocene remains from the latter locality.

CONSERVATION STATUS:

Global Justification

An endemic species to South Africa. While declining in parts of its range, the species is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, its known large population (there are many records of this species occurring in high numbers in coastal caves), and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008z; IUCN, 2009; Jacobs and Monadjem, 2017).

Assessment History

Global

2016: LC ver 3.1 (2001) (Jacobs and Monadjem, 2017). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008z; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004w; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016c). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

The species is threatened in parts of its range by disturbance of cave roosts (often by recreational and tourism activities), and the conversion of suitable foraging habitat to agricultural use (Jacobs *et al.*, 2008z; IUCN, 2009; Jacobs and Monadjem, 2017).

CONSERVATION ACTIONS:

Jacobs and Monadjem (2017) the species is recorded from more than 10 protected areas including: West Coast National Park; De Hoop Nature Reserve; Garden Route National Park; Langeberg Nature Reserve; Addo Elephant National Park; Great Fish Nature Reserve; Kologha Forest Reserve and Kubusi Indigenous State Forest. While no urgent conservation interventions are necessary, the species would benefit from further protected area establishment once key roost sites have been identified; and artificial wetlands in agricultural landscapes should be managed for biodiversity by conserving patches of native vegetation around the waterbodies (Sirami *et al.*, 2013). Further studies are needed into the distribution of this bat it may occur in southern Namibia (Sirami *et al.*, 2013).

GENERAL DISTRIBUTION:

Rhinolophus capensis is restricted to the coastal belt of the Northern Cape, the Western Cape and the Eastern Cape of South Africa, as far east along the coast as the vicinity of East London (Csorba *et al.*, 2003: 8; Stoffberg, 2008: 2). Odendaal *et al.* (2014: 4) indicate that the geographic range of *R. capensis* is determined by two environmental gradients that influence the regional rainfall patterns. First, there is the increasing aridity towards the north and secondly a seasonality shift from west to east, whereby the rains are dominant during the winter in the west, then becoming aseasonal and finally being dominant during the summer in the extreme east.

Simmons (2005: 352) follows Ansell and Dowsett (1988: 33) and Koopman (1993a: 164), who list South Africa, Zimbabwe and Mozambique, but does indicate doubt about its occurrence outside of South Africa. Koopman (1993a: 164) states that the records from Zambia and Malawi are erroneous. Griffin (1999: 32), however, suspects its occurrence in Namibia. In the RSA, the species' distribution is best predicted by biome: desert, Albany thicket, fynbos and grassland (Babiker Salata, 2012: 50, 118).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 277,925 km^2 (or 4 % of the total surface of the area).

Native: South Africa (Eastern Cape Province, Northern Cape Province, Western Cape Province) (Ellerman *et al.*, 1953; Maree and Grant, 1997; Csorba *et al.*, 2003: 8; Monadjem *et al.*, 2010d: 556).
Presence uncertain: Namibia.

FUNCTIONAL MORPHOLOGY:
Jacobs *et al.* (2007a), at De Hoop, South Africa, found *R. capensis* to have a lower mean wing loading and aspect ratio than *R. clivosus*, but no differences in their mean shape indices.

Amador *et al.* (2019: Suppl.) [referring to Jacobs *et al.* (2007a)] mention a wing loading value of 7.3 Pa, aspect ratio 5.6 for a wingspan of 29 cm and a wing area of 148 cm^2 and a body mass of 11 g.

SEXUAL DIMORPHISM:
At De Hoop, South Africa, Jacobs *et al.* (2007a) found females were heavier than males, but there were no differences in forearm length, or wingspan.

ECHOLOCATION:
Jacobs *et al.* (2007a) reported a peak frequency of 83.9 (± 1.2) kHz for individuals from South Africa.

Moir (2020: 29) and Moir *et al.* (2021a: 371) recorded 19 calls from one specimen in southern KwaZulu-Natal or Eastern Cape (RSA) with the following parameters: F_{max}: 81.72 ± 1.09 (80.63 - 82.81) kHz, F_{min}: 78.87 ± 0.96 (77.91 - 79.83) kHz, F_{char}: 79.83 ± 0.98 (78.85 – 80.84), F_{knee}: 80.41 ± 1.01 (79.39 – 81.43) kHz and duration: 8.49 ± 1.41 (7.09 - 9.90) ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 4 *Rhinolophus capensis* calls from the Kruger Park (RSA): F_{min}: 76.2 ± 2.1 (73.2 77.9) kHz, Duration: 25.9 ± 15.8 (9.6 42.1) ms, F_{max}: 84.5 ± 1.0 (83.2 85.5) kHz, F_{knee}: 83.7 ± 1.0 (82.2 84.3) kHz, F_{char}: 83.9 ± 0.7 (82.8 84.4) kHz,

Odendaal and Jacobs (2009: 62) found some sort of local dialects in the echolocation calls for South African *R. capensis*: 84.60 ± 0.82 kHz at De Hoop, 85.84 ± 0.73 kHz at Table Farm, and 80.66 ± 0.50 kHz at Steenkampskraal, which is probably the result of interactions with other *Rhinolophus* species: *R. swinnyi* at Steenkampskraal, and *R. darlingi* at Table Farm, as well as with *R. clivosus*. Bastian and Jacobs (2013: 18) and Odendaal *et al.* (2013: 112) indicate that the peak frequency ranges from 75.7 kHz at the western end of the species' coastal distribution in South Africa to 85 - 86.5 kHz at the eastern end. This increase seems to be linked with the mean annual rainfall (Odendaal *et al.*, 2013). Bastian and Jacobs (2013: 18) also found that the 85 kHz specimens were able to discriminate between 85 kHz calls from conspecifics and calls from *R. damarensis*, which also peaks at 85 kHz. The 75 kHz specimens were unable to make that discrimination.

Odendaal and Jacobs (2010b: 240) reported that there was no relation between body size and peak frequency across populations. However, nasal chamber length was found to be the best predictor on peak frequency. They also found that in each population, the females were larger than the males and produced calls with higher frequencies, and therefore suggest that there might be a potential social role for the peak frequency.

When flying with conspecifics, Fawcett *et al.* (2013: 49) found that the terminal FM sweep became longer and wider in bandwidth than when flying alone. Fawcett *et al.* (2015: 693), furthermore, found that *R. capensis* produced longer frequency-modulated downward sweeps at the end of their call when they flew together with bats from the same species or with *Miniopterus natalensis* than when they flew alone. Additionally, when they were flying with *R. clivosus* (a larger high-duty cycle bat), its calls were shorter than when flying alone or with other *R. capensis* individuals.

Bastian and Jacobs (2015) investigated the ability for *R. capensis* to discriminate their own calls from those of allopatric (*R. damarensis*) and sympatric (*R. clivosus*) congeners. The bats had no problems with the calls from *R. clivosus*, but the calls from *R. damarensis* could only be discriminated by one of the test groups.

Flight room experiments by Finger *et al.* (2019: 128) indicated that emitted calls were of higher intensity when the bats flew in an uncluttered (empty) vs. cluttered (82 % vegetated) flight room.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach (1986) reported 2*n* = 58, FN = 60, BA = 4, and the X and Y chromosomes as submetacentric. Erasmus and Rautenbach (1984: 94) mention 52 acrocentric and four bi-armed autosomal chromosomes, resulting in 60 autosomal arms.

Protein / allozyme
See Maree and Grant (1997).

HABITAT:
Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *R. capensis* activity was not significantly, nor positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *R. capensis* preferentially flew near trees, orchards surrounding wetlands and over these wetlands (Sirami *et al.*, 2013: 35).

HABITS:
Jacobs *et al.* (2007a) at De Hoop, South Africa found that the average estimated flying height above ground 1.00 ± 0.77 m, *n*= 11. At the same locality, Thomas and Jacobs (2013: 129) found that Lepidoptera eating bats (e.g., *R. capensis* and *Nycteris thebaica*) emerged earlier than bats feeding on Diptera (e.g., *Tadarida aegyptiaca*).

ROOST:
Czenze *et al.* (2021: 3) found that these bats preferred to roost in places where the maximum temperature was well below 30* C, and where the maximum roost temperature was about 10* C lower than the temperature outside.

DIET:
Jacobs *et al.* (2007a) at De Hoop, South Africa, found that the diet mainly comprised Lepidoptera and Coleoptera with lesser amounts of Neuroptera, Hemiptera and Diptera. The mean size of measurable prey taken by *R. capensis* was smaller than that taken by *R. clivosus*, although the range of prey sizes taken by the two species overlapped (Jacobs *et al.*, 2007a).

PREDATORS:
Avery *et al.* (2005: 1054) found this species in pellets from *Tyto alba* (Scopoli, 1769) in South Africa.

POPULATION:
Structure and Density
This species is common throughout its range (Bernard, 2013a), and is relatively well represented in museums (Monadjem *et al.*, 2010d). Skinner and Chimimba (2005) state that 'they are abundant in the Western Cape and the Eastern Cape, where there are many records from coastal caves. It can be found in colonies consisting of thousands of individuals (Herselman and Norton, 1985; Taylor, 2000; Skinner and Chimimba, 2005). Example, there are an estimated 19,000 individuals in De Hoop Guano Cave (McDonald *et al.*, 1990b).

Trend
2016: Stable (Jacobs and Monadjem, 2017).
2008: Decreasing (Jacobs *et al.*, 2008z; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Bojarski and Bernard (1992) [in Anthony (2000: 16)] report that immunocytochemical indices of gonadotropic function rise significantly during the spermatogenic period, coincident with high plasma testosterone levels.

Bernard (1985: 129) and Martin and Bernard (2000: 36) mention that spermatogenesis starts in spring (October in South Africa) and ends after early winter (May) although sperm remain in the caudae epididymides through winter (May to September). Copulation and ovulation occur in August to September, at the end of winter hibernation. Parturition occurs in November and December after a gestation period of three to four months (see also Bernard, 1984; Krutzsch, 2000).

Bernard (1985: 134) indicates that females do not become reproductively mature in their first year, and that males would only be able to mate in their second year.

PARASITES:
ACARI
Myobiidae
Bochkov and Fain (2003: 41) reported the presence of *Neomyobia africanoides* Kellmann, 1964 and *Neomyobia (Neomyobia) jacksoni* (Radford, 1940) in South Africa.

DIPTERA
Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub-Saharan Africa (Haeselbarth *et al.*, 1966: 100). de Groot *et al.* (2020: Suppl.) indicate that this parasitic fly might also be a host for the fungal parasite *Dimeromyces capensis* A. Weir.

Nycteribiidae
Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108).
Dick *et al.* (2023) mentioned fly as *Nycteribia schmidlii scotti* Falcoz, 1923 and they also mentioned *Phthiridium scissum* (Speiser, 1900) from the RSA.

SIPHONAPTERA
Ischnopsyllidae
Rhinolophopsylla ashworthi (Waterson, 1913) known only from a few specimens from the Cape Province (King William's Town, Willowmore and Oudtshoorn), South Africa (Haeselbarth *et al.*, 1966: 191). *Rhinolophopsylla capensis* Jordan and Rothschild, 1921 (Haeselbarth *et al.*, 1966: 191).

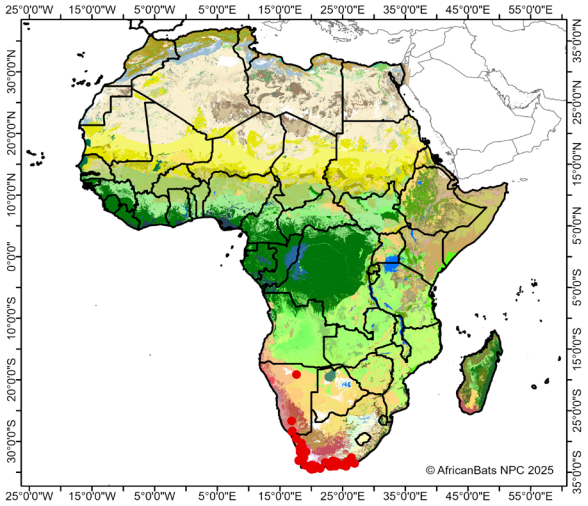

Figure 84. Distribution of *Rhinolophus capensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Namibia, South Africa.

Rhinolophus cervenyi Benda, Uvizl, Eiseb and Avenant, 2024

*2024. *Rhinolophus cervenyi* Benda, Uvizl, Eiseb and Avenan, Mammalia, xxx (x): xxx. Publication date: 25 March 2024. Type locality: Lesotho: Sehlabathebe National Park [29 52 02 S 29 07 15 E, 2417 m]. Holotype: NMP 97760: ad ♀, skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12730: alcoholic (skull not removed). Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12731: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12732: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12733: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12734: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12735: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMB 12736: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMP 97756: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMP 97757: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMP 97758: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMP 97759: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. Paratype: NMP 97761: skull and alcoholic. Collected by: Nico Loubser Avenant, Petr Benda and Jaroslav Červený; collection date: 17 February 2013. - Etymology: In honour of Professor Jaroslav Červený (Prague, Czech Republic) who significantly contributed to the research of the African bat fauna, and mainly, discovered the bat colony that provided the type series (Benda *et al.*, 2024: 15)..

TAXONOMY:
Specimens of this species had been identified as *Rhinolophus clivosus* in the past or - more recently - *Rhinolophus acrotis* (Taylor *et al.* (2024: 11).

Taylor *et al.* (2024: 11) also indicated that the close-matching cyt-b sequences of *R. cervenyi* and the southern clade of *R. damarensis* may be explained by recent mtDNA introgression.

COMMON NAMES:
English: Červený's Horseshoe Bat. German: Lesotho-Hufeisennase.

GENERAL DISTRIBUTION:
Benda *et al.* (2024: 15) mention that this species is known from 12 locations in Lesotho and two in the RSA. Taylor *et al.* (2024: 11) confirmed its occurrence in the Maloti Drakensberg in the Free State and KwaZulu-Natal provinces and from the Mpumalanga Escarpment, extending also into the KwaZulu-Natal midlands.

Native: Lesotho; South Africa.

ECHOLOCATION:
Benda *et al.* (2024: 15) mention that 22 females from the Uintjiesburg Farm (South Africa) produced a resting frequency in the range of 83.3 - 86.2 kHz (mean 84.9 kHz).

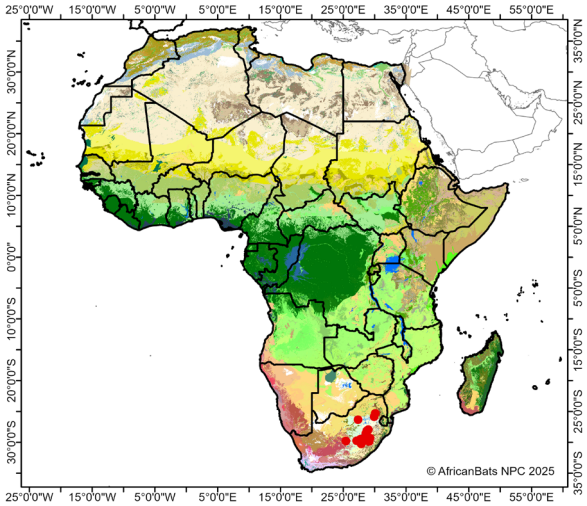

Figure 85. Distribution of *Rhinolophus cervenyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Lesotho, South Africa.

Rhinolophus cf. hillorum Tanshi, Chigozie Obitte, Monadjem and Kingston, 2022

2022. *Rhinolophus cf. hillorum* Tanshi, Chigozie Obitte, Monadjem and Kingston, Acta Chiropt., 23 (2): 313 (for 2021). Publication date: 14 February 2022.

TAXONOMY:
Tanshi *et al.* (2022a: 328) compared one specimen from the Sapoba Forest Reserve (Nigeria) to be different from six other specimens they examined, and tentatively assigned this specimen to *Rhinolophus* cf. *hillorum* pending detailed morphological and molecular analyses. They also point out that the Sapoba Forest Reserve is situated in lowland forest, whereas *Rhinolophus hillorum* is an inhabitant of mountain ranges.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Tanshi *et al.* (2022a: 314) reported that the records from Nigeria mentioned by Cotterill (2002a: 175) as *Rhinolophus hillorum* should be assigned to this species.

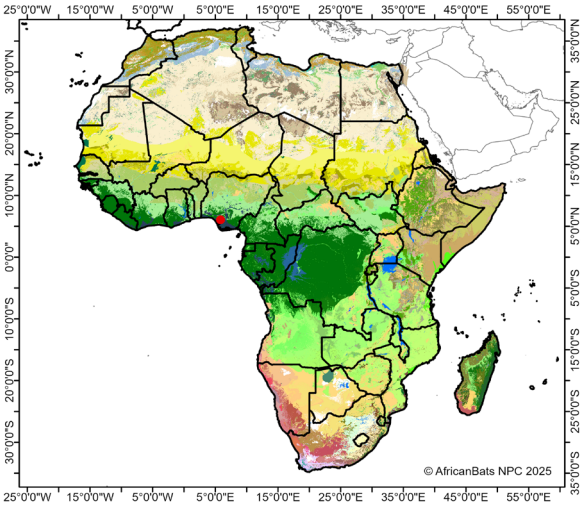

Figure 86. Distribution of *Rhinolophus* cf. *hillorum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Nigeria.

Rhinolophus clivosus Cretzschmar, 1828

*1828. *Rhinolophus clivosus* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 47, pl 18. Type locality: Saudi Arabia: Red Sea Coast: Al Muwaylih [=Mohila] [ca. 27 49 N 35 30 E]. [Goto Description]. Paratype: SMF 12311: skin only. Lectotype: SMF 4371: mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1826. Old catalog: II.F.4.a; see Mertens (1925: 20). - Comments: Allen (1939a: 74) mentions "1826" (as mentioned on the title page) as year of publication of Cretzschmar's work, other authors mention it as "1827", "1828", "1830-1831". - Etymology: From the masculine Latin adjective *clivósus*, meaning "characterized by slopes, steep", referring to a seemingly unreliable

distinctive character of the noseleaf "*Rhinolophus apparato olfactorio externo clivis gradatim elatis non dissimili*" (Cretzschmar 1828) (see Lanza *et al.* (2015: 80). (Current Combination).

1904. *Rhinolophus Andersoni* Thomas, Ann. Mag. nat. Hist., ser 7, 14 (80): 156. Publication date: 1 August 1904. Type locality: Egypt: Eastern desert of Egypt [ca. 22 N 35 E]. [Goto Description]. Holotype: NHMUK 1904.11.4.2: imm ♂. Collected by: Arthur M. MacKilligan; collection date: 3 August 1903; original number: 26. - Comments: Kock (1969a: 113) mentions: "Eastern Desert, im Gebiet des Wadi Alagi, 22 N 35 E, Sudan".

1905. *Rhinolophus acrotis brachygnathus* K. Andersen, Ann. Mag. nat. Hist., ser 7, 15 (85): 73. Publication date: 1 January 1905. Type locality: Egypt: Giza province: Giza [30 01 N 31 13 E]. [Goto Description]. Holotype: NHMUK 1892.9.9.7: ad ♂, alcoholic (skull not removed). Collected by: Dr. John Anderson; collection date: 16 December 1891. See Qumsiyeh (1985: 35). Paratype: [Unknown] |TS99|: imm ♀, alcoholic (skull not removed). See Qumsiyeh (1985: 35).

1934. *Rhinolophus acrotis schwarzi* Heim de Balsac, Bull. Mus. natn. Hist. nat., Paris, sér 2, 7: 483. Publication date: November 1934. Type locality: Algeria: Sahara, Tassai des Azdjers: Djanet [24 34 N 09 30 E]. [Goto Description]. Holotype: MNHN ZM-2006-246: ♀, skull and alcoholic. Collected by: Dr. Henry Foley; collection date: 1934. Paratype: MNHN ZM-2006-247: ♀, skull only. Collected by: Dr. Henry Foley; collection date: 1934. Paratype: MNHN ZM-2006-248: ♀, skull only. Collected by: Dr. Henry Foley; collection date: 1934.

2019. *R[hinolophus] clivosus 4:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 10. Publication date: 22 August 2019. (Name Combination).

2019. *Rhinolophus clivossis:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

? *Rhinolophus clivosus brachygnathus:* (Name Combination).

? *Rhinolophus clivosus clivosus:* (Name Combination).

Taxonomy:

ferrumequinum species group (Csorba *et al.*, 2003: 35 - 39; Simmons, 2005: 353). See Csorba *et al.* (2003: 36 - 37) for review of taxonomy.

Uvizl *et al.* (2024: 1) and Benda *et al.* (2024: 2) indicate that *R. clivosus* s.l. covers three species: one occurring in the Palaearctic and Saharo-Arabian (*R. clivosus* s.str.), a Cyrenaican endemic (*R. horaceki*) and one distributed widely in the Afro-tropics (*R. acrotis*). Benda *et al.* (2024: 12) also split off the population from Lesotho and surrounding South Africa as a new species (*R. cervenyi*).

Note: Most of the information previously (prior to ACR 2024) reported for this species pertains to *Rhinolophus acrotis augur* and has been moved to sections covering that subspecies.

Common Names:

Afrikaans: Geoffroy se saalneusvlermuis, Geoffroy-saalneusvlermuis, Geoffroyse vlermuis. Arabian: Khafash abu hadweh arabi, Khaffash. Chinese: 佐氏菊头蝠. Czech: vrápenec pouštní, wrápenec pahrbečný, vrapenec pahrbeční. Dutch: Geoffroy's hoefijzerneus. English: Arabian Horseshoe Bat, Cretzschmar's Horseshoe bat, Geoffroy's Horseshoe Bat. French: Rhinolophe de Cretzschmar, Rhinolophe de Geoffroy. German: Arabian Horseshoe Bat, Geoffroys Hufeisennase. Hebrew: פרסף הנגב, Parsaf HaNegev. Italian: Rinòlofo di Cretzschrnar, Fèrro di cavàllo di Cretzschmar. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura gigante.

Etymology of common name:

Colloquial name after E. Geoffroy Saint-Hilaire, who collected bats in Egypt during the early part of the nineteenth century (see Taylor, 2005).

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough globally to qualify for listing in a more threatened category (Kock *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017cy).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cy). 2008: LC ver 3.1 (2001) (Kock *et al.*, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004an; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Conservation actions:

Kock *et al.* (2008a) [in IUCN (2009)] reported that in view of the species wide range it seems likely that it is present in several protected areas. All bats, including *Rhinolophus clivosus*, are protected by national legislation in Jordan (Amr *pers. comm.,* 2004). Bats of the genus *Rhinolophus* are generally susceptible to indirect poisoning through the local use of insecticides; there is a need to evaluate the impact of this threat on populations (especially in southwest Asia), and to investigate alternative methods of insect control (Kock *pers. comm.,* 2004).

General distribution:

Rhinolophus clivosus is restricted to north(eastern) Africa and in parts of southwest Asia, including western areas of the Arabian Peninsula. In North Africa it has been recorded from Egypt. In southwest Asia, it ranges from Israel, Jordan and the Sinai Peninsula of Egypt in the north, through the western part of the Arabian Peninsula of Saudi Arabia, Yemen and Oman,

with a few additional records of the species from central regions of the Arabian Peninsula.

Benda *et al.* (2024: 2) restrict the distribution of *Rhinolophus clivosus* s.s. to the Palaearctic and the Saharo-Arabian area. The Cyrenaican pouplations are assigned to *R. horaceki* and the remaining African populations belong to *R. acrotis*.

ZMB has two specimens from the Central African Republic, that seem to be outliers (both as *clivosus* or *acrotis*).

Native: Afghanistan; Algeria; Angola; Burundi; Cameroon; Chad; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 556); Djibouti (Pearch *et al.*, 2001: 397); Egypt; Eritrea; Eswatini (Monadjem, 2005: 5; Monadjem *et al.*, 2010d: 557, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 133); Israel; Jordan; Kenya (Lavrenchenko *et al.*, 2004b: 133); Lesotho (Lynch, 1994: 190; Monadjem *et al.*, 2010d: 556); Liberia; Libyan Arab Jamahiriya; Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Monadjem *et al.*, 2010d: 556); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 556; Monadjem *et al.*, 2010c: 377); Namibia (Cotterill, 2004a: 261); Oman; Rwanda; Saudi Arabia; Somalia; South Africa (Monadjem *et al.*, 2010d: 556); Sudan; Tanzania (Stanley and Goodman, 2011: 41); Turkmenistan; Uganda (Kityo and Kerbis, 1996: 63); Yemen; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 557); Zimbabwe (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 557).

Presence uncertain: Palestinian Territory, Occupied.

General description of external morphology:

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on both the dorsal and ventral sides of the proximal arm and moderate on both the dorsal and ventral sides of the plagiopatagium.

Dental Formula:

Kock *et al.* (2002a: 507) mention that all Arabian and northeastern African *R. clivosus* have lost the small anterior upper premolar (except for some populations in northwestern Ethiopia and northwestern Somalia, which probably should be assigned to *acrotis*).

Detailed morphology:

Baculum

See Thomas (1997) and Csorba *et al.* (2003: 36).

Skull

Jacobs *et al.* (2013b: 76) found that *R. clivosus* has a smaller nasal capsule volume than predicted from its size.

Echolocation:

In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for 10 calls: F_{start}: 73.1 ± 1.9 (71.5 - 77.0) kHz, F_{end}: 73.8 ± 2.3 (70.0 - 77.0) kHz, F_{peak}: 84.4 ± 0.4 (83.5 - 85.0) kHz, Pulse duration: 48.0 ± 4.8 (43.0 - 59.0) ms, and Inter-pulse interval: 39.6 ± 12.9 (27.0 - 59.0) ms.

From Israel, Hackett *et al.* (2016: 223) reported 66 calls with these values: Pulse duration: 54.48 ± 11.22 ms, F_{start}: 78.92 ± 5.18 (69.3 - 88.8) kHz, F_{end}: 78.81 ± 5.26 (68.3 - 88.8) kHz, F_{peak}: 85.18 ± 0.57 (83.4 - 88.8) kHz.

For 18 calls from 3 *Rhinolophus clivosus* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 90.63 ± 0.68 kHz, F_{knee}: 89.93 ± 0.98 kHz, F_{min}: 74.44 ± 6.15 kHz, F_{max}: 91.85 ± 0.33 kHz, Bandwidth: 17.41 ± 6.41 kHz, Duration: 34.49 ± 7.33 ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 90.39 ± 0.55 kHz, F_{max}: 92.56 ± 0.57 kHz, F_{min}: 75.01 ± 3.16 kHz.

Molecular Biology:

Karyotype

Both Đulić and Mutere (1974) reported $2n$ = 58,.FN = 62, BA = 6, a large acrocentric X chromosome, and a small acrocentric Y chromosome.

Population:

Trend

2016: Unknown (Monadjem *et al.*, 2017cy).
2008: Unknown (Kock *et al.*, 2008a; IUCN, 2009).
R. clivosus populations within the Asia Minor and Levant region have an unknown population trend, under predictive climate change scenarios (Bilgin *et al.*, 2012: 433).

Parasites:

Hirst (1923: 989) mentions that Kolenati gave "*R. clivosus* [= *R. blasii*]" as host for the mite *Periglischrus interruptus* Kolenati, but that he corrected this later to *R. euryale*. Kolenati gave a new name to a mite from a *R. clivosus* specimen from Egypt: *Periglischrus glutinimargo*.

From Jordan, Benda *et al.* (2010b: 229) reported the presence of a bat fly: *Phthiridium biarticulatum* Hermann, 1804 (Nycteribiidae) and a flea *Rhinolophopsylla unipectinata unipectinata*

(Taschenberg, 1880) (Ischnopsyllidae). Additionally, they also mention literature date for *Phthiridium integrum* from Saudi Arabia and Yemen, *Ascodipteron africanum rhinolophi* Jobling, 1958 (Streblidae) from Yemen, and five mites from Yemen: *Trombicula knighti* Radford, 1954, *T. filamentosa* Radford, 1953, *T. brevitarsa* Radford, 1952, *Brennanella longispina* Radford, 1953, and *Labidocarpus nasicolus* Lawrence, 1938.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following bat flies: Nycteribiidae: *Nycteribia schmidlii schmidlii* Schiner, 1853; and Streblidae: *Raymondia huberi huberi* Frauenfeld, 1856.

Streblidae
Brachytarsina (Brachytarsina) flavipennis Macquart, 1851 and *Raymondia huberi* Frauenfeld, 1855 from Algeria (Bendjeddou *et al.*, 2017: 15).

Brachytarsina sp. flies were also reported by Lutz *et al.* (2021: Suppl.)

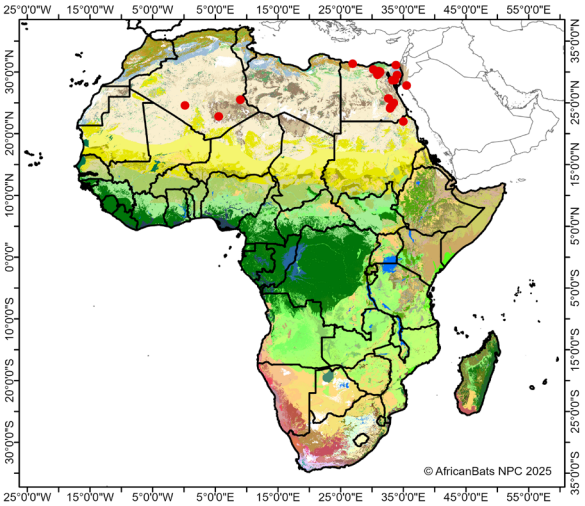

Figure 87. Distribution of *Rhinolophus clivosus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Algeria, Cameroon, Egypt, Saudi Arabia, Somalia.

Rhinolophus cohenae Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012

*2012. *Rhinolophus cohenae* Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, PLoS ONE, 7(9): 16. Publication date: 12 September 2012. Type locality: South Africa: Mpumalanga: Barberton: Mountainland Nature Reserve [25 43 08 S 31 15 58 E, 690m]. Holotype: DNSM 8626: ad ♂, skull and alcoholic. Collected by: Lientjie Cohen (Mpumalanga Park). Baculum prepared. Skull and mandible in good condition (Taylor *et al.*, 2012c: 16). Paratype: DNSM 11620: ad ♂, skull and alcoholic. Collected by: Dr Samantha Stoffberg and Lientjie Cohen; collection date: 27 September 2009. Paratype: DNSM 11918: ad ♂, skull and alcoholic. Collected by: Dr Samantha Stoffberg and Lientjie Cohen; collection date: 27 September 2009. Paratype: DNSM 11919: ad ♂, skull and alcoholic. Collected by: Dr Samantha Stoffberg and Lientjie Cohen; collection date: 27 September 2009. Paratype: DNSM 7886: ad ♂, skull and alcoholic. Collected by: Lientjie Cohen (Mpumalanga Park); collection date: 27 September 2004. - Etymology: Recognition of Lientjie Cohen who collected the type specimen and contributed significantly to the conservation of bats in South Africa, particularly in Mpumalanga Province. The species name combines the surname Cohen and genitive singular case-ending "ae" indicative of feminine gender (Taylor *et al.*, 2012c: 17). - ZooBank: D0E1C9DD-7D36-4C01-AE0D-60AD474960A0. (Current Combination).

TAXONOMY:



Figure 88. *Rhinolophus cohenae* from Mpumalanga, South Africa.

Based on mitochondrial and nuclear DNA sequences and morphological and morphometric data, Taylor *et al.* (2012c) found that the *Rhinolophus hildebrandtii* group includes more species than previously recognized.

COMMON NAMES:
English: Cohen's Horseshoe Bat. German: Cohens Hufeisennase.

CONSERVATION STATUS:
Global Justification
Cohen *et al.* (2017) report that this recently described species endemic to South Africa and known from the Mpumalanga Escarpment, and from a few records in the southeast of Limpopo Province with an estimated extent of occurrence of 15,640 km^2. There are inferred to be fewer than 1,000 mature individuals (and certainly fewer than 10,000) in the population. Colonies are usually small, numbering only a few individuals. The greatest number of mature individuals counted at a single site was ± 40. All recorded

colonies are suspected to comprise the same subpopulation. An ongoing decline is inferred to be taking place as a result of loss of habitat due to poor land-use management practices, mining activities, agricultural intensification as well as infestation by alien invasive plant species. Further field surveys and vetting of museum records are needed to more accurately delimit the distribution range of the species. Currently, list the species as Vulnerable C2a(ii) and D1.

Assessment History
Global
2016: VU C2a(ii); D1 ver 3.1 (2001) (Cohen *et al.*, 2017).

Regional
South Africa: 2016: VU C2a(ii), D2 ver 3.1 (2001) (Cohen *et al.*, 2016).

MAJOR THREATS:
Cohen *et al.* (2017) reports that the Mpumalanga Tourism and Parks Agency (MTPA) mapped all development applications received at a cadastral scale over a 14-year period (2000-2014), which showed that greatest pressure for land-use change has come from prospecting applications (54% of the land surface area) and mining (25% of land surface area) (Lötter *et al.*, 2014). A major threat within this species' range is mining (legal, illegal and recommissioning of old mines). Future developments at the above rates or even higher are likely to cause further detriment towards natural ecosystems and processes and in particular, disturb or destroy foraging grounds and roosting and maternity sites, or alter key micro-climates needed by the species. Additionally, loss of natural habitat around roost sites through poor land-use management practices, (such as inappropriate burning regimes, overgrazing and alteration of vegetation structure negatively affect foraging areas and prey base), land development activities including agricultural intensification (Driver *et al.*, 2012), and alien invasive plant infestations are causing a decline in available habitat for foraging.

Climate change may also influence micro-climate distribution. This species is very dependent on suitable subterranean environments for roosting and maternity requirements and associated natural habitats for foraging. These sites are limited throughout its distribution range and beyond. The effects of climate change can severely impact on the survival of this species if the above is not provided for and not adequate for habitation anymore (Cohen *et al.*, 2017).

CONSERVATION ACTIONS:
Cohen *et al.* (2017) reports that the species occurs in the Mariepskop Primary Conservation Area and Barberton Mountainlands Nature Reserve. No specific conservation actions directed towards this species at the moment. The MTPA has developed the Mpumalanga Biodiversity Sector Plan (MBSP) that indicates areas of high conservation value and is based on a systematic conservation plan which considers the distribution of all species and their habitat, sets quantitative targets for these and tries to find the most sufficient selection of areas to meet these targets. A few *R. cohenae* localities fall within the boundaries of protected areas but most are situated on private land. The MBSP has categorised areas in term of. its biodiversity value and *R. cohenae* localities located within the Protected Area and Critical Biodiversity and Ecological Support Areas will potentially receive the best protection measures from a land development perspective where certain activities will not be allowed or be restricted. With regards to all other areas, the MBSP land-use guidelines should also be followed and Environmental Impact Assessment legislative tools applied.

GENERAL DISTRIBUTION:
Known only from three closely-spaced localities in Mpumalanga Province of South Africa in the vicinity of Nelspruit Taylor *et al.* (2012c: 17).

Accurate delimitation of this species' range is subject to further collecting and reappraisal of existing museum material, previously referred to as *R. hildebrandtii*.

Native: South Africa (Taylor *et al.*, 2012c: 17).

ECHOLOCATION:
Lowest recorded peak frequency 33.0 kHz in the holotype; mean 32.86 ± 0.24 kHz, n= 7 in type series Taylor *et al.* (2012c: 16).

POPULATION:
Structure and Density
Cohen *et al.* (2017) report that In total, 240 individuals have been counted in surveys but this is an underestimate. The total population is thus inferred to be fewer than 1,000 mature individuals and thus certainly fewer than 10,000 mature individuals, as this species is encountered in small groups of which around 40 individuals was the highest number counted at a single site. All recorded colonies are suspected to be part of one subpopulation.

Trend
Decreasing (Cohen *et al.*, 2017).

PARASITES:
DIPTERA
Streblidae
Raymondia hardyi Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254; based on a record by Theodor (1968), who mentioned "*R. hildebrandtii*" as host).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Africa.

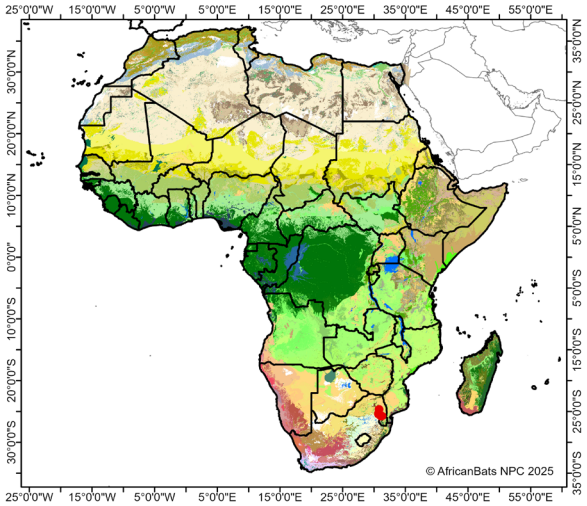

Figure 89. Distribution of *Rhinolophus cohenae*.

Rhinolophus damarensis Roberts, 1946

*1946. *Rhinolophus darlingi damarensis* Roberts, Ann. Transv. Mus., 20 (4): 303. Type locality: Namibia: Damaraland: Okahandja district: Oserikari. [Goto Description]. Holotype: TM 9474: ad ♀, skin and skull. Collected by: Austin Roberts; collection date: 10 August 1941. Note: Caught in bedroom at night.
2013. *Rhinolophus d. damarensis:* Jacobs, Babiker, Bastian, Kearney, van Eeden and Bishop, PLoS ONE, 8 (12): d82614 (Suppl). Publication date: 3 December 2013.
2024. *Rhinolophus cf. damarensis:* Taylor, Kearney, Clark, Howard, Mdluli, Markotter, Geldenhuys, Richards, Rakotoarivelo, Watson, Balona and Monadjem, 30 (6): 13. Publication date: 5 June 2024. (Name Combination).
? *Rhinolophus damarensis:* (Name Combination, Current Combination).
? *Rhinolophus darlingi:* (Name Combination).

TAXONOMY:


Figure 90. A male *Rhinolophus damarensis* (TM 48040) caught at Taung, North-West Province, South Africa.

Jacobs *et al.* (2013a: 12) showed that *R. darlingi* (*sensu lato*) was polyphyletic comprising two non-sister lineages (*R. darlingi* (*sensu stricto*) and *R. damarensis*), with disjunct distributions in southern Africa, which diverged about 9.7 Mya. They further showed that despite the genetic divergence between the two lineages (*R. darlingi* (*sensu stricto*) and *R. damarensis*) echolocation frequencies as well as skull and post-cranial morphology, apart from bacula, were highly convergent.

Based on DNA sequencing, morphometrics, and echolocation data, Jacobs *et al.* (2013a: 1, 12) concluded that the western population of *R. darlingi* represents a separate species [= *R. damarensis*], which was separated from the eastern population some 9.7 Mya. Within the *R. damarensis* clade, two lineages can be seen: a northern (where the type of *damarensis* falls) and a southern linage, which diverged about 5 Mya (Jacobs *et al.*, 2013a: 12).

COMMON NAMES:
English: Damara Horseshoe Bat. German: Damara-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) [as part of *R. darlingi*] in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008aa; IUCN, 2009). While Monadjem *et al.* (2017bl) report that with an Extent of Occurrence of 17,3750 km^2 and an estimated population size of 20,000 individuals, this species qualifies as Least Concern; however, the population trend should be closely monitored since there is an ongoing

threat of loss of roost sites, as old mines are being re-opened for mining.

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bl). 2008: LC ver 3.1 (2001) [as part of *R. darlingi*] (Jacobs *et al.*, 2008aa; IUCN, 2009). 2004: LC ver 3.1 (2001) [as part of *R. darlingi*] (Jacobs *et al.*, 2004v); IUCN, 2004). 1996: LR/lc [as part of *R. darlingi*] (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016i). 2004: NT ver 3.1 (2001) [as part of *R. darlingi*] (Friedmann and Daly, 2004).

MAJOR THREATS:
The species is potentially threatened by the re-opening of mine adits, as well as re-use of old mines (Monadjem *et al.*, 2017bl).

CONSERVATION ACTIONS:
Monadjem *et al.* (2017bl) report that there are no direct conservation measures in place. It has however been recorded from formally protected Richtersveld National Park and the Augrabies Falls National Park.

GENERAL DISTRIBUTION:
Rhinolophus damarensis occurs primarily in the arid areas of Namibia, but also extends to Angola and the Northern Cape and North West provinces of South Africa (Palmeirim *et al.*, 2023: 313).

ECHOLOCATION:
In South Africa, Maluleke *et al.* (2017: 7347) studied the variation in echolocation calls along a latitudinal gradient between 16 and 32° S. They observed resting frequencies of 85.43 ± 1.3 kHz and average call duration of 31.14 ± 5.9 ms, with a slight sexual dimorphism: in females the frequencies varied between 84.4 ± 0.7 kHz and 87.6 ± 1.1 kHz in the different localities, and in males between 84.4 kHz ± 0.9 to 86.9 ± 1.1 kHz. The only factor they found to be responsible for the divergence in resting frequency was annual mean temperature.

MOLECULAR BIOLOGY:
Genetics
Jacobs *et al.* (2013a: 12) sequenced the Cytochrome *b* gene from the type specimen of *R. d. damarensis* Roberts, 1924 (TM 9474) (Genbank Nr- KF683224), which grouped distinctly from the eastern populations now referred to as *R. darlingi* (*sensu stricto*). Two lineages which within the *R. damarensis* clade can be seen a northern (where the type of *damarensis* falls, and a southern linage.

POPULATION:
Structure and Density
It occurs in small colonies of less 100 individuals per colony (Monadjem *et al.*, 2017bl).

Trend
Unknown (Monadjem *et al.*, 2017bl).

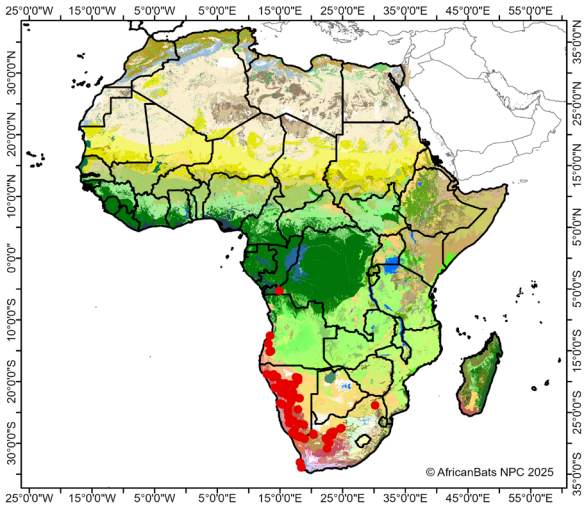

Figure 91. Distribution of *Rhinolophus damarensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Congo (Democratic Republic of the), Namibia, South Africa.

Rhinolophus darlingi K. Andersen, 1905

*1905. *Rhinolophus Darlingi* K. Andersen, Ann. Mag. nat. Hist., ser 7, 15 (85): 70. Publication date: 1 January 1905. Type locality: Zimbabwe: Mashonaland: Mazoe [17 30 S 31 03 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1895.8.27.1: ad, skull only. Collected by: James Johnston ffolliot Darling Esq. Collection date: 13 June 1895; original number: 35. Paratype: NHMUK [a]. Paratype: NHMUK [b]. Paratype: NHMUK [c]. Paratype: NHMUK [d]. Paratype: NHMUK [e]. - Etymology: In honour of J. ff. Darling, a mining engineer, who first collected this species in Mazoe, Zimbabwe, in the early part of the twentieth century (see Smithers, 1983: 126; Taylor, 2005). (Current Combination).

1924. *Rhinolophus darlingi barbertonensis* Roberts, Ann. Transv. Mus., 10: 59. Publication date: 31 January 1924. Type locality: South Africa: SE Transvaal province: Barberton district: Louw's creek. [Goto Description]. Holotype: TM 2476: ad ♀, skin and skull. Collected by: Austin Roberts; collection date: 14 March 1920. Note: Caught in old mine drive.

2013. *R[hinolophus] d[arlingi] barbetonensis:* Jacobs, Babiker, Bastian, Kearney, van Eeden and Bishop, PLoS ONE, 8 (12): 3. Publication date: 3 December 2013. (Lapsus).

2016. *Rhinolophus darling:* Hoffmaster and Vonk, Behav. Sci., 6 (25): 1. Publication date: 20 November 2016. (Lapsus).
2022. *Rhinolophus darlingi barbetonensis:* Chidoti, De Nys, Pinarello, Mashura, Missé, Guerrini, Pfukenyi, Cappelle, Chiweshe, Ayouba, Matope, Peeters, Gori, Bourgarel and Liégeois, Viruses, 17 (781): Suppl. Publication date: 9 April 2022. (Lapsus).
? *Rhinolophus darlingi darlingi:* (Name Combination).
? *Rhinolophus darlingi:* (Current Spelling).

TAXONOMY:
Jacobs *et al.* (2013a: 12) showed that *R. darlingi* (*sensu lato*) was polyphyletic, comprising two non-sister lineages (*R. darlingi* (*sensu stricto*) and *R. damarensis*), with disjunct distributions in southern Africa, which diverged about 9.7 Mya. They further showed that despite the genetic divergence between the two lineages (*R. darlingi* (*sensu stricto*) and *R. damarensis*) echolocation frequencies as well as skull and post-cranial morphology, except for the bacula, were highly convergent.

R. darlingi is embedded in the *fumigatus* clade (Csorba *et al.*, 2003: 39 - 40; Simmons (2005: 354) that includes – *R. damarensis*, *R. fumigatus*, *R. eloquens* and *R. hildebrandtii* (Jacobs *et al.* (2013a: 12).

However, Taylor *et al.* (2024: 4) indicate that the taxonomic position of *Rhinolophus darlingi* within the genus is rather ambiguous as it morphologically seems to belong to the *ferrumequinum* group, but molecularly to the *fumigatus* group. Hence, they retain it in its own group (*darlingi*).

R. darlingi includes *R. d. barbertonensis* Roberts, 1924.

COMMON NAMES:
Afrikaans: Darling se saalneusvlermuis, Darling-saalneusvlermuis. Czech: vrápenec Darlingův. English: Darling's Horseshoe Bat. French: Fer-à-Cheval de Darling, Rhinolophe de Darling. German: Darlings Hufeisennase. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura de Darling.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
R. darlingi is represented intermittently in the upper Pleistocene and in the very late Holocene at Border Cave (Avery, 1991: 6).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008aa; IUCN, 2009; Monadjem *et al.*, 2017cv).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cv). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008aa; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004v); IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016j). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
Jacobs *et al.* (2008aa) [in IUCN (2009)] and Monadjem *et al.* (2017cv) reported that there appear to be no major threats to this species as a whole.

CONSERVATION ACTIONS:
This species is present within several protected areas. Further taxonomic studies are needed for populations recorded outside of southern Africa. No direct conservation measures are currently needed for the species (Jacobs *et al.*, 2008aa; IUCN, 2009; Monadjem *et al.*, 2017cv).

GENERAL DISTRIBUTION:
Rhinolophus darlingi is largely distributed in southern Africa with some additional records outside of this area. Skinner and Chimimba (2005) report that it has been recorded from Namibia and northeastern Botswana; that it is widely distributed in Zimbabwe; in South Africa, where its distribution is best predicted by geology (Babiker Salata, 2012: 50), it is known from Limpopo Province, eastern Mpumalanga, northern Gauteng, in parts of the Eastern Cape and the Northern Cape, and from KwaZulu-Natal. In much of eastern Mozambique; and in the lowveld and Lubombo regions of Swaziland. It is unclear if the species is present in Lesotho. Outside of southern Africa, it has been recorded from Benguela in Angola, Banagi in Tanzania, and possibly from Nigeria suggesting a wider distribution than is currently known (Skinner and Chimimba, 2005). Herkt *et al.* (2017: Appendix S9), however, found that there are substantial differences in terms of occupied ecological niches between the populations from southern Africa and those from Nigeria, which support the statement in IUCN (2013) that they may represent a

separate species, which was tentatively identified as *Rhinolophus* aff. *darlingi* by Tanshi *et al.* (2022a: 314)

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,217,047 km^2.

CAS has 5 specimens from the Pyramids of Giza, Egypt, which may be possible misidentifications as these seem to be well outside of the distribution range of the species.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 557); Botswana (Monadjem *et al.*, 2010d: 557); Burundi; Congo (The Democratic Republic of the); Eswatini (Monadjem *et al.*, 2010d: 558, Monadjem *et al.*, 2021: 5); Kenya; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 557); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 557); Namibia (Monadjem *et al.*, 2010d: 557); South Africa (Monadjem *et al.*, 2010d: 557); Tanzania; Zambia (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 558); Zimbabwe (Monadjem *et al.*, 2010d: 558).

Presence uncertain: Lesotho; Nigeria.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.8 Pa, aspect ratio 6.3 for a wingspan of 30 cm and a wing area of 138 cm^2 and a body mass of 11 g.

ECHOLOCATION:
Jacobs *et al.* (2007a) reported a peak frequency of 88.1 (± 2.0) kHz for individuals from South Africa (detector type not reported). For individuals from Swaziland Taylor (1999b) using a Petterssen D980 at Mlawula reported a F_{max}: 86.2 ± 0.1 kHz, while Monadjem *et al.* (2007a) using an Anabat detector at a number of localities reported a F_{max}: 85.8 ± 0.36 kHz. Taylor (2000) reported a constant frequency component of 86 kHz. Monadjem *et al.* (2017c: 179) registered the following parameters: F_{min}: 74.3 ± 4.28 (70.8 - 79.1) kHz, F_{knee}: 85.7 ± 0.46 (85.2 - 86.1) kHz, F_c: 85.6 ± 0.38 (85.2 - 85.8) kHz and duration: 26.5 ± 3.74 (22.6 - 30.0) ms. They also indicated that the maximum detection distance was 2 m.

One call from Waterberg, South Africa had the following parameters: F_{max}: 87.4 kHz, F_{min}: 84.2 kHz, F_{knee}: 85.6 kHz, F_{char}: 85.1 kHz, duration: 28.0 ms (Taylor *et al.*, 2013b: 19). These authors also reported an additional four calls from Swaziland: F_{max}: 85.8 ± 0.25 (85.5 - 86.0) kHz, F_{min}: 74.5 ± 4.54 (72.3 - 76.1) kHz, F_{knee}: 84.8 ± 0.52 (84.1 - 85.2) kHz, F_{char}: 85.2 ± 0.54 (84.5 - 85.6) kHz, duration: 17.8 ± 3.39 (13.3 - 21.5) ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 8 calls of 1 bat: F_{max}: 91.04 kHz, F_{min}: 78.67 kHz, F_{knee}: 89.02 kHz, F_{char}: 90.15 kHz, slope: -222.94 OPS, duration: 37.63 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 4 *Rhinolophus darlingi* calls from the Kruger Park (RSA): F_{min}: 70.4 ± 4.3 (67.6 - 76.8) kHz, duration: 27.3 ± 1.0 (26.5 - 28.7) ms, F_{max}: 82.0 ± 3.7 (80.1 - 87.5) kHz, F_{knee}: 80.7 ± 3.6 (78.8 - 86.1) kHz, F_{char}: 80.8 ± 3.5 (79.0 - 86.1) kHz.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 80.76 ± 3.55 kHz, F_{max}: 81.95 ± 3.70 kHz, F_{min}: 70.38 ± 4.32 kHz.

88 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 72 - 76 kHz, F_{max}: 85 - 86 kHz, F_{char}: 84 - 85 kHz, F_{knee}: 84 - 85 kHz and duration 13 - 21ms.

For 34 calls from 5 *Rhinolophus darlingi* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 83.49 ± 1.37 kHz, F_{knee}: 83.36 ± 0.85 kHz, F_{min}: 73.36 ± 4.77 kHz, F_{max}: 84.65 ± 1.50 kHz, Bandwidth: 11.29 ± 3.95 kHz, Duration: 31.95 ± 6.92 ms.

Jacobs (2016: 119) indicates that the second harmonic of this bat coincides with the fourth harmonic of *R. hildebrandtii*, which possibly might illustrate "harmonic hopping".

MOLECULAR BIOLOGY:
Karyotype
Both Peterson and Nagorsen (1975) and Rautenbach (1986) reported, for specimens from Zimbabwe and South Africa respectively, 2*n* = 58, FN = 60, BA = 4, and subtelocentric X and Y chromosomes. Erasmus and Rautenbach (1984: 94) mention 52 acrocentric and four bi-armed autosomal chromosomes, resulting in 60 autosomal arms.

Genetics
Jacobs *et al.* (2013a: 12) sequenced the Cytochrome *b* gene from the type specimen of *R. d. barbetonensis* (sic) Roberts 1924 (TM 2476) (Genbank Nr- KF683217), which grouped with specimens collected from the type locality of the type of *R. darlingi* (Mazoe, Zimbabwe).

ROOST:
These bats roost in caves, abandoned mine-adits, cavities and fissures in rock or in piles of boulders, large hollow trees or disused buildings. They generally form small groups, but at least one group of about 160 animals has been reported. In these groups, they form clusters, but the animals do not touch one another (Happold and Happold, 2023: 82).

PREDATORS:
Based on Fenton *et al.* (1981), Gual-Suárez and Medellín (2021: Suppl.) reported that this species accounted for 0.5 % of the food items taken by *Nycteris grandis*.

Malan *et al.* (2022: 167) reported one individual found in a pellet from a bat hawk (*Macheiramphus alcinus* Bonaparte, 1850.

POPULATION:
Structure and Density
Rhinolophus darlingi is a locally common species that, while usually found in small numbers, can be represented by hundreds of bats in a colony (Skinner and Chimimba, 2005) (Jacobs *et al.*, 2008aa; IUCN, 2009; Monadjem *et al.*, 2017cv).

Trend
2016: Unknown (Monadjem *et al.*, 2017cv).
2008: Unknown (Jacobs *et al.*, 2008aa; IUCN, 2009).

POSTNATAL DEVELOPMENT:
Hoffmaster and Vonk (2016: 1) refer to Carter and Wilkinson (2013), who suggest that *R. darlingi* mothers, cooperating to keep all of the offspring warm, increase the probability of their own offspring's survival.

PARASITES:
DIPTERA
Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100).

Nycteribiidae
Nycteribia scissa rhodesiensis Theodor, 1957 from Zimbabwe and Malawi (Haeselbarth *et al.*, 1966: 108). *Nycteribia tecta* Theodor,1957 from Zimbabwe and South Africa, but Haeselbarth *et al.* (1966: 110) suggests these may represent a distinct subspecies.

Dick *et al.* (2023) mentioned that *Phthiridium rhodesiense* (Theodor, 1957), *Phthiridium scissum* (Speiser, 1900) and *Phthiridium tectum* (Theodor, 1957), have been found on *Rhinolophus darlingi*.

SIPHONAPTERA
Pulicidae
Echidnophaga aethiops Jordan and Rothschild, 1906 locality not mentioned (Haeselbarth *et al.*, 1966: 135).

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in one individual from Limpopo Province, South Africa, none were tested positive (0/1).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested five individuals from three localities using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) tested five individual brains, from three localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

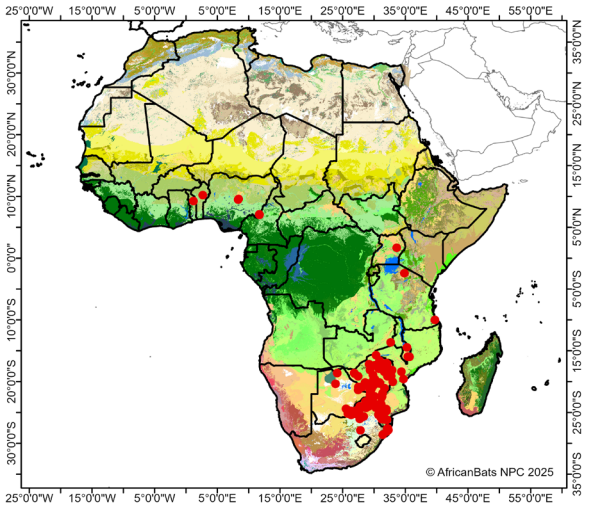

Figure 92. Distribution of *Rhinolophus darlingi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Eswatini, Kenya, Malawi, Mozambique, Nigeria, South Africa, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Rhinolophus deckenii Peters, 1868

*1868. *Rhinolophus Deckenii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 705 (for 1867). Type locality: Tanzania: Zanzibar coast (mainland opposite Zanzibar). [Goto Description]. Holotype: ZMB 3269: ad ♀, alcoholic (skull missing). Collected by: Baron Karl Klaus von der Decken; collection date: undated. - Etymology: In honour of baron Karl Klaus Von der Decken (1833 - 1865), collector of the type specimen. (Current Combination).
? *Rhinolophus deckeni:* (Alternate Spelling).
? *Rhinolophus deckenii:* (Current Spelling).

TAXONOMY:



Figure 93. *Rhinolophus deckenii*, Zanzibar Island.

Treated as a subspecies of *clivosus* by Hayman and Hill (1971: 23); but see Koopman (1975: 386). *ferrumequinum* species group (Csorba *et al.*, 2003: 41 - 42; Simmons, 2005: 354). See Csorba *et al.* (2003: 41) for remarks on taxonomy.

COMMON NAMES:
Chinese: 德氏菊头蝠. Czech: vrápenec východoafrický. English: Decken's Horseshoe Bat, Eastern Africa horseshoe bat. French: Fer-à-Cheval d'Afrique orientale, Rhinolophe de Decken, Rhinolophe d'Afrique orientale. German: Deckens Hufeisennase. Italian: Rinòlofo di Dècken, Fèrro di cavàllo di Dècken.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened (NT ver 3.1 (2001)) as its global population is suspected to have declined by 25-30% over the past 15 years (two generations) and is expected to continue to decline over next 7.5 years (one generation; generation length = 7.5 years, Pacifici *et al.*, 2013), making it close to qualifying as Vulnerable under A4c (Jacobs *et al.*, 2008ab; IUCN, 2009; Shapiro *et al.*, 2020a). Its extent of occurrence (EOO), area of occupancy (AOO), and habitat is projected to continue to decline due to continuing threats from forest loss and degradation and cave loss, degradation, and disturbance (Shapiro *et al.*, 2020a).

Assessment History
Global
2019: NT A4c ver 3.1 (2001) (Shapiro *et al.*, 2020a). 2008: NT ver 3.1 (2001) (Jacobs *et al.*, 2008ab; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004p; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Jacobs *et al.* (2008ab) [in IUCN (2009)] and Shapiro *et al.* (2020a) reported that this species is presumably threatened by the logging and conversion of forest land to agricultural use, especially in coastal areas. For example, deforestation of coastal forest in northern Mozambique is progressing at an alarming rate; the Chinizua forest (where one of the two Mozambique specimens was captured) has virtually disappeared due to logging. Cave disturbance and degradation are also key threats in some areas (Shapiro *et al.*, 2020a).

CONSERVATION ACTIONS:
There appear to be no direct conservation measures in place. It has been recorded from some National Parks and Forest Reserves in Tanzania, including the Udzungwa National Park (Stanley *et al.*, 2005b) and the Uzungwa Scarp Forest Reserve (Trentin and Rovero 2011). It has been recorded from within the greater Gorongosa protected area. There is a need to maintain areas of suitable forest habitat for this species. Further research is needed into the species taxonomy, biology and overall natural history (Jacobs *et al.*, 2008ab; IUCN, 2009; Shapiro *et al.*, 2020a)..

GENERAL DISTRIBUTION:
Rhinolophus deckenii, a little-known East African species has been recorded from Uganda, Kenya, and Tanzania (including the islands of Pemba, and Unguja [=Zanzibar] [see O'Brien, 2011: 286]). It has recently been found in Mozambique.

Native: Kenya; Mozambique (Monadjem *et al.*, 2010d: 558; Monadjem *et al.*, 2010c: 378); Tanzania (including the islands of Zanzibar and Pemba) (Stanley and Goodman, 2011: 42); Uganda.

ECHOLOCATION:
Monadjem *et al.* (2010c: 378) reported from Mozambique that the peak echolocation frequency of a single male was recorded at 72 kHz (ANABAT).

POPULATION:
Structure and Density
Small colonies of less than 20 individuals. It is reported to be locally common in some areas, such as the Manga Forest Reserve, Tanzania (Doggart *et al.*, 1999b) (Jacobs *et al.*, 2008ab; IUCN, 2009) and Mozambique Monadjem *et al.*, 2010d: 558; Monadjem *et al.*, 2010c: 378).

Trend
2019: Decreasing (Shapiro *et al.*, 2020a). 2008: Decreasing (Jacobs *et al.*, 2008ab; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Pakenham (1984: 30) reported he captured pregnant females in October 1938 on Zanzibar.

PARASITES:
DIPTERA
Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100).

Nycteribiidae
Nycteribia tecta Theodor 1957 from Kenya, Uganda, Tanzania and the Sudan (Haeselbarth *et al.*, 1966: 110). Dick *et al.* (2023: 80) mentioned this fly as *Phthiridium tectum* (Theodor, 1957).

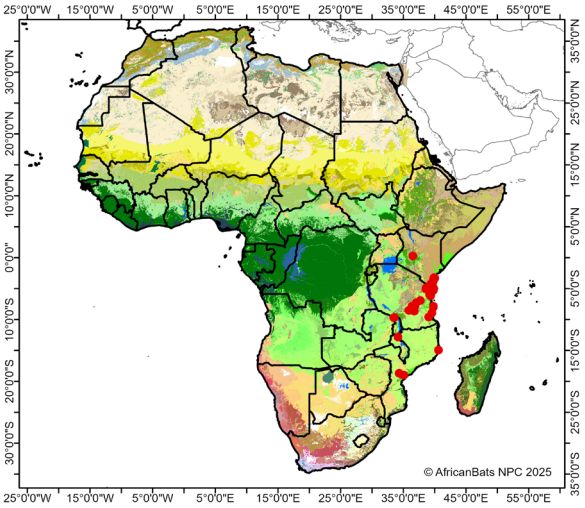

Figure 94. Distribution of *Rhinolophus deckenii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Malawi, Mozambique, Tanzania.

Rhinolophus denti Thomas, 1904

*1904. *Rhinolophus Denti* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (77): 386. Publication date: 1 May 1904. Type locality: South Africa: Northern Cape province: [formerly Bechuanaland]: Kuruman [26 28 S 22 27 E, 1 300 m]. [Goto Description]. Holotype: NHMUK 1904.4.8.2: ♂. Collected by: Captain R.E. Dent; collection date: 24 January 1904; original number: 7. - Etymology: In honour of R.E. Dent (Smithers, 1983: 130; Skinner and Smithers, 1990; Taylor (2005), the collector of the type specimen. (Current Combination).

1960. *Rhinolophus denti knorri* Eisentraut, Stuttg. Beitr. Naturk., 39: 3. Publication date: 1 June 1960. Type locality: Guinea: 12 km W Kolenté, Salung Plateau: Nyembaro [ca. 10 05 N 12 30 W]. [Goto Description]. Holotype: SMNS 6111: ad ♂, skin and skull. Collected by: Hans Knorr; collection date: 27 November 1956. Dieterlen *et al.* (2013: 293) mention the locality for this specimen as "Salung-Plateau near Nyembaro-Nerebili, 10 km western of Kolenté, 400 m, Guinea". Paratype: SMNS 6112: ad ♀, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Paratype: SMNS 6112a: ad ♀, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Paratype: ZFMK MAM-1959.0174: ♂, skin and skull. Collected by: Hans Knorr; collection date: 15 November 1956; original number: 90. See Hutterer and Peters (2010: 11). Paratype: ZFMK MAM-1959.0175: ♂, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. See Hutterer (1984: 30), Hutterer and Peters (2010: 11).. - Comments: Considered a valid subspecies by Grubb *et al.* (1998: 78). Type specimen in the SMNS.

2019. *R[hinolophus] cf. denti:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 7. Publication date: 22 August 2019. (Name Combination).

? *Rhinolophus cf. denti TD-2019*

? *Rhinolophus denti denti:* (Name Combination).

? *Rhinolophus denti:* (Current Spelling).

TAXONOMY:



Figure 95. A female *Rhinolophus denti* (TM 48035) caught at Taung, North-West Province, South Africa.

Placed within the *capensis*-group (Csorba *et al.*, 2003: 9 - 10; Simmons, 2005: 354). Possibly includes *R. swinnyi* (see Roberts, 1914; Csorba *et al.*, 2003: 9 - 10). Two subspecies are currently recognised, besides the nominate form described from the Northern Cape Province of South Africa (and including Namibia, Botswana and Zimbabwe), also *R. d. knorri* Eisentraut, 1960 from Guinea (and including Ghana) (Csorba *et al.*, 2003: 9 - 10; Simmons, 2005: 354). *R. d. knorri* is slightly smaller than the nominate form especially in the length of tibia and ear (Csorba *et al.*, 2003: 9 - 10). See Csorba *et al.* (2003: 9 - 10) for further remarks on taxonomy.

Taylor *et al.* (2024: 7) found that arid-adapted *R. denti* from the western Escarpment (southern Africa) diverged from *R.* cf. *denti* from central Africa (W DRC and Gabon) at 3.13 (1.44 - 4.96) Mya and these two clades formed an unresolved polychotomy at about 5.51 (3.48 - 8.07) Mya (at the Pliocene/Miocene boundary) with *R. rhodesiae* and *R. namuli* (temperate forests in eastern Escarpment, SEAMA and EARS) and *R. simulator* (savannas from northern South Africa to Ethiopia).

COMMON NAMES:

Afrikaans: Dent se saalneusvlermuis, Dent-saalneusvlermuis, Dentse Vlermuis. Czech: vrápenec Dentův. English: Dent's Horseshoe Bat. French: Rhinolophe de Dent. German: Dents Hufeisennase. Portuguese: Morcego ferradura de Dent.

SIMILAR SPECIES:

R. swinnyi (Shortridge, 1934; Roberts, 1914; 1946: 304). Shortridge (1934) was incorrect though, in indicating that Hewitt (1913) described a new subspecies of *R. denti*, from Pirie in the Eastern Cape province of South Africa, when it was actually *R. swinnyi piriensis* (Hewitt, 1913: 402).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Avery and Avery (2011: 16) indicate that material from the eastern part of the Northern Cape province in South Africa, that was previously assigned to *R. capensis* should probably be assigned to *R. denti*.

CONSERVATION STATUS:

Global Justification

Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ak; IUCN, 2009; Monadjem *et al.*, 2017bd).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bd). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008ak; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004ak; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: NT D1 ver 3.1 (2001) (Schoeman *et al.*, 2016a). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:

Jacobs *et al.* (2008ak) [in IUCN (2009)] and Monadjem *et al.* (2017bd) reported there appear to be no major threats to this species. It might be locally threatened in parts of its range by disturbance to roosting caves.

CONSERVATION ACTIONS:

There appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further studies are needed into the distribution of this species (particularly in West and Central Africa) (Jacobs *et al.*, 2008ak; IUCN, 2009; Monadjem *et al.*, 2017bd).

GENERAL DISTRIBUTION:

Rhinolophus denti is widely, but patchily, recorded in West and southern Africa. It ranges from southeastern Senegal, through northern parts of West Africa to northeastern Ghana; in Central Africa it appears to have only been recorded from eastern Congo and southern Angola; in southern Africa, it is present in Namibia, northwestern and southwestern Botswana and northern parts of South Africa, where the species' distribution is linked with land use/land cover (Babiker Salata, 2012: 50).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 781,091 km^2.

A record from Gambia is doubtful according to Kock *et al.* (2002b: 85), since it is possibly of an adolescent *R. landeri*, as is the record from Côte d'Ivoire (Csorba *et al.*, 2003: 10) that is also apparently a *R. landeri* (see Simmons, 2005: 354). Records have been reported from Zimbabwe (Smithers and Wilson, 1979: 57; Fenton and Bell, 1981). However, Smithers (1983) later indicated three records from northeastern Zimbabwe in Smithers and Wilson (1979) and Csorba *et al.* (2003: 10) are misidentifications.

Herkt *et al.* (2017: Appendix S9) found that there are major differences between the occupied ecological niches for *denti* from southwestern Africa and *knorri* from West Africa.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 558); Botswana (Smithers, 1971; Csorba *et al.*, 2003: 10; Monadjem *et al.*, 2010d: 558); Ghana (Csorba *et al.*, 2003: 10); Guinea (Csorba *et al.*, 2003: 10); Guinea-Bissau (Rainho and Ranco, 2001: 48; Simmons, 2005: 354); Mozambique (Smithers and Lobão Tello, 1976; Csorba *et al.*, 2003: 10; Smithers and Lobão Tello, 1976); Namibia (Ellerman *et al.*, 1953; Kock and Howell, 1988; Csorba *et al.*, 2003: 10; Monadjem *et al.*, 2010d: 558); Nigeria (Tanshi *et al.*, 2022a: 314); Senegal; South Africa (Northern Cape Province (Ellerman *et al.*, 1953; Herselman and Norton, 1985; Rautenbach, 1986; Monadjem *et al.*, 2010d: 558; Csorba *et al.*, 2003: 10), North West Province (James, 1986; Csorba *et al.*, 2003: 10), Free State Province (Watson, 1998; Monadjem *et al.*, 2010d: 558)).

Bates *et al.* (2013: 338) reject the presence of *R. denti* in the Republic of Congo.

GEOGRAPHIC VARIATION:
See "Taxonomy" section.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Smithers (1983), Skinner and Smithers (1990), Taylor (2000), Csorba *et al.* (2003: 9 - 10), Taylor (2005).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Smithers (1983), Skinner and Smithers (1990), Taylor (2000), Csorba *et al.* (2003: 9 - 10), Taylor (2005).

DETAILED MORPHOLOGY:
Skull
Of the skull, teeth and noseleaves see Csorba *et al.* (2003: 9 - 10).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Jacobs *et al.* (2007a)] mention a wing loading value of 4.7 Pa, aspect ratio 6 for a wingspan of 27 cm and a wing area of 122 cm^2 and a body mass of 6 g.

SEXUAL DIMORPHISM:
Five mensural characters (forearm length, fourth metacarpal length, width across the upper canines, rostral width, and length of the mandibular toothrow) showed significant variation between the sexes in an analysis of specimens from Koegelbeen Cave in the Northern Cape Province of South Africa (Rautenbach, 1986).

ECHOLOCATION:
For individuals at Sengwa in Zimbabwe Jacobs (1996) and Fenton and Bell (1981) reported a maximum frequency of 110 kHz. Jacobs *et al.* (2007a) reported a similar peak frequency of 110.9 ± 1.7 kHz for individuals in South Africa.

Jacobs (2016: 119) indicates that the second harmonic of this bat coincides with the fourth harmonic of *R. capensis*, which possibly might illustrate "harmonic hopping".

For the Boundou cave in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data for *Rhinolophus* cf. *denti*: 6 FF: F_{pmin}: 88.2 ± 8.6 kHz, F_{pmax}: 110.5 ± 3.9 kHz, F_{pmean}: 101.5 ± 1.2 kHz, F_{ppeak}: 101.7 ± 1.2 kHz, F_{flat}: 101.2 ± 1.3 kHz, F_{knee}: 100.6 ± 1.4 kHz, F_{mean}: 101 ± 1.4 kHz, Duration: 32 ± 17.5 ms; 1 M: F_{pmin}: 85.5 kHz, F_{pmax}: 103.5 kHz, F_{pmean}: 99.3 kHz, F_{ppeak}: 99.3 kHz, F_{flat}: 98.4 kHz, F_{knee}: 99.2 kHz, F_{mean}: 99.4 kHz, Duration: 18.5 ms.

MOLECULAR BIOLOGY:
Karyotype
Peterson and Nagorsen (1975) reported the diploid number as 2*n* = 58, aFN = 62, BA = 6, X = ST, Y =?, based on specimens from Zimbabwe. These results were supported by Rautenbach (1986) who also reported the Y chromosome to be metacentric. Karyologically identical to *R. swinnyi* (Csorba *et al.* (2003: 9 - 10).

HABITAT:
Found in relatively arid regions (Csorba *et al.*, 2003: 9 - 10). Even the most south easterly record in Africa comes from the drier south-western part of the Free State Province of South Africa (Watson, 1998).

HABITS:
In northwestern Namibia a specimen shot by Shortridge (1934: 52) at "Rua Cana Falls" had a slow fluttering *Kerivoula*-like flight, and several other individuals were observed "circling low among trees and bushes near the Cunene River on bright moonlight nights". Found roosting at Drotsky's Cave in Namibia throughout the year (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2005).

ROOST:
Shortridge (1934: 52) records finding a single individual, at Louisvale in the Northern Cape Province of South Africa, inside a low water culvert occupied by a small colony of *Nycteris*. Shortridge, 1934: 52) also records finding two individuals "hanging from the thatched roof inside a small native house at Kaoko-Otavi" in the north western part of Namibia. Also found in caves (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2005). At Drotsky's Cave in Namibia the bats were "clinging to the sides of stalactites…hanging freely from the sides in open clusters", and were found in semi-dark 90 m from the cave entrance and in total darkness deep in the cave (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2005). Notes on an index card for specimens in the Transvaal Museum, from a cave near Warrenton in the Northern Cape Province of South Africa, indicate the cave was wet with water on the floor and dripping from stalactites, and that the bats congregated in separate groups. James (1986: 218) recorded a single individual at a disused quarry near Buxton in the North West Province, roosting on the ceiling of a "ruined mine structure which formed a 2 x 2 x 20 m cement, semi-dark room in a hillside".

Weber and Fahr (2006: 4) indicate that, in Guinea, *R. denti* largely or exclusively depends on the availability of caves as day roosts.

MIGRATION:
May not migrate as *R. denti* has been found roosting at Drotsky's Cave in Namibia throughout the year (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2005).

DIET:
Insectivorous (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2000; 2005).

POPULATION:
Structure
The species is known from fewer than 100 in colonies in West Africa, and fewer than 200 colonies in southern Africa (Jacobs *et al.*, 2008ak; IUCN, 2009; Monadjem *et al.*, 2017bd).

Density
"Sparsely distributed", with no records of large colonies (Shortridge, 1934:52). At Drotsky's Cave in Namibia the bats were observed "clinging to the sides of stalactites in dozens" (Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2005). Herselman and Norton (1985: 92) indicated that this species had not been collected from the Northern Cape province in the "last half century" and could be considered as "extremely rare, possibly extinct, in the Cape Province". Yet, specimens in the Transvaal Museum, collected from the Northern Cape Province of South Africa between 1983 and 1988, indicate that at three different visits; 12, 71 and 15 specimens were taken from Koegelbeen Cave, 12 specimens were taken on a single date from a cave near Warrenton, and 11 specimens were taken on a single date from a locality near Postmasberg.

Trend
2016: Unknown (Monadjem *et al.*, 2017bd).
2008: Unknown (Jacobs *et al.*, 2008ak; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Notes on an index card for specimens in the Transvaal Museum, from a cave near Warrenton in the Northern Cape Province of South Africa, indicate that on 14th of June 1983 the bats were in torpor.

PARASITES:
Brennan *et al.* (2015: 145) found no antibodies against *Pseudogymnoascus destructans* (White-nose syndrome) in blood samples from bats from Botswana.

VIRUSES:
Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that two out of three examined South African *R. denti* specimens tested positive for *Paramyxovirus* sequences.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 12 individuals from three localities using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) tested 15 individual brains, from two localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

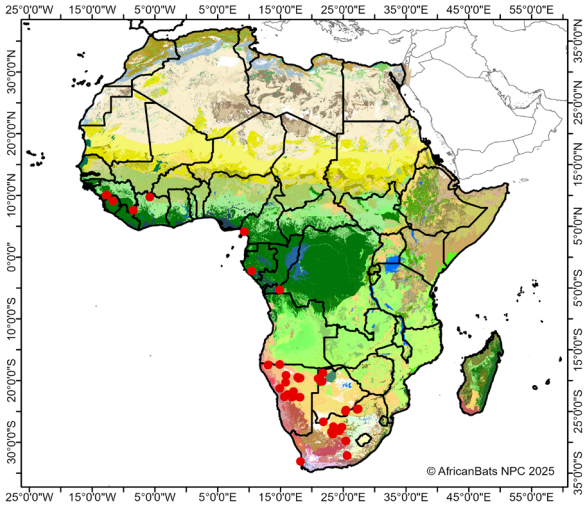

Figure 96. Distribution of *Rhinolophus denti*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Guinea, Namibia, Sierra Leone, South Africa.

Rhinolophus dobsoni Thomas, 1904

1904. *Rhinolophus Dobsoni* Thomas, Ann. Mag. nat. Hist., ser 7, 14 (80): 156, footnote. Publication date: 1 August 1904. Type locality: Sudan: Kordofan [ca. 13 00 N 30 00 E]. [Goto Description]. Holotype: NHMUK 1847.5.27.49: ♀. Thomas (1904d: 156) mentioned the registration number for the holotype as "47.5.7.49", but Patterson *et al.* (2024: Suppl.) mentioned "1847.5.27.49". Cross-checking with the NHMUK online catalog proved this latter number to be correct (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/3621169).

? *Rhinolophus landeri dobsoni:* (Name Combination).

TAXONOMY:
Patterson *et al.* (2024: 4, 12) consider *dobsoni* to be a valid species, based on cyt b sequences, which are different from both *Rhinolophus landeri* and *Rhinolophus webalai*.

COMMON NAMES:
English: Dobson's horseshoe bat. German: Dobson-Hufeisennase

GENERAL DISTRIBUTION:
Patterson *et al.* (2024: 12, Suppl.) mention this species to occur in North Africa and provide records from Sudan (Kordofan and Gallabat, near the Ethiopian border). We tentatively include the "*landeri*" specimens from Ethiopia.

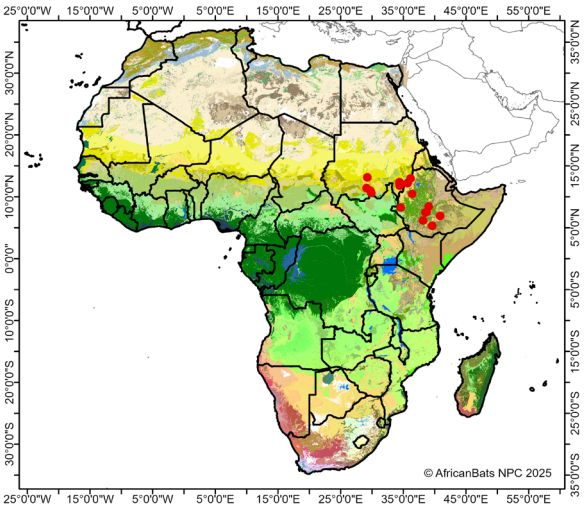

Figure 97. Distribution of *Rhinolophus dobsoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Sudan.

Rhinolophus eloquens K. Andersen, 1905

*1905. *Rhinolophus Hildebrandti eloquens* K. Andersen, Ann. Mag. nat. Hist., ser 7, 15 (85): 74. Publication date: 1 January 1905. Type locality: Uganda: Entebbe [00 04 N 32 28 E, 3 800 ft]. [Goto Description]. Holotype: NHMUK 1899.8.4.4: ad, skull only. Collected by: Sir Frederick John Jackson. See Andersen (1905a: 75). Topotype: ROM 68683: ad ♀, alcoholic (skull not removed). Collected by: Theo Simpson Jones; collection date: 4 July 1963. - Etymology: From the Latin masculine adjective *èloquens*. Andersen (1905a) provides no etymological information; however, it is possible that this *Rhinolophus* is "eloquent" from a phylogenetic and zoogeographical point of view, as Andersen (1905a: 75) writes that "The present form is of great interest from phylogenetic no less than from a zoogeographical point of view" (see Lanza *et al.*, 2015: 93).

1922. *Rhinolophus hildebrandti perauritus* de Beaux, Atti Soc. ital. Sci. nat., 61: 22. Publication date: February 1922. Type locality: Somalia: Territory of the Rahanuin. [Goto Description].

2016. *Rhinolophus eloquensis:* Amori, Segniagbeto, Decher, Assou, Gippoliti and Luiselli, Zoosystema, 38 (2): 219. Publication date: 24 June 2016. (Lapsus).
? *Rhinolophus aethiops eloquens:* (Name Combination).
? *Rhinolophus cf. eloquens DMR-2017*
? *Rhinolophus eloquens eloquens:* (Name Combination).
? *Rhinolophus eloquens:* (Name Combination, Current Combination).
? *Rhinolophus fumigatus eloquens:* (Name Combination).

TAXONOMY:
Included as subspecies in *aethiops* by Kock (1969a: 121). Includes *perauritus*; see Koopman (1975: 389). *fumigatus* species group (Csorba *et al.*, 2003: 47 - 48; Simmons, 2005: 354). See Csorba *et al.* (2003: 48) for remarks on taxonomy.

COMMON NAMES:
Chinese: 乌干达菊头蝠. Czech: vrápenec ugandský. English: Eloquent Horseshoe Bat. French: Rhinolophe éloquent. German: Andersens Hufeisennase. Italian: Rinòlofo eloquènte, Fèrro di cavàllo eloquènte.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017cj).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cj). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008ac; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004u; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Rhinolophus eloquens is threatened by the general conversion of its habitat to agricultural use (Jacobs *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017cj).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008ac) [in IUCN (2009)] and Monadjem *et al.* (2017cj) reported there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research needed into the distribution, natural history and threats to this bat.

GENERAL DISTRIBUTION:
Rhinolophus eloquens is endemic to Central and Eastern Africa. It has been recorded from southern Sudan, eastern Democratic Republic of the Congo, Rwanda, Uganda, Kenya, Somalia and the islands of Pemba, Unguja [=Zanzibar], and Mafia in Tanzania (see O'Brien, 2011: 286).

Native: Congo, (Democratic Republic of) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 558); Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Kenya; Rwanda; Somalia; Sudan; Tanzania (United Republic of); Uganda.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017cj).

Trend
2016: Unknown (Monadjem *et al.*, 2017cj). 2008: Unknown (Jacobs *et al.*, 2008ac; IUCN, 2009).

PARASITES:
PROTOZOA
Babyesiza *et al.* (2025: 4) reported *Trypanosoma livingstonei* from Ugandan *Rhinolophus eloquens*.

HEMIPTERA
Polyctenidae
Androctenes horvathi Jordan 1912 recorded from Kenya and Sudan (Haeselbarth *et al.*, 1966: 17), and from South Africa and South Sudan by Szentiványi *et al.* (2022: 5)

DIPTERA
Nycteribiidae
Nycteribia hoogstraali Theodor, 1957 from the Torit district in the Sudan (Zumpt 1966: 109). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114). *Phthiridium hoogstraali* (Theodor, 1957) (Lutz *et al.*, 2021: Suppl.). These two bat flies were also mentioned by Dick *et al.* (2023).

Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in subsaharan Africa (Haeselbarth *et al.*, 1966: 100). Jobling (1954) as mentions *Raymondia intermedia* Jobling, 1936 as possible parasite of *R. eloquens* (see also Shapiro *et al.*, 2016: 255). *Raymondia seminuda* Jobling, 1954 (Shapiro *et al.*, 2016: 255).
Raymondia sp. was found in three Kenyan bats by Lutz *et al.* (2021: Suppl.).

ACARI
Trombiculidae
Stekolnikov (2018a: 50) reported the presence of *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957.

VIRUSES:
Filoviridae - Filoviruses
Marburgvirus
Kuzmin *et al.* (2010b: 353) detected MARV RNA in 3.6 % of the examined *R. eloquens* in the DRC.

Luis *et al.* (2013: suppl.) report the presence of Lake Victoria marburg virus.

Crowley *et al.* (2020: 5) pointed out that the infected *R. eloquens* specimens were co-roosting with positive *R. aegyptiacus* and that they were possibly infected by spill-over from the latter species.

Rhabdoviridae
Vesiculovirus
Mount Elgon bat virus (MEBV)
Reported by Luis *et al.* (2013: suppl.) although they remark that the bat might have been a *R. hildebrandti*.

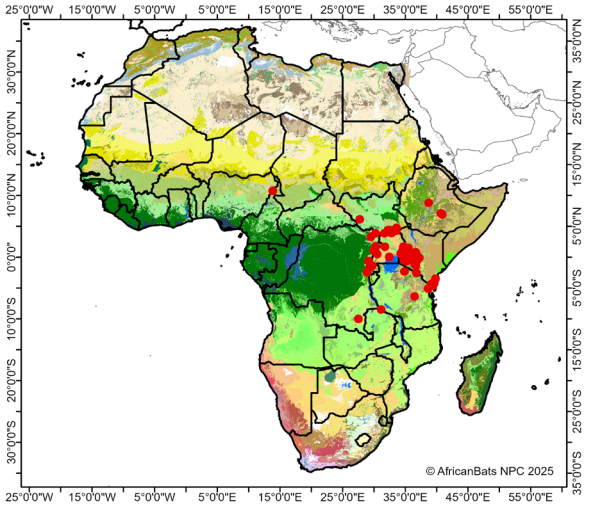

Figure 98. Distribution of *Rhinolophus eloquens*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Ethiopia, Kenya, Rwanda, South Sudan, Sudan, Tanzania, Uganda.

Rhinolophus euryale Blasius, 1853

*1853. *Rhinolophus euryale* Blasius, Arch. Naturgesch. Berlin, 19 (1): 49, 52, 54. Publication date: 1853. Type locality: Italy: Milan. - Etymology: Referring to "*Euryale*", one of the Gorgons (see Palmer, 1904: 279). (Current Combination).
1867. *Rhinolophus algirus* Loche, Exploration scientifique de l'Algerie pendant les années 1840, 1841, 1842. Mammifères, Cheiroptères, 83. Publication date: 1867. Type locality: Algeria: "Jardin Marengo". - Comments: Allen (1939a: 74) states that this name is not certainly identifiable but may possible prove to supersede *barbarus* if the types can be found. Ellerman and Morrison-Scott (1951: 120) include it with a question mark in the synonymy of *R. euryale barbarus*.
1896. *Hipposiderus euryale:* Thomas, Ann. Mus. civ. Stor. nat. Genova, (2) 17 (37): 105. (Name Combination).
1904. *E[uryalus] atlanticus* K. Andersen and Matschie, Sber. Ges. naturf. Freunde Berlin, 77. Type locality: France: Indre-et-Loire: St. Paterna. Holotype: ZMB 12963: ♂, alcoholic (skull not removed). Collected by: Nitsche; collection date: 6 April 1893; original number: (formerly ZMB 6705). See Turni and Kock (2008: 28). Paratype: MNHN ZM-MO-1879-2030: alcoholic (skull not removed). Collected by: The Lataste collection. See Rode (1941: 238).
1904. *E[uryalus] Cabreræ* K. Andersen and Matschie, Sber. Ges. naturf. Freunde Berlin, 78. Type locality: Spain: Madrid: Alcata de Henares [40 25 N 03 43 W]. Holotype: ZMB 12964: ♀, alcoholic (skull not removed). Original number: ex. Museum Madrid. See Turni and Kock (2008: 28). - Comments: Mentioned as *cabrerai* by Trouessart, 1910 (see Cabrera, 1914: 83).
1970. *R[hinolophus] euryole:* Rushton, Ann. Génét. Sél. anim., 2 (4): 463. (Lapsus).
1970. *Rhinolophus euroyle:* Rushton, Ann. Génét. Sél. anim., 2 (4): 466. (Lapsus).

TAXONOMY:
Revised by DeBlase (1972). Gaisler (2001: 68) does not recognises subspecies. *euryale* species group (Csorba *et al.*, 2003: 14 - 16; Simmons, 2005: 354 - 355). See Csorba *et al.* (2003: 16) for remarks on taxonomy.

COMMON NAMES:
Albanian: Lakuriq nate hundëpatkua i Mesdheut. Arabian: Khaffash. Armenian: Հարաւային պայտաքիթ. Azerbaijani: Cənub nalburunu. Basque: Ferra-saguzar mediterraneo. Belarusian: Падкаванос міжземнаморскі. Bosnian: Mediteranski potkovasti šišmiš. Breton: Frigribell greizdouarel. Bulgarian: Южен подковонос. Castilian (Spain): Murciélago mediterráneo de herradura, Rinolofo mediterraneao de herradura, Murciélago de herradura mediterráneo. Catalan (Spain): Ratpenat de ferradura mediterrani, Rat penat mediterrani de ferradura, Ratapinyada mediterrània de ferradura. Croatian: Južni

potkovnjak, Mediteranski potkovasti šišmiš. Czech: Vrápenec jižní, Vrápenec středozemský. Danish: Middelhavehestekonæse. Dutch: Paarse hoefijzerneus. English: Mediterranean Horseshoe Bat. Estonian: Vahemere sagarnina. Finnish: Välimerenherkko. French: Rhinolophe euryale. Frisian: Pearse hoefizernoas. Galician (Spain): Morcego de ferradura mediterráneo, Morcego mediterráneo de ferradura. Georgian: სამხრეთული ცხვირნალა. German: Mittelmeerhufeisennase, Mittelmeer-Hufeisennase, Gleichsatteligen Kammnase. Greek: Μεσορινόλοφος. Hebrew: פרסף בהיר, Parsaf Bahir. Hungarian: Kereknyergű patkósdenevér, Kereknyergû patkósorrú denevér, Rinolophos i mesogiaki. Italian: Rinolofo mediterraneo, Rinolofo Eurìale, Ferro di cavallo Eurìale, ferro di cavallo mediterraneo. Irish Gaelic: Crú-ialtóg Mheánmhuirí. Latvian: Vidusjuras pakavdegunis. Lithuanian: Pietinis pasagnosis. Luxembourgish: Mëttelmier-Huffeisennues. Macedonian: Медитерански потковичар, Juzhen Potkovichar. Maltese: Rinolofu tal-Mediterran. Montenegrin: Južni potkovičar. Norwegian: Middelhavshesteskonese. Polish: Podkowiec śródziemnomorski. Portuguese: Morcego-de-ferradura-mediterrânico. Rhaeto-Romance: Rinolof mediterran. Romanian: Liliacul mediteranean cu potcoavă, Liliac-sudic. Russian: Подковонос южный, Южный подковонос [= Yuzhnyj podkovonos]. Serbian: Средоземни потковичар [= Sredozemni potkovičar]. Scottish Gaelic: Crudh-ialtag Meadhan-thìreach. Slovak: Podkovár južný. Slovenian: Južni podkovnjak. Swedish: Medelhavshästskonäsa. Turkish: Akdeniz Nalburunlu Yarasası. Ukrainian: Підковик (Підковоніс) південний. Welsh: Ystlum pedol Môr y Canoldir.

Similar Species:

Puechmaille and Teeling (2013: 252) point out that visual identification of hibernating bats might be problematic in the case of *R. euryale* and *R. mehelyi*, as bat they originally identified as *R. mehelyi* turned out to belong to the other species after using non-invasive genetic tests on the animals' droppings.

Conservation status:

Global Justification

Many range states have reported that populations have declined, and colonies have disappeared over the last 27 years (= 3 generations). It is inferred that overall population decline has approached 30 % over that period (although the population is now stable and or even increasing in some areas, e.g., France), so the species is assessed as Near Threatened (approaching A2c) (NT ver 3.1 (2001)) (Hutson *et al.*, 2008o; IUCN, 2009; Juste and Alcaldé, 2016a).

Assessment History

Global

2016: NT ver 3.1 (2001) (Juste and Alcaldé, 2016a). 2008: NT ver 3.1 (2001) (Hutson *et al.*, 2008o; IUCN, 2009). 1996: VU A2c ver 2.3 (1994).

Regional

None known.

Major threats:

Threats include loss of foraging habitat, and disturbance and loss of underground habitats. On a landscape scale, fragmentation and loss of linear elements such as hedgerows and riparian vegetation is a problem because such elements are used as landscape references for commuting. The species' strong dependence upon caves for roosting makes it particularly sensitive to cave disturbance, such as that from caving or tourism. Tourist disturbance of caves affects the species in several range states. The use of organochlorine pesticides is believed to have contributed to the earlier dramatic decline of the species in France (Brosset *et al.*, 1988). In North Africa, threats include habitat loss due to agriculture (livestock) and human disturbance (Hutson *et al.*, 2008o; IUCN, 2009; Juste and Alcaldé, 2016a).

Aerial hawking, water stress, and its small distribution range are believed to be the most important risk factors for this species linked with climatic change (Sherwin *et al.* (2012: 174).

Conservation actions:

Juste and Alcaldé (2016a) supports Hutson *et al.* (2008o) [in IUCN (2009)] who reported *Rhinolophus euryale* is protected by national legislation in most range states. There are also international legal obligations for protection of this species through the Bonn Convention (Eurobats) and Bern Convention, where these apply. It is included in Annex II (and IV) of EU Habitats and Species Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. There is some habitat protection through Natura 2000, and some roosts are already protected by national legislation). The species is directly or indirectly benefiting from EU LIFEfunded projects in France, Spain and Italy. No specific measures are in place in North Africa.

General distribution:

Rhinolophus euryale is a western Palaearctic species, occurring in southern Europe, north-west

Africa (known range extends across northern Morocco, Algeria, and Tunisia), and the Near East. There is only a single record from Cyprus, but this is regarded by most authors to be *R. mehelyi*. It is widely distributed over its range, and is found from sea level to 1,000 m.

Native: Abkhasia; Albania; Algeria (Csorba *et al.*, 2003: 16); Andorra; Armenia; Azerbaijan; Bosnia and Herzegovina; Bulgaria; Croatia; France (Corse) (Csorba *et al.*, 2003: 16); Georgia; Gibraltar; Greece (East Aegean Is.); Holy See (Vatican City State); Hungary; Iran (Csorba *et al.*, 2003: 16), Islamic Republic of; Iraq; Israel (Csorba *et al.*, 2003: 16); Italy (Sardinia, Sicily); Jordan; Lebanon [see Horáček *et al.* (2008: 55)] (Csorba *et al.*, 2003: 16); Macedonia, the former Yugoslav Republic of; Monaco; Montenegro; Morocco (Csorba *et al.*, 2003: 16; El Ibrahimi and Rguibi Idrissi, 2015: 359; Dbiba *et al.*, 2025: 6); Palestinian Territory, Occupied; Portugal (Csorba *et al.*, 2003: 16); Romania; Russian Federation; San Marino; Serbia; Slovakia; Slovenia; Spain; Syrian Arab Republic (Csorba *et al.*, 2003: 16); Tunisia (Csorba *et al.*, 2003: 16; Dalhoumi *et al.*, 2016b: 867); Turkey (Csorba *et al.*, 2003: 16).
Regionally extinct: Switzerland.
Presence uncertain: Cyprus [see Benda *et al.* (2007: 71)]; Egypt; Turkmenistan.

Detailed morphology:

Baculum
See Csorba *et al.* (2003: 15).

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Salsamendi *et al.* (2005)] mention a wing loading value of 7.9 Pa, aspect ratio 6.2 and tip shape index of 2.78 for a wingspan of 30 cm and a wing area of 150 cm^2 and a body mass of 12 g.

In their study on take-off performance, Gardiner *et al.* (2014: 1059) determined a wing beat frequency of 11.48 ± 0.50 Hz.

Echolocation:

The data for 38 animals from Greece were the following: F_{start}: 91.8 ± 5.00 kHz, F_{end}: 88.7 ± 3.49 kHz, F_{peak}: 104.8 ± 0.96 kHz, bandwidth: 3.5 ± 1.05 kHz, duration 53.8 ± 20.42 ms and interpulse interval: 84.5 ± 30.01 ms (Papadatou *et al.*, 2008b: 132).

Walters *et al.* (2012: suppl.) report the following figures for 26 calls (15 sequences) from French and Italian bats: duration: 35.23 ± 18.06 ms, F_{max}: 102.28 ± 1.20 kHz, F_{min}: 88.22 ± 4.30 kHz, bandwidth: 14.06 ± 3.69 kHz, F_{peak}: 101.68 ± 2.18 kHz.

Animals from Tunisia emitted sounds at 102.39 ± 1.01 kHz (105.0 - 106.5 kHz; Dalhoumi *et al.*, 2016b: 866).

Schuchmann *et al.* (2012: 161) found that both sexes were able to recognize the sex of conspecifics from their echolocation calls.

Luo *et al.* (2019a: Supp.) reported the following data (for two calls): F_{peak}: 104.8, 102.4 kHz, F_{start}: 91.8, 93.8 kHz, F_{end}: 88.7, 89.1 kHz, and duration: 53.8, 40.6 ms.

Molecular Biology:

Karyotype
Both Bovey (1949) and Capanna and Manfredi Romanini (1971) reported 2*n* = 58, FN = 60. Rushton (1970: 463) also reported 2*n* = 58, FN=60, with two (sub)metacentric, 24 acrocentrics, and 2 minute pairs or acrocentric chromosomes. The X chromosome is reported as submetacentric and the Y chromosome as minute. Zima *et al.* (1992a) reported 2*n*=58, FN=60, BA=4, a submetacentric X chromosome and a metacentric Y chromosome for a specimen from Greece.

Capanna and Civitelli (1964a: 371) reported 2*n* = 58, including 24 acrocentric pairs, 2 metacentric pairs and two pairs of very small chromosomes. The X chromosome was reported as a large submetacentric and the Y as a very small one.

Genetics
In their study of mitochondrial DNA, Budinski *et al.* (2019: 770, 772) found that northern African *R. euryale* clustered together with the samples from Europe and Turkey in Clade III, indicating that these orignated from the same source population.

Habitat:

Russo *et al.* (2005: 327) and Goiti *et al.* (2003: 75; 2008: 498 - 499) indicate that, in Spain, *R. euryale* always foraged in areas where there were trees or hedgerows, and never over open meadows, pastures, heath, gorse- or fern-covered areas (or any other open habitats). About 96 % of the bats they tagged, used hedgerows to forage in. The second most frequented habitat (90 %) was broad-leaved woodland, whereas isolated trees were visited between 1 and 12 %. Exotic tree plantations (e.g., *Eucalyptus* formed the least preferred habitat. Furthermore, the breeding colony size was found to be positively correlated with the availability of edges around breeding sites.

Habits:

From the Iberian Peninsula, Goiti *et al.* (2006: 141) reported that during pre-breeding foraging

occurred on average within 1.3 km, and at most 4.2 km from the roost. For lactating females, the average distance was 4.3 km, and a maximum distance from the roost of 9.2 km was observed. In the same period, males foraged closer (mean 1.9 km). During the post-lactation period, adults travelled a mean of 4.6 km, whereas juveniles flew on average only 2.6 km.

ROOST:
Based on data from Sardinia, Russo *et al.* (2014: 9) rule out that *R. euryale* and *R. mehelyi* compete for roosting sites.

DIET:
In northern Spain, Goiti *et al.* (2008: 496 - 497) examined 810 faeces from 168 bats. These showed that the bat's diet included 10 prey categories, of which the Lepidoptera (moths) formed the staple diet (between 68 and 99 % of the diet). Moths are also the most important prey during lactation and post-lactation. Another important prey item, although very seasonal and especially prebreeding, was the beetle *Rhizotrogus* (Scarabaeidae). Other food items (in descending rank) included lacewings (Neuroptera, Chrysopidae and Hemerobiidae), craneflies (Diptera, Tipulidae), brachyceran flies, Psocoptera, and Hymenoptera. Diets were similar for adults and juveniles. In the same area, Aldasoro *et al.* (2019: 9) found the following prey groups (in descending order of occurrence): Lepidoptera (100 %), Diptera (94 %), Neuroptera (22 %), Ephemenoptera (17 %), Hemiptera (11 %), Hymentoptera (6 %) and Trichoptera (6 %). Arrizabalaga-Escudero *et al.* (2019: 1) found that seasonality was the most important factor explaining the dietary variation in adult bats. They also found that young bats ate slower, smaller and lighter moths, suggesting that they still need to acquire the skills to capture the same prey items as adults.

In the southwestern Iberian peninsula, Arrizabalaga-Escudero *et al.* (2018: Suppl.) identified the following food items from faecal samples of *R. euryale* (food items marked with an asterisk were also found in faecal samples of *R. mehelyi*): Coleoptera (Cerambycidae: *Arhopalus ferus* (Mulsant, 1839)*); Diptera (Tachinidae: unidentified*: *Phryno vetula* (Meigen, 1824); Muscidae: *Polietes lardarius* (Fabricius, 1781)); Lepidoptera (Crambidae: *Calamotropha paludella* (Hübner, 1824)*; *Metasia ophialis* (Treitschke, 1829); *Ostrinia nubilalis* (Hübner, 1796)*; Erebidae *Catocala nymphaea* (Esper, 1787); *Catocala nymphagoga* (Esper, 1787)*; *Lygephila lusoria* (Linnaeus, 1758); Gelechiidae: *Teleiopsis* sp.*; Geometridae: *Aplasta ononaria* (Füssli, 1783); *Camptogramma bilineata* (Linnaeus, 1758)*; *Ennomos quercaria* (Hübner, 1813)*; *Gymnoscelis rufifasciata* (Haworth, 1809); *Idaea ochrata/rufaria*; *Pachycnemia hippocastanaria* (Hübner, 1799)*; *Rhoptria asperaria* (Hübner, 1817)*; Noctuidae: *Acronicta rumicis* (Linnaeus, 1758); *Agrotis segetum/trux**; *Agrotis ipsilon* (Hufnagel, 1766)*; *Amphipyra tragopoginis* (Clerck, 1759); *Apamea monoglypha/sicula*; *Apamea arabs* Oberthur, 1881; *Autographa gamma/pulchrina**; *Calophasia platyptera* (Esper, [1788])*; *Cosmia trapezina* (Linnaeus, 1758); *Mythimna albipuncta* (Denis & Schiffermüller, 1775)*; *Mythimna loreyi/sicula**; *Peridroma saucia* (Hübner, 1808)*; *Polyphaenis sericata* (Esper, 1787)*; *Sesamia nonagrioides* (Lefèbvre, 1827)*; Nolidae: *Meganola strigula* (Denis & Schiffermüller, 1775); Praydidae: *Prays fraxinella* Bjerkander, 1784*; Pyralidae: *Ephestia mistralella* (Millière, 1874); *Pempelia palumbella* (Denis & Schiffermüller, 1775)*; *Phycita* sp.; Tortricidae: *Cnephasia* sp. 1*; *Cnephasia* sp. 2*); Neuroptera (Chrysopidae: *Chrysoperla* sp.*; *Cunctochrysa albolineata* (Killington, 1935); *Pseudomallada flavifrons* (Brauer, 1851); Myrmeleontidae: *Distoleon tetragrammicus* (Fabricius, 1798)*); Orthoptera (Tettigoniidae: *Tessellana tessellata* (Charpentier 1825)). Of the 62 prey taxa, 32 (representing over 75 % of all food items) were consumed by both bat species.

Andreas *et al.* (2013) using faecal analysis of *R. euryale* from southern Slovakia, showed that this species mainly fed on medium-sized moths (25 - 40 mm) (%f = 60; %vol = 74) and the diet of *R. euryale* contained Neuroptera (Hemerobiidae) (%f = 2.2; %vol = 0.3), nematoceran Diptera (%f = 13.3; %vol = 9.1) and Trichoptera (%f = 6.7; %vol = 3.6). In the same area (and northern Hungaria), Miková *et al.* (2013: 848) investigated the relation between food and ambient temperature during winter.

Ahmim and Moali (2013: 175) examined droppings from northern Algeria, which contained mainly Insecta (96.19%) and Chilopoda (3.81%). Diptera accounted for 29.00 % (Culicidae: 14.29 %, Chironomidae/Ceratopogonidae: 7.14 %, and Tipulidae: 5.71 %. Lepidoptera were the second most important order and accounted for 19.08 %. Andreas *et al.* (2023: 7) suggest that the high proportion of Diptera in the diet of Algerian *R. euryale* indicates that the bats' foraging area was mainly concentrated over or near of some water bodies or in some quite wet patches in relatively dry areas in the transit zone between Mediterranean arboreal habitats and desert landscapes.

Laurent (1944a: 13) tried to (force) feed captive animals with mealworms (*Tenebrio molitor*), but these were rejected.

Gardiner *et al.* (2014: 1058) assessed its foraging strategy as "low altitude slow aerial hawking", with no observations of gleaning.

In Hungary, Maxinová *et al.* (2017a: 98) examined "non-consumptive faeces" (produced during hibernation after no feeding activity) and found these not to contain any insect DNA, but rather bat DNA as well as peptides belonging to other craniates and eukaryotes. They also found bacterial peptides and one Nematode. Furthermore, the high concentration of inorganic material suggest that drinking as well as direct sediment consumption occur inside the cave environment during the hibernation period. They conclude that winter arousals are primarily aimed at regulating the water balance. Maxinová *et al.* (2017b: 93) also found that the bat's digestive enzymes (amylase, chitobiase, endochitinase and glukosaminidase) remained active during the entire hibernation period.

POPULATION:
Structure and Density
According to Hutson *et al.* (2008o) [in IUCN (2009)] supported by Juste and Alcaldé (2016a), *R. euryale* is an infrequent species. Summer colonies number ca. 50 - 1,500 individuals (S. Aulagnier *pers. comm.,* 2007). Winter clusters typically number up to 2,000 animals. It occurs in large vulnerable colonies and is considered threatened in many range states. Large population declines have been reported in several European countries, including Spain (Palomo and Gisbert, 2002). In France, the population declined by ca. 70 % between 1940 and 1980, although subsequently the trend appears to have stabilised (Brosset *et al.*, 1988; S. Aulagnier *pers. comm.,* 2007). Apart from *R. blasii*, which may have gone extinct in the country, *R. euryale* is probably the rarest rhinolophid in Italy, and anecdotal evidence suggests that a number of colonies have declined in the past few decades (D. Russo *pers. comm.,* 2006). The species has a very small and declining population in Portugal (Rodrigues *et al.*, 2003; Cabral *et al.*, 2005). It is stable and common in the central and eastern Balkans (M. Paunovic *pers. comm.,* 2007).
There is little information on population trends outside Europe, although it is suspected that continuing declines have also occurred in at least parts of the non-European range. For example, in Iran the species is no longer found in caves which 30 years ago held 20,000 individuals of different species (M. Sharifi *pers. comm.,* 2005).

Trend
2016: Decreasing (Juste and Alcaldé, 2016a).
2008: Decreasing (Hutson *et al.*, 2008o; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 13 years, and Ibáñez *et al.* (2018: 80) recaptured a male bat in La Rioja (Spain) that was banded 21 years before.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 121) indicate that males need about 27 months to reach sexual maturity, whereas females need between 15 and 27 months.

Szekely *et al.* (2015: Suppl.) mention that both males and females become sexually mature after 821 days (= about 27 months). The gestation period takes 90 days, after which a young is born with a weight of 3.89 g (adult: 8.2 g).

POSTNATAL DEVELOPMENT:
In Iran, Eghbali *et al.* (2017: 276) found that the young's body mass increased linearly until day 23, when it attained 74.29 % of the mean mass of adult females. Its body mass increased (from 3.58 g at birth) by 0.36 g per day and its forearm length increased (from 20.10 mm at birth) by 1.41 mm/day. By day 70, the epiphysal gap was closed. The wing load decreased by 0.09 Nm^{-2}/day until day 36, and subsequently increased again to a maximum of 6.56 ± 0.30 Nm^{-2} by day 80.

PARASITES:
Hirst (1923: 989) mentions that Kolenati described a mite (*Periglischrus interruptus*) from a bat, he originally identified as "*R. clivosus* [= *R. blasii*]", but that he corrected this later to *R. euryale*.

Ševčík *et al.* (2012: 35) report on the presence of the bat flies *Nycteribia schmidlii schmidlii* Schiner, 1853 and *Phthiridium biarticulatum* Hermann, 1804 on bats from Cyprus.

The bat flies *Brachytarsina flavipennis* Macquart, 1851 (Streblidae) and *Phthiridium biarticulatum* Hermann, 1804 (Nycteribiidae) were reported from Jordan by Benda *et al.* (2010b: 238). Benda *et al.* (2010b: 238) also refer to previous reports from Turkey mentioning the following parasites: *Nycteribia pedicularia* Latreille, 1805, *N. schmidlii* Schiner, 1853, *N. kolenatii* Theodor and Moscona, 1954, *N. vexata* Westwood, 1835, *Brachytarsina flavipennis* Macquart, 1851, and *Rhinolophopsylla u. unipectinata* (Taschenberg,

1880) and in Palestine *Penicillidia conspicua* Speiser, 1901 and *P. dufourii* (Westwood, 1835).

From Tunisia, Vermeil (1960: 738) reported the presence of the Nycteribiids *Nycteribia latreillii* Leach, 1817 and *Nycteribia vexata vexata* Westwood, 1835.

Bendjeddou *et al.* (2017: 15) and Khelfaoui *et al.* (2018: 67) reported the following ectoparasites from Algeria: Nycteribiidae: *Nycteribia (Nycteribia) pedicularia* Latreille, 1805, *Penicillidia (Penicillidia) dufourii* Westwood, 1835 and *Phthiridium biarticulatum* Hermann, 1804; Streblidae: *Brachytarsina flavipennis* Macquart, 1851; Siphonaptera: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes vespertilionis* Koch, 1844.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes vespertilionis* Koch, 1844; Nycteribiidae: *Nycteribia pedicularia* Latreille, 1805, *Nycteribia vexata* Westwood, 1835, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Eyndhovenia euryalis oudemansi* (Eyndhoven, 1941); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851.

From non-specified areas, Haelewaters *et al.* (2018: 974) reported the Nycteribiid *Penicilidia conspicua* Speiser, 1901, which might be a host for the fungus *Arthrorhynchus nycteribiae* (Peyr.) Thaxt (see also de Groot *et al.*, 2020: Suppl.). Other nycteribiid flies reported by Júnior *et al.* (2020: Suppl.) include: *Basilia italica* Theodor, 1954, *Basilia nana* Theodor, 1954, *Basilia nattereri* (Kolenati, 1857), *Nycteribia kolenati* Theodor and Moscona, 1954, *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* (Latreille, 1805), *Nycteribia vexata* Westwood, 1835, *Penicillidia conspicua* Speiser, 1901, *Phthiridium biarticulatum* Hermann, 1804.

Maliničová *et al.* (2017: 211) investigated the gut microflora of Hungarian *R. euryale* during hibernation and found that the number of enterobacteria and enterococci decreased during hibernation and were restored at the end of hibernation.

VIRUSES:

Adenoviridae

Mastadenovirus

This virus was mentioned by Nieto-Rabiela *et al.* (2019: Suppl.).

Coronaviridae - Coronaviruses

Luis *et al.* (2013: suppl.) mention the presence of a SARS coronavirus-related virus.

Alphacoronavirus

Reported from Germany by Kohl and Kurth (2014: 3112).

Ar Gouilh *et al.* (2018: 90) reported the EPI 10 virus from an *R. euryale* from Morocco.

Betacoronavirus

Reported from Bulgaria and Germany by Kohl and Kurth (2014: 3112).

Orthomyxoviridae

Despite sampling and testing of 2 individuals of this species, no evidence of influenza A-like viruses (Orthomyxoviridae) were obtained (Fereidouni *et al.*, 2015).

Picornaviridae

The presence of Picornavirus was mentioned by Nieto-Rabiela *et al.* (2019: Suppl.).

Rhabdoviridae

Lyssavirus

Serra-Cobo *et al.* (2018: 2) found one out of 31 Algerian bats testing seropositive for European bat lyssavirus1 and none of the twelve Moroccan bats.

Vesiculovirus

Luo *et al.* (2025: 9) found 2 out of 41 bats from Morocoo and Algeria testing positive for a new virus species: *Vesiculovirus mediterranean*.

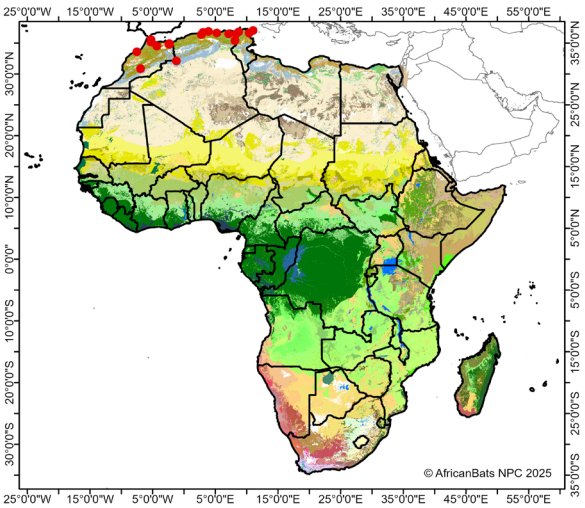

Figure 99. Distribution of *Rhinolophus euryale*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Egypt, France, Morocco, Tunisia.

Rhinolophus ferrumequinum (Schreber, 1774)

*1774. *Vespertilio ferrum-equinum* Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, 1 (8): pl 62, upper fig + 1 (9): 174. Publication date: 1774. Type locality: France: "France". - Etymology: From the Latin "*ferrum*" meaning iron and "*equus*" meaning horse.
1792. *Vespertilio ferrum-equinum major* Kerr, Animal Kingdom, 1 (1): xvii, 99. Type locality: France. - Comments: This might be an African form, but we lack further information.
1803. *major* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, ???. - Comments: This might be an African form, but we lack further information.
1961. *Rhinolophus ferrumequinum millali:* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, 155: ?. Type locality: Morocco. - Comments: This is a fossil form from the Miocene-Pliocene. (Name Combination).
1986. *Rhino!ophus ferrumeginum:* Castiblanco de V., Jaramillo and Muñoz, Actual Biol., 15 (56): 27. Publication date: April-June 1986. (Lapsus).
2018. *Rh[inolophus] ferrimequinum:* Khelfaoui, Kebaci and Benyacoub, Bull. Soc. zool. France, 143 (2): 67. (Lapsus).
? *Rhinolophus ferrumequinum 1:* (Name Combination).
? *Rhinolophus ferrumequinum ferrumequinum:* (Name Combination).
? *Rhinolophus ferrumequinum:* (Name Combination, Current Combination).

TAXONOMY:
Taxonomic revisions by Felten *et al.* (1977), Strelkov *et al.* (1978), Kryštufek (1993) and Thomas (1997). Thomas (1997) recognized seven subspecies based on morphological characters (*R. f. ferrumequinum* in Europe and northwest Africa, *R. f. creticum* in Crete, *R. f. irani* in Iran, Iraq and Turkmenistan, *R. f. proximus* from Afghanistan and Pakistan to India, *R. f. tragatus* in north India and China, *R. f. korai* in Korea and *R. f. nippon* in Japan). *ferrumequinum* species group (Csorba *et al.*, 2003: 42 - 45; Simmons, 2005: 355). See Csorba *et al.*, 2003: 44 - 45) for further remarks on the taxonomy.

Based on cytochrome *b* analyses, Koh *et al.* (2014: 97) indicate that northern African populations form one clade with specimens from Europe and western Asia, which is different from three other clades: far-eastern Asia, eastern China and central China.

COMMON NAMES:
Albanian: Lakuriq nate hundëpatkua i madh. Arabian: Khafash abu hadwa kabir, Khaffash. Armenian: Մեծ պայտաքիթ. Azerbaijani: Böyük nalburun. Basque: Ferra-saguzar handi. Belarusian: Падкаванос вялікі. Bosnian: Veliki potkovasti šišmiš. Breton: Frigribell vras. Bulgarian: Голям подковонос. Castilian (Spain): Murciélago grande de herradura, Rinolofo grande de herradura. Catalan (Spain): Rat penat gran de ferradura, Ratapinyada gran de ferradura, Ratpenat de ferradura gran. Croatian: Veliki potkovnjak, Veliki potkovasti šišmiš. Czech: Vrápenec velký, wrápenec podkowní, podkováček, podkováček, obecný, vrápenec podkovní, vrápenec podkovníček, vrápenec veliký, veliký vrápenec podkovní, vrápeník podkovní, vrápenec podkrovní. Danish: Stor hestekonæse. Dutch: Grote hoefijzerneus. English: Larger Horseshoe Bat, Greater Horseshoe Bat. Estonian: Suur-sagarnina. Finnish: Euroopanisoherkko. French: le grand rhinolophe fer à cheval, Grand rhinolophe, Grand Fer-à-Cheval. Frisian: Grutte hoefizernoas. Galician (Spain): Morcego de ferradura grande. Georgian: დიდი ცხვირნალა. German: Große Hufeisennase, Großhufeisennase, Hufeisennase. Greek: Τρανορινόλοφος. Hebrew: פרסף גדול, parsaf gadol. Hungarian: Nagy patkósdenevér nagy patkósorrú denevér, Rhinolophos i megali. Irish Gaelic: Crú-ialtóg mhór. Italian: Rinolofo maggiore, Ferro di Cavallo Maggiore. Latvian: Lielais pakavdegunis. Lithuanian: Didysis pasagnosis. Luxembourgish: Grouss Huffeisennues. Macedonian: Голем потковичар [= Golem Potkovichar]. Maltese: Rinolofu Kbir, Farfett il-Lejl tan-Nala kbir. Montenegrin: Veliki potkovičar. Nepali: Thulo Ghodnale Chamero. Norwegian: Storhesteskonese, Stor hesteskonese. Polish: Podkowiec duŻy. Portuguese: Morcego-de-ferradura-grande. Rhaeto-Romance: Rinolof grond, Nas fier-chaval grond. Romanian: Liliacul mare cu potcoavă, Liliac-mare-cupotcoavã. Russian: Подковонос большой, Болъшой подковонос [= Bolshoj podkovonos]. Serbian: Велики потковичар [= Veliki potkovičar]. Scottish Gaelic: Crudh-ialtag mhòr. Slovak: Podkovár veľký. Slovenian: Veliki podkovnjak, mali podkovnjak. Swedish: Större hästskonäsa. Turkish: Büyük Nalburunlu Yarasa. Ukrainian: Підковик (Підковоніс) великий [= Pidkovyk velykyy]. Welsh: Ystlum pedol mwyaf.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Lavocat (1961) described a new subspecies found in deposits of the Mio-Pliocene, at Beni Mellal. See Butler (1978).

CONSERVATION STATUS:
Global Justification
This species has a large range. Although there have been marked and well-documented declines in some areas, the species remains widespread, abundant, and apparently stable in other areas. Assessed as Least Concern (LC ver 3.1 (2001))

(Aulagnier *et al.*, 2008a; IUCN, 2009; Piraccini, 2016b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Piraccini, 2016b). 2008: LC ver 3.1 (2001) (Aulagnier *et al.*, 2008a; IUCN, 2009). 2000: LR/nt. 1996: LR/nt ver 2.3 (1994).

Regional
None known.

MAJOR THREATS:
Piraccini (2016b) supports Aulagnier *et al.* (2008a) [in IUCN (2009)] who reported the main threats are fragmentation and isolation of habitats, change of management regime of deciduous forests and agricultural areas, loss of insects due to pesticide use, and disturbance and loss of underground habitats and attics. In northwest Europe, habitat change is likely to have been amongst the major causes of declines, the conversion of woodland and small-field landscape to large-scale agricultural land being particularly damaging. While declines elsewhere, particularly in eastern Europe, may currently not be so marked, the loss of cultural landscapes in those countries as they move towards western-style economies may have significant effects in the near future. The use of pesticides has been a recognized threat to the insect food, particularly where these have been directed against the larvae of favoured food items, such as melolonthid beetles, larvae of noctuid moths or crane-flies. Favoured prey may be affected secondarily by pesticide use, such as the loss of dung fauna from the use of persistent anti-parasitic drugs (avermectins) on cattle. Populations in caves and other underground habitats have suffered from increased disturbance (for example by tourist visits to caves). In buildings, colonies may be affected by human intolerance, renovation work or the application of pesticides, such as some of those used for the remedial treatment of timbers (Hutson *et al.*, 2001). In South Asia, this species is threatened by deforestation, generally resulting from logging operations and the conversion of land for agricultural and other uses. Disturbance to roosting sites is likely to be a potential threat to the populations of this species (Molur *et al.*, 2002).

Concerning climatic change, the most important risk factors identified by Sherwin *et al.* (2012: 174), are water stress, aerial hawking and long-distance dispersal.

CONSERVATION ACTIONS:
Piraccini (2016b) supports Aulagnier *et al.* (2008a) [in IUCN (2009)] who reported *Rhinolophus ferrumequinum* has been the subject of widespread conservation activity, especially in Europe. Until recently, this has concentrated on roosts in buildings and caves. Many buildings used as roosts have management agreements and many underground sites have been protected. Nevertheless, sites continue to be lost or damaged. More recently, attention has turned to identifying more precisely the food and foraging requirements. A European meeting (Germany, May 1995) discussed the status and conservation needs for the species on a pan-European scale. The Bern Convention has commissioned a Europe-wide Species Action Plan under the Pan-European Biological and Landscape Diversity Strategy (Ransome and Hutson, 2000). It is protected by national legislation in some range states. There are international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in parts of its range where these apply. It is included in Annex II (and IV) of the European Union Habitats Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. There is some habitat protection through Natura 2000 (some roosts are already protected by national legislation).

Flanders and Jones (2009: 894) point out that, in the U.K., management of broad-leaved woodland areas in close proximity (within 4 km) of transitional roosts (used in spring and autumn) should be enhanced.

There are no specific conservation measures in place for the species in North Africa or South Asia. Populations should be monitored to record changes in abundance and distribution (Molur *et al.*, 2002).

GENERAL DISTRIBUTION:
Rhinolophus ferrumequinum has a wide range in the Palaearctic, occurirng from North Africa (north of 32° N - Ransome (2023: 840)) and southern Europe through south-west Asia, the Caucasus, Iran, Afghanistan, Pakistan and the Himalayas to south-eastern China, Korea, and Japan (Csorba *et al.*, 2003; Abe *et al.*, 2005). It usually occurs below 800 m asl but can be found up to 3,000 m asl in the Caucasus depending on roost availability and humidity (K. Tsytsulina *pers. comm.,* 2005).

Native: Abkhasia; Afghanistan; Albania; Algeria; Andorra; Armenia; Austria; Azerbaijan; Bangladesh; Bhutan; Bosnia and Herzegovina;

Bulgaria; China; Croatia; Cyprus; Czech Republic; France (Corse); Georgia; Germany; Gibraltar; Greece (Kriti); Hungary; India; Iran, Islamic Republic of; Iraq; Israel; Italy (Sardinia, Sicilia); Japan; Jordan; Kazakhstan; Korea, Democratic People's Republic of; Korea, Republic of; Kyrgyzstan; Lebanon; Liechtenstein; Luxembourg; Macedonia, the former Yugoslav Republic of; Moldova; Monaco; Montenegro; Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 358; Dbiba *et al.*, 2025: 6); Nepal; Pakistan; Palestinian Territory, Occupied; Poland; Portugal; Romania; Russian Federation; San Marino; Saudi Arabia; Serbia; Slovakia; Slovenia; Spain (Baleares); Switzerland; Syrian Arab Republic; Tajikistan; Tunisia (Dalhoumi *et al.*, 2014: 53, 2016b: "3"; 2019b: 26); Turkey; Turkmenistan; Ukraine; United Kingdom; Uzbekistan.
Possibly extinct: Malta.
Regionally extinct: Belgium; Netherlands.

BIOGEOGRAPHY:
See Rossiter *et al.* (2007).

GEOGRAPHIC VARIATION:
Benda *et al.* (2014c: 16) mention that the Libyan *R. ferrumequinum* specimens are very small in size, and even the smallest within the Mediterranean range of this species, which led to their confusion with *R. clivosus*.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Lucati and López-Baucells (2016: Suppl.) and Zortéa and Silva (2017: 80)refers to an albino specimen that was reported from "South Africa?" by Allen (1939b).

DETAILED MORPHOLOGY:
Baculum
See Csorba *et al.* (2003: 43).

Other
Forman (1973) [in Scillitani *et al.* (2005: 302)] regards the stomach of this bat as primitive for the order and probably represents the ancestral condition of lower Eutheria, because it presents a number of features in common with Insectivora.

R. ferrumequinum is one of the few bat species, where the females can have a baubellum (*os clitoris*) (Lough-Stevens *et al.* (2017: 1078).

FUNCTIONAL MORPHOLOGY:
Kobayashi (2018: 69) found that the bat's *M. quadriceps femoris* has a short muscle belly attached to the proximal portion of the femur and that the insertional tendon of this muscle and its patellar ligament are very thin. These features indicate that *R. ferrumequinum* cannot exert a strong and long-distance extension of its knee joints, which results in the inability to crawl.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.2 Pa, aspect ratio 6.1 and tip shape index of 2.13 for a wingspan of 33 cm and a wing area of 182 cm^2 and a body mass of 23 g.

In their study - covering the entire distribution range of *R. ferrumequinum* - Jiang *et al.* (2019: 1) found that populations with long forearms in both sexes occurred in areas with higher mean temperatures in the warmest quarter and lower mean temperatures in the coldest quarter.

ECHOLOCATION:
Fukui *et al.* (2011: 1548) report that, in Japan, the detection range for *Rhinolophus ferrumequinum* calls is less than 5 metres.
Jones and Siemers (2010: 450) indicate that juveniles emit lower frequencies than adults, and Jones and Ransome (1993: 125) found that the young's resting constant-frequency (RF) values are at least partially determined by their mother's RF. Jones and Ransome (1993: 125) furthermore report that calls of *R. ferrumequinum* specimens aged between 1 and 28 years vary seasonally and over a lifetime in a predictable manner.
Barclay and Jacobs (2022: 138) [referring to Jones and Ransome (1993)] mention that calls change over the entire lifetime of individuals, initially increasing and then decreasing in the CF frequency.

For 28 Greek specimens, Papadatou *et al.* (2008b: 132) report a start frequency of 66.5 ± 3.23 kHz, a terminating frequency of 64.9 ± 4.33 kHz, and a bandwidth of 3.9 ± 1.34 kHz. The duration of the call is 53.8 ± 10.50 ms, and the interpulse interval is 92.1 ± 24.94 ms.
Andrews *et al.* (2006: 199) analysed 500 echolocation calls from UK bats, and found an average frequency of 83.8 ± 0.4 kHz and 21.0 ± 6.4 ms duration. Another set of 500 calls had an average frequency of 84.0 ± 0.5 kHz and a duration of 31.9 ± 9.5 ms. Social calls were emitted at frequencies between 15 and 29 kHz and their duration was between 4 and 49 ms (p. 201).
Walters *et al.* (2012: suppl.) report the following figures for 30 calls from bats from France, Switzerland and the UK: duration: 50.08 ± 13.52 ms, F_{max}: 81.66 ± 1.68 kHz, F_{min}: 70.29 ± 3.62 kHz, bandwidth: 11.37 ± 3.19 kHz, F_{peak}: 81.46 ± 1.65 kHz.

Dalhoumi *et al.* (2016b: 866) reported a long constant frequency part between 85 and 88 kHz

for Tunisian animals. For Morocco, Disca *et al.* (2014: 226) indicate that the type of call is FM-FC-FM, with F_{peak}: 84.6 ± 0.8 kHz and duration: 30.3 ± 7.6 ms. Ait-Abdesselam *et al.* (2025: 40) reported a peak frequency between 84.4 and 87.8 kHz for Aigerian bats.

Luo *et al.* (2019a: Supp.) reported the following data (for two calls): F_{peak}: 82.3, 78.7 kHz, F_{start}: 69.3, 66.5 kHz, F_{end}: 70.3, 64.9 kHz, and duration: 49.4, 53.8 ms.

From experiments in a flight tunnel, Koselj and Siemers (2013: 81) found that *R. ferrumequinum* bats can extract information from echolocation calls produced by conspecifics. This could facilitate sensory cooperation among echolocating bats.

In China, Sun *et al.* (2013: 1) found regional differences in the resting frequency of echolocation calls of *R. ferrumequinum* which were significantly correlated with geographic distance and mean annual temperature.

Besides the ultrasound calls used in echolocation, Andrews and Andrews (2003: 221) also report on twelve types of ultrasound social calls, which were in the range of 20 to 29 kHz and had a duration of 1 to 49 ms. Furthermore, there were also low frequency (audible) social calls (1 - 10 kHz).

Molecular Biology:

Karyotype

Makino (1948), Capanna and Civitelli (1964a: 363), Rushton (1970: 463), Baker *et al.* (1974; 1975) and Qumsiyeh *et al.* (1986) all reported 2*n* = 58, FN = 60, a submetacentric X chromosome, and an acrocentric Y chromosome. Volleth and Eick (2012: 167) reported 2*n* = 58 and 28 as segment number. In Turkey, Arslan and Zima (2014: 7) found 2*n* = 58, FNa = 60-62, FN = 64-66, a metacentric X and an acro-/metacentric Y. The autosomal chromosomes consist of two medium-sized bi-armed pairs and 26 acrocentric pairs, but they indicate that one of the acrocentric pairs is considered by some other authors to be bi-armed, leading to the different FN and FNa values. Capanna and Civitelli (1964a: 371) mention 24 pairs of acrocentric chromosomes, 2 metacentric pairs, and 2 pairs of very small chromosomes; the X chromosome was reported as a large submetacentric and the Y as a very small one.

Genetics

See Rossiter *et al.* (2007).

Other

Tournayre *et al.* (2019: 12285-12286) found high genetic differentiation between bats from western France and the Basque country on the one hand and bats from Tunisia on the other hand. This might indicate that *R. ferrumequinum* was already present in northern Africa before the Late Glacial Maximum (LGM) and that no re-colonisation from Europe occurred post-LGM. However, further investigation is necessary, especially into the potential pathways (e.g., the Strait of Gibraltar).

Habitat:

In the U.K., Flanders and Jones (2009: 891) reported that on an overall area of about 632 ha used by a colony of *R. ferrumequinum* specimens, 28.7 % consisted of pasture, 26.6 % of broad-leaved woodland, 16.1 % of arable, 8.2 % of mixed woodland, 6.7 % urban, 5.8 % scrub, 4.3% grassland, 1.6 % heathland, 1.4 % water, and 0.7 % coniferous woodland. They also reported the following habitat preferences (high to low): pasture, broad-leaved woodland, mixed woodland, water, scrub, grassland, urban, coniferous woodland, heathland, and arable. Fukui *et al.* (2011: 1551) indicate that, in Japan, this species prefers natural forest gaps over artificially made gaps as in the latter debris is generally removed, leaving no tree branches for it to hang from while scanning for prey.

Habits:

Park *et al.* (2000) [in Sherwin *et al.* (2012: 172)] found that *R. ferrumequinum* was longer active when the temperatures were higher than 10 °C, which they considered to be a thermal threshold for insect activity.

Diet:

Flanders and Jones (2009: 892) examined 1,580 bat droppings in the U.K. and found that Lepidoptera (moths) were the most abundant prey. In spring, *Melolontha melolontha* (May bugs), beetles of the genus *Geotrupes* (dor beetles), Trichoptera (caddis flies), Tipulidae (crane flies), Ichneumonidae (ichneumonid wasps), and Lepidoptera were contributing to the diet. In autumn, the two beetle species were replaced by representatives of the genus *Aphodius* (dung beetles), and additional to the other groups of insects, Diptera (mainly dung flies) were also part of the main prey types.

Andreas *et al.* (2013) using faecal analysis of *R. euryale* from southern Slovakia, showed that this species fed mainly on large moths (>40mm) (%f = 54; %vol = 89) and comprised also Coleoptera (%f = 19.5; %vol = 4.82), represented by Scarabaeidae, Elateridae and Curculionoidea.

In northern Spain, Aldasoro *et al.* (2019: 9) found the following prey groups (in descending order of occurrence): Diptera, Lepidoptera, Coleoptera, Neuroptera, Hemiptera and Trichoptera.

In northern Algeria, Ahmim and Moali (2013: "2") found that *R. ferrumequinum* fed on three groups of arthropods: Insecta (95.31 % [Diptera: 34.56 % and Lepidoptera: 24.13 %]), Chilopoda (4.49 %) and Araneida (0.20 %). The largest groups within the Diptera were Culicidae (10.40 %), Chironomidae/Ceratopogonidae (10.94 %) and Tipulidae (4.28 %).

In Libya, Benda *et al.* (2014c: 19) examined faecal pellets and found one set to contain 84 % by volume larger moths, 9 % ants and 7 % beetles, whereas a second set contained only Lepidoptera with wingspans of ca. 40 mm.

POPULATION:
Structure and Density
Rhinolophus ferrumequinum is an infrequent species in most parts of its range, although in at least parts of southwest Asia and the Caucasus it is abundant and widespread (it is the most frequently reported species in Turkey: A. Karataş *pers. comm.,* 2005), with populations in Iran and Turkey considered to be stable (A. Karataş, M. Sharifi and K. Tsytsulina *pers. comm.,* 2005), although it may be decreasing in Russian parts of the Caucasus (S. Kruskop *pers. comm.,* 2005). Summer colonies of c. 30 - 200 individuals (up to 400 animals), and winter clusters of up to 500 animals are typical.
In Europe, the two most widespread *Rhinolophus* species, *R. ferrumequinum* and *R. hipposideros*, are of particular conservation concern and are the subject of considerable research and monitoring. *R. ferrumequinum* has shown marked declines in range in northwest Europe within the last 100 years (e.g., United Kingdom, Germany, Austria), and has gone extinct in some countries (e.g., Belgium, Netherlands). However, there are signs of stabilisation and/or recovery in some northwest European countries (Hutson *et al.*, 2001). For example, in the UK the species declined massively in the past, but it is now stable at a low population level (around 5,000 individuals) (Ransome and Hutson, 2000). However, in Austria declines continue, with population reductions of 70 % in the last 10 years (from 100 to 30 breeding individuals: Spitzenberger (2002); F. Spitzenberger *pers. comm.,* 2006). In other parts of Europe, trends vary and are generally less well known: in Malta the species has gone extinct, in Portugal and Spain the trend is not known (although some colonies have disappeared in Spain) (Palomo and Gisbert, 2002; Cabral *et al.*, 2005), in Croatia the population is thought to be stable (N. Tvrtkovic *pers. comm.*), and in Romania the population has been slowly increasing since 1989 due to reduced use of pesticides and a return to traditional agriculture with colonies of up to 800 individuals. In Switzerland the species is very rare (3 maternity roosts with some 200 individuals), but the population trend appears stable (H. Kraettli *pers. comm.*, 2006). In its north African and south Asian range the population size and trends are unknown (Aulagnier *et al.*, 2008a; IUCN, 2009; Piraccini, 2016b).

Trend
2016: Decreasing (Piraccini, 2016b). 2008: Decreasing (Aulagnier *et al.*, 2008a; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 30.5 years.

ACTIVITY AND BEHAVIOUR:
In the U.K., Flanders and Jones (2009: 891) reported a maximum nightly foraging range of between 2.17 and 2.44 km, and the foraging area averaged 148.1 ha. Fukui *et al.* (2011: 1551) [referring to Jones and Rayner (1989)] indicate that *R. ferrumequinum* is a "flycatcher" species, meaning that it hangs from tree branches while scanning for its prey.

Smotherman *et al.* (2016: 537) refer to Ma *et al.* (2006) in describing the song-like structure for this species as consisting of different syllable types in series.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 121) mention that males attain sexual maturity between 15 and 51 months, whereas this for females is between 15 and 39 months. Szekely *et al.* (2015: Suppl.) report 730 days (about 24 months) for both sexes.

Gharaibeh (1997: 55) mentions lactating females and juveniles from the cave at Djebel Oust (Tunisia) on 29 July 1996. Benda *et al.* (2014c: 16) collected a pregnant female on 28 May at Nanatalah (Libya).

Kurta and Kunz (1987: 82) report that, at birth, the young weights about 29.3 % of the mother's body mass (5.8 versus 19.8 g), and that its forearm length is about 36.0 % of the mother's length (25.3 versus 70.3 mm).

The gestation period takes 80 days (with the young having a birth weight of 5.8 g - 25.4 % of

the adult), and weaning occurs after 60 days (Szekely *et al.*, 2015: Suppl.).

MATING:
Fenton (1984) [in Keeley and Keeley (2004: 117)] reports the existence of copulatory plugs. For *R. ferrumequinum*, these plugs are formed from male secretions, and probably serve to prevent further insemination by other males, rather than preventing sperm leakage from the female's reproductive trace (in that case the plugs would probably be made by the females). However, Rossiter *et al.* (2000b) mention that these plugs can be ejected by the females, which would allow additional matings.

Webber *et al.* (2017: Suppl.) indicated that the mating system was polygynandrous, but in Britain, Rossiter *et al.* (2000a: 545) found that mating was polygynous, but six females gave birth to young fathered by the same male in different years. This seems to indicate fidelity for either mating sites or individuals or from sperm competition. Females start visiting males for mating in autumn, so breeding partnerships are primarily determined by the female. Mating occurs in territory sites occupied by single males, which can be born both within and outside the female's own natal colony. Relatedness between parents, however, was no less than the average recorded for male/female pairs. Gene flow between colonies is likely to be primarily mediated by both female and male dispersal during the mating period rather than more permanent movements.

Liu *et al.* (2013a: 2179) describe the vocal communications during mating in China. They suggest these calls can serve as an indicator for the female bats to recognize the mating male in order to maintain mate fidelity as greater horseshoe bats are sexually segregated before mating.

PARASITES:
Seurat (1930: 488) and Beaucournu and Kock (1996) mentioned *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921 on bats from Algeria (although the prior used the genusname *Rhinopsylla*).

Aellen (1955b) reported the following nycteribid flies on bats from Morocco and Algeria: *Nycteribia (Nycteribia) schmidli* Schiner, 1853, *Nycteribia (Stylidia) biarticulata* Hermann, 1804, and *Penicillidia dufouri* (Westwood, 1835).

Other ectoparasites reported from Algeria by Bendjoudi *et al.* (2019: 71) and Khelfaoui *et al.* (2018: 67) include: Ixodidae: *Ixodes vespertilionis* Koch, 1844; Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856); Ischnopsyllidae: *Araeopsylla gestroi* (Rothschild, 1906); Streblidae: i Brachytarsina flavipennis Masquart, 1851; Nycteriibidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia schmidlii* Schiner, 1853, *Nycteribia pedicularia* Latreille, 1805, *Penicilidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* Hermann, 1804.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Ischnopsyllus octactenus* (Kolenati, 1856), *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes vespertilionis* Koch, 1844; Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Eyndhovenia euryalis euryalis* (Canestrini, 1884); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851;

In Europe Genov *et al.* (1992) reported the presence of the following Nematodes: *Molinostrongylus skrjabini* Skarbilovitch, 1934 and *M. alatus* (Ortlepp, 1932).

DIPTERA
Ševčík *et al.* (2012: 35) report on the presence of the bat flies *Phthiridium biarticulatum* Hermann, 1804, *Phthiridium biarticulatum* Hermann, 1804, and *Brachytarsina flavipennis* Macquart, 1851 on bats from Crete and Cyprus. *Phthiridium biarticulatum* was also reported on *R. ferrumequinum* from Jordan by Benda *et al.* (2010b: 226), and from Algeria by Bendjeddou *et al.* (2013: 325). The latter authors also found *Brachytarsina flavipennis* Masquart, 1851 and *Penicillidia dufouri* (Westwood, 1825) (Diptera: Nycteribiidae). Bendjeddou *et al.* (2017: 15) added two additional Nycteribiidae: *Nycteribia (Listropoda) schmidlii schmidlii* Schiner, 1853 and *Phthiridium biarticulatum* Hermann, 1804 and one Siphonaptera: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921.

Haelewaters *et al.* (2018: 794) also reported *Penicillidia conspicua* Speiser, 1901 and *P. fulvida*, Bigot, 1885, *Phthiridium biarticulatum* Hermann, 1804, which all might be hosts for the fungus *Arthrorhynchus nycteribiae*.

Nycteribiidae
Nycteribia kolenati Theodor & Moscona, 1954 was reported by Haelewaters *et al.* (2017: 1) from *R. ferrumequinum* from Hungary. Vermeil (1960) reported two bat flies from Tunisian *R.*

ferrumequinum: *Nycteribia biarticulata* Hermann, 1804 and *Nycteribosca kollari* Frauenfeld, 1855.

Other nycteribiid flies reported by Júnior *et al.* (2020: Suppl.) (not specifically from Africa) include: *Basilia italica* Theodor, 1954, *Basilia nana* Theodor, 1954, *Basilia nattereri* (Kolenati, 1857), *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* (Latreille, 1805), *Nycteribia vexata* Westwood, 1835, *Phthiridium biarticulatum* Hermann, 1804.

ACARI

Trombiculidae

Stekolnikov (2018a: 186) mentioned *Sasatrombicula cherrata* (Taufflieb, 1960) from Oued Cherrat (Morocco).

VIRUSES:

In Italy, Balboni *et al.* (2010: 216) reported two *R. ferrumequinum* specimens, which tested positive for a fragment of RNA-dependent RNA polymerase (RdRp) gene of viruses related to *Coronavirus*. Phylogenetic analysis showed a close correlation between one of these and SARS-related CoV belonging to the genus *Betacoronavirus* (see also de Jong *et al.*, 2011: 10).

Nieto-Rabiela *et al.* (2019: Siuppl.) mentioned the following list of viruses: Adeno associated virus, Astrovirus, Banna virus isolate, Bat calicivirus, Bat circovirus, Bat coronavirus, Bat gammaretrovirus, Bat hepevirus, Bat herpesvirus, Bat mastadenovirus, Bat paramyxovirus, Bat parvovirus, Bat polyomavirus, Bat rhabdovirus, Betacoronavirus, European bat lyssavirus, Hantavirus, Issyk Kul virus, Picornavirus, Puumala virus, *Rhinolophus ferrumequinum* herpesvirus 1, *Rhinolophus ferrumequinum* papillomavirus, *Rhinolophus ferrumequinum* paramyxovirus, Roseolovirus, SARS.

Adenoviridae

Mastadenovirus

Kohl and Kurth (2014: 3111) report this virus from Hungary.

Astroviridae

Luis *et al.* (2013: suppl.) report on the presence of an unassigned astrovirus.

Bunyaviridae

Hantavirus

de Jong *et al.* (2011: 9), Luis *et al.* (2013: suppl.) report Hantaan virus occurring on this species, as well as an unassigned Issyk-kul virus (Keterah virus).

Coronaviridae - Coronaviruses

Luis *et al.* (2013: suppl.) mentions the presence of Coronavirus BatCoV BB98-15 and SARS coronavirus.

Alphacoronavirus

Kohl and Kurth (2014: 3112) report this virus to be present in German bats.

Betacoronavirus

This virus was reported from bats from Germany and Bulgaria by Kohl and Kurth (2014: 3112).

Flaviviridae

Flavivirus

Japanese encephalitis virus was reported by Luis *et al.* (2013: suppl.).

Orthomyxoviridae

Despite sampling and testing of 2 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

Papillomaviridae

Papillomavirus

This virus was reported from Spanish bats by Kohl and Kurth (2014: 3113).

Rhabdoviridae

Lyssavirus - Rabies related viruses

de Jong *et al.* (2011: 9) report the presence of European bat lyssavirus 2. Serra-Cobo *et al.* (2018: 2) found one seropositive bat among the 47 tested for European bat lyssavirus 1 in Algeria and eight out of 67 tested in Morocco.

"Various European bat lyssaviruses" were reported by Kohl and Kurth (2014: 3114) from various European countries.

Vesiculovirus

Luo *et al.* (2025: 9) found 15 out of 126 bats from Morocco and Algeria testing positive for a new virus species: *Vesiculovirus mediterranean*..

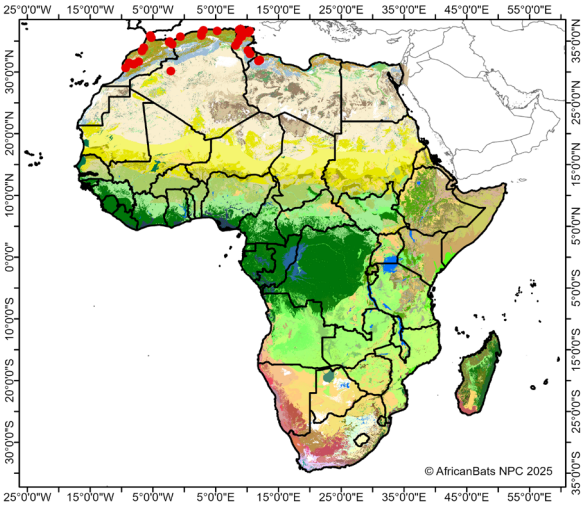

Figure 100. Distribution of *Rhinolophus ferrumequinum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Algeria, Libya, Morocco, Tunisia.

Rhinolophus fumigatus Rüppell, 1842

*1842. *Rhinolophus fumigatus* Rüppell, Mus. Senckenberg., 3 (2): 132. Type locality: Ethiopia: Shoa province: Shoa province [ca. 09 00 N 39 00 E]. [Goto Description]. Lectotype: SMF 4372: ad, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1841. Presented/Donated by: Wilhem Peter Edward Simon Rüppell. See Andersen (1904c: 451). Mertens (1925: 20). Turni and Kock (2008) mention this specimen (old catalog SMF II.F.7.a) as Lectotype. Cotype: SMF II.F.7b:; collection date: 1841. Presented/Donated by: Wilhem Peter Edward Simon Rüppell. See Andersen (1904c: 451). - Etymology: From the passive Latin perfect participle *fumigàtus* meaning "smoked", referring to the fur colour of the species (see Lanza *et al.*, 2015: 96). (Current Combination).

1869. *Rhinolophus æthiops* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 637 (for 1868). Type locality: Namibia: Damaraland: Otjimbingue [22 15 S 16 10 E]. Syntype: ZMB 3295: ♂, skull and alcoholic. Collected by: Missionary Hahn. See Turni and Kock (2008). Syntype: ZMB 50073: ♀, alcoholic (skull not removed). Collected by: Missionary Hahn. Formerly second specimen with number ZMB 3295; see Turni and Kock (2008: 30). - Comments: Turni and Kock (2008: 30) referring to Csorba *et al.* (2003: 50) mention that ZMB 3295 might possibly represent a species distinct from *fumigatus*.

1877. *Rhinolophus macrocephalus* Heuglin, Reise in Nordost Afrika, 2: 22. Publication date: 1877. Type locality: Ethiopia: Tigre province: As(s)am river: Adowa [14 10 N 38 54 E, 1 900 m]. Syntype: SMNS 1059: imm ♀, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. See Andersen (1904c: 451), Dieterlen *et al.* (2013: 294). Syntype: SMNS 1059a: imm ♀. Collected by: Martin Theodor von Heuglin. Syntype: SMNS 1059b: ad ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1862. See Andersen (1904c: 451), Dieterlen *et al.* (2013 294).

1885. *Rhinolophus antinorii* Dobson, Ann. Mus. civ. Stor. nat. Genova, (2) 2: 16. Publication date: 22 May 1885. Type locality: Ethiopia: Shoa province: Daimbi.

1905. *Rhinolophus fumigatus exsul* K. Andersen, Ann. Mag. nat. Hist., ser 7, 15 (85): 74. Publication date: 1 January 1905. Type locality: Kenya: Kitui [01 22 S 38 01 E, 3 500 ft]. [Goto Description]. Holotype: NHMUK 1901.5.6.3: ad, skin only. Collected by: Mrs. Hildegarde Beatrice Hinde; collection date: 3 January 1901; original number: 68. See Andersen (1905a: 74). - Comments: Considered a valid subspecies by Ansell and Dowsett (1988: 32).

1913. *Rhinolophus foxi* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 314. Publication date: 1 March 1913. Type locality: Nigeria: Northern Nigeria, Bauchi plateau: Kabwir [09 24 N 09 34 E, 2 500 ft]. [Goto Description]. Holotype: NHMUK 1913.2.5.1: ad ♂. Collected by: Mr. J.C. Fox and The Cambridge University Mission; collection date: 14 November 1912; original number: 45. Presented/Donated by: Mr. J.C. Fox.

1914. *Rhinolophus acrotis:* G.M. Allen, Bull. Mus. comp. Zool., 58 (7): 346. - Comments: Preoccupied by *acrotis* Heuglin, 1861.

1917. *Rhinolophus abæ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 428. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 49113: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 15 December 1911; original number: 1756.

1939. *Rhinolophus aethiops diversus* Sanborn, Field Mus. Nat. Hist., Zool. Ser., 24 (5): 42. Publication date: 19 September 1939. Type locality: Senegal: Bakel [14 54 N 12 26 W]. [Goto Description]. Holotype: NHMUK 1919.7.7.2774: ad ♀, alcoholic (skull not removed). Collection date: 27 September 1887. Formerly in the Lataste collection (see: 42). - Comments: Considered a valid subspecies by Grubb *et al.* (1998: 77), but they also remark that it might be a subspecies of *aethiops*.

2019. *R[hinolophus] fumigatus/eloquens 1:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol.,
19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).

2019. *R[hinolophus] fumigatus/eloquens 2:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).

2019. *R[hinolophus] fumigatus/eloquens 3:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).
2022. *R[hinolophus] fumigatus/eloquens 0:* Flanders, Frick, Nziza, Nsengimana, Kaleme, Dusabe, Ndikubwimana, Twizeyimana, Kibiwot, Ntihemuka, Cheng, Muvunyi and Webala, Biodivers. Data J., 10 (e83547): Suppl. Publication date: 19 May 2022. (Name Combination).
? *[Rhinolophus] fumigates:* Zhou, Guillén-Servent, Lim, Eger, Wang and Jiang, J. Mamm., 90 (1): 64. Publication date: February 2009. (Lapsus).
? *Rhinolophus abae:* (Alternate Spelling).
? *Rhinolophus aethiops:* (Alternate Spelling).
? *Rhinolophus fumigatus abae:* (Name Combination).
? *Rhinolophus fumigatus aethiops:* (Name Combination).
? *Rhinolophus fumigatus foxi:* (Name Combination).
? *Rhinolophus fumigatus fumigatus:* (Name Combination).
? *Rhinolophus fumigatus/eloquens complex sp. 1 TD-2019*
? *Rhinolophus fumigatus/eloquens complex sp. 2 TD-2019*
? *Rhinolophus fumigatus/eloquens complex sp. 3 TD-2019*
? *Rhinolophus fumigatus/eloquens complex sp. 8 TD-2019*

TAXONOMY:
Does not include *eloquens* or *perauritus* but does include *aethiops*; see Koopman (1975: 389 - 390). *fumigatus* species group (Csorba *et al.*, 2003: 48 - 51; Simmons, 2005: 356). See Csorba *et al.* (2003: 49 - 50) for remarks on taxonomy, e.g., that *fumigatus* and *aethiops* are probably different species.

Jacobs *et al.* (2016g: 94) refer to Dool *et al.* (2016b), who found that *R. fumigatus* from the western part of Southern Africa seems to be a distinct but sister lineage to *R. fumigatus* from the eastern half of Africa.

Taylor *et al.* (2024: 9) recognized two subspecies in southern Africa: *Rhinolophus fumigatus aethiops* from the arid savanna of the western Escarpment [= lineage 6 of Demos *et al.* (2019a)] and *Rhinolophus fumigatus fumigatus* from the mesic savanna woodland of the eastern Escarpment.

COMMON NAMES:
Afrikaans: Rüppell se saalneusvlermuis, Rüppell-saalneusvlermuis. Chinese: 达马拉菊头蝠. Czech: vrápenec kouřový. English: Rüppell's Horseshoe Bat, Smoky Horseshoe Bat, Abyssinian Horseshoe Bat. French: Rhinolophe de Rüppell. German: Rüppells Hufeisennase, Rüppells Hufeisennase, Shoa Kamnase. Italian: Rinòlofo affumicàto, Fèrro di cavàllo affumicàto. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura da Damarlandia.

ETYMOLOGY OF COMMON NAME:
The colloquial name refers to the describer of the species (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017be).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017be). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008al; IUCN, 2009). 2004: LC ver 3.1 (2001) (IUCN, 2004; Jacobs *et al.*, 2004aj). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016k). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to *Rhinolophus fumigatus* as a whole (Jacobs *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017be).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008al) [in IUCN (2009)] and Monadjem *et al.* (2017be) reported that in view of the species wide range in East and southern Africa, it seems probable that it is present in several protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Rhinolophus fumigatus is widely, but patchily, recorded over much of sub-Saharan Africa. It ranges from Senegal and The Gambia in the east, through West and Central Africa to Ethiopia and Eritrea in the east, and from here through East and southern Africa as far south as Namibia and north-eastern South Africa.

A record from "Mapti, Bankass, Morocco" in the MNHN is rejected by Dbiba *et al.* (2025: 13) and probably originates from Mali. The reason being that the collector (Laurent Granjon) seems to have no connection with Morocco.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,246,343 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 558; Taylor *et al.*, 2018b: 62); Benin (Capo-Chichi *et al.*, 2004: 162); Botswana (Cotterill, 2004a: 261); Burkina Faso (Kangoyé *et al.*, 2015a: 610); Burundi; Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 558); Côte d'Ivoire; Eritrea; Ethiopia; Gabon; Gambia; Ghana; Guinea; Kenya; Liberia; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 558); Mali (Meinig, 2000: 105); Mauritania; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 558; Monadjem *et al.*, 2010c: 378); Namibia (Monadjem *et al.*, 2010d: 559); Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; South Africa (Monadjem *et al.*, 2010d: 559); Sudan; Tanzania (Stanley and Goodman, 2011: 42); Togo; Uganda; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 559); Zimbabwe (Monadjem *et al.*, 2010d: 559).

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.7 Pa, aspect ratio 6.7 and tip shape index of 2.67 for a wingspan of 33 cm and a wing area of 165 cm^2 and a body mass of 13 g.

Sexual dimorphism:

Kangoyé *et al.* (2015a: 610) found no differences in body measurement of males and females from Burkina Faso, but the cranial measurements of the males were on average larger than those of the females.

Echolocation:

Jacobs *et al.* (2007a) reported a F_{peak} 53.8± 0.2 kHz for individuals South Africa. Monadjem *et al.* (2010c: 378) reported from Mozambique the F_{peak} of a single male was 54 kHz (ANABAT).

1 call of tye FM/CF/FM was recorded by Manga Mongombe (2012: 79) from Maroua (Cameroon) with the following parameters: F_{max}: 62.6 kHz, F_{min}: 61.6 kHz, F_{mean}: 61.9 kHz, F_{knee}: 61.7 kHZ, F_{char}: 61.6 kHz, and duration: 0.57 ms.

Kangoyé *et al.* (2015a: 610) reported that five males from Burkina Faso called at 54.2 ± 0.4 (53.4-54.4) kHz.

In Sierra Leone, a flying bat was recorded by Weber *et al.* (2019: 21) at 51.5 kHz.

For two calls from the Aberdares Range in Kenya, Eisenring *et al.* (2016: SI 2) gave the following values: F_{peak}: 57.9 ± 1.1 (57.2 - 58.7) kHz, F_{max}: 106.7 ± 4.3 (103.7 - 109.8) kHz, F_{min}: 54.3 ± 0.3 (54.0 - 54.5) kHz, duration: 52.5 ± 4.7 (49.2 - 55.8) ms, Interpulse interval: 0.7 ± 0.1 (0.6 - 0.8) ms.

For a bat from the Kalahari Desert, Adams and Kwiecinski (2018: 4) reported: F_{char}: 53.9 kHz, F_{max}: 54.4 kHz, F_{min}: 53.6 kHz, and duration: 40.1 ms.

Weier *et al.* (2020: Suppl.) reported on four calls from the Okavango River Basin with the following characteristics: F_{max}: 53.19 ± 0.60 kHz, F_{min}: 51.44 ± 1.67 kHz, F_{knee}: 52.59 ± 0.78 kHz, F_{char}: 52.74 ± 0.66 kHz, slope: 0.31 ± 5.49 OPS, duration: 10.24 ± 5.89 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 83 *Rhinolophus fumigatus* calls from the Kruger Park (RSA): F_{min}: 50.2 ± 2.6 (43.4 - 54.2) kHz, Duration: 25.4 ± 8.6 (6.3 - 41.5) ms, F_{max}: 55.8 ± 0.9 (53.2 - 57.7) kHz, F_{knee}: 54.7 ± 0.7 (52.5 - 56.2) kHz, F_{char}: 54.7 ± 0.6 (52.7 - 55.9) kHz.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 54.70 ± 0.60 kHz, F_{max}: 55.80 ± 0.90 kHz and F_{min}: 50.20 ± 2.60 kHz.

Jacobs (2016: 119) indicates that the second harmonic of this bat coincides with the third harmonic of *R. hildebrandtii*, which possibly might illustrate "harmonic hopping".

Molecular Biology:

Karyotype

Rautenbach (1986) reported 2*n* = 58, FN = 60, BA = 4, a subtelocentric X chromosome, and a metacentric Y. Koubínová *et al.* (2010b: 394) reported for Senegal similar results to Rautenbach (1986), but there were only two pairs of small meta- and submetacentric autosomes, and the remaining 26 pairs were acrocentric, a medium sized acrocentric (no. 15) had an achromatic gap near the centromere, while the X was a medium sized subtelocentric, and the Y was dot-like. Koubínová (2013: 7) reported the karyotype as: 2*n* = 58, FNa = 60, FN = 64.

Habitat:

In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported that this species was only found in disturbed habitats in the Afromontane forest biome.

HABITS:
Happold and Happold (2023: 84) mention that these bats can take off from the ground, but probably can not hover.

ROOST:
Lelant and Chenaval (2011d: 13) report on a colony of over 1,000 animals inhabiting a very old Baobab tree (*Adansonia digitata*) in Fadgal, Senegal. In Malawi, Happold and Happold (2023: 84) found groups of up to 10 - 15 individuals.

POPULATION:
Structure and Density
It is a locally common species that can be encountered as large colonies. Colonies in southern Africa tend to be smaller (Jacobs *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017be).

Trend
2016: Unknown (Monadjem *et al.*, 2017be).
2008: Unknown (Jacobs *et al.*, 2008al; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Happold and Happold (1990b: 566) reported births in Malawi early in the wet season, and females were in "fairly close reproductive synchrony".

A pregnant female was collected in August 1992 in the East Usambara Mountains (Tanzania) (Stanley and Goodman, 2011: 42).

PARASITES:
HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 5 *R. fumigatus* specimens from East Africa and found two of them infected with *Nycteria* sp. Rosskopf *et al.* (2018: Suppl.) mentioned the (same?) record from Malawi.

Fain (1959b: 340) mentions that one of the paratypes of *Nycteridocoptes eyndhoveni* Fain, 1959 (Acari: Sarcoptidae) was collected from a "*R. aethiops*" specimen Kambisa, Angola.

HEMIPTERA
Polyctenidae
Androctenes horvathi Jordan, 1912 recorded from Transvaal, South Africa (Haeselbarth *et al.*, 1966: 17, host referred to as *R. eloquens*), and from Malawi by Curran *et al.* (2022: 237) and Szentiványi *et al.* (2022: 5).

ACARI
Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides rhinolophi* Fain, 1959 on Angolan *R. fumigatus*.

Myobiidae
Bochkov and Fain (2003: 14) reported on one female and one nymph of *Neomyobia (Neomyobia) jacksoni* (Radford, 1940).

Trombiculidae
Zajkowska *et al.* (2018: 149) mentioned the presence of *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957.

DIPTERA
Streblidae
Ascodipteron brevior Maa, 1965, female cysts found at the base of the ears in Congo, Namibia and South Africa (Haeselbarth *et al.*, 1966: 106). *Brachytarsina africana* (Walker, 1849) has a wide distribution in sub-Saharan Africa (Haeselbarth *et al.*, 1966: 100, host refered to as *R. eloquens*). *Raymondia intermedia* Jobling, 1936 (Shapiro *et al.*, 2016: 255).

Nycteribiidae
Nycteribia scissa sudanica Theodor, 1957 from Ethiopia, the Sudan and the Congo (Haeselbarth *et al.*, 1966: 108). *Penicillidia fulvida* (Bigot ,1885) (Haeselbarth *et al.*, 1966: 114, host referred to as *R. foxi*). Verrett *et al.* (2022: 8) reported the same parasite from Kenyan *Rhinolophus fumigatus* 2, 3, 4 and 8.

Dick *et al.* (2023: 77) mentioned that *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) has been found on *Rhinolophus fumigatus* and on *Rhinolophus fumigatus* clades 2/3/4/8. *Phthiridium hoogstraali* (Theodor, 1957) has been found on *Rhinolophus fumigatus* clade 1/3/4, and *Phthiridium scissum* on *Rhinolophus fumigatus* clade 2/3.

SIPHONAPTERA
Ischnopsyllidae
Rhinolophopsylla ectopa (Jordan, 1937) was reported on "*R. aethiops*" from Kenya by Beaucournu and Kock (1996).

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Rhinolophus fumigatus*: Coronaviruses and Paramyxoviruses.

Coronaviridae - Coronaviruses
Alphacoronavirus
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in 204 individuals from Oriental Province, DRC, one tested positive (1/204, 0.5 %).

UTILISATION:
Lelant and Chenaval (2012: 15) report on the use of *R. fumigatus* specimens in traditional medicine in Senegal.

Friant *et al.* (2022: 11) [referring to Lelant and Chenaval (2012)] mention that traditional healers frequently use heads and whole bodies of these bats in potions to treat mental illnesses.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Eritrea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Malawi, Mali, Mauritania, Morocco, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

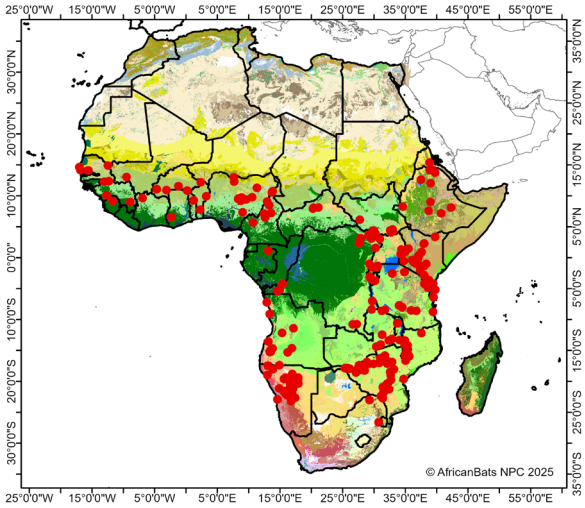

Figure 101. Distribution of *Rhinolophus fumigatus*.

Rhinolophus guineensis Eisentraut, 1960

*1960. *Rhinolophus landeri guineensis* Eisentraut, Stuttg. Beitr. Naturk., 39: 1, fig 1. Publication date: 1 June 1960. Type locality: Guinea: foot of Kelesi Plateau: Tahiré [ca. 10 05 N 12 30 W, 500 m]. [Goto Description]. Holotype: SMNS 6103: ad ♂, skin and skull. Collected by: Hans Knorr; collection date: 5 October 1956. Paratype: SMNS 6104: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6105: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6106: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6107: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6108: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6109: ad, alcoholic (skull not removed). Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: SMNS 6113: ad, skin and skull. Collected by: Hans Knorr; collection date: 19 November 1956. Dieterlen *et al.* (2013: 294) mention Salung Plateau near Nyembaro, 10 km W of Kolenté, Guinea as locality. Paratype: ZFMK MAM-1959.0176: ♀, skin and skull. Collected by: Hans Knorr; collection date: 5 October 1956; original number: 29. Paratype: ZFMK MAM-1959.0177: ♂, skin and skull. Collected by: Hans Knorr; collection date: 23 November 1956; original number: 137. See Hutterer (1984: 30), Hutterer and Peters (2010: 11). - Etymology: Refers to country from which the type specimen was collected.

? *Rhinolophus guineensis:* (Name Combination, Current Combination).

TAXONOMY:
Meester *et al.* (1986) state that Rosevear (1965) and Kock (1969a) regard *guineensis* Eisentraut, 1960, from Guinea, as subspecifically distinct from *landeri*. Hayman and Hill (1971), on the other hand, consider it a synonym, while Böhme and Hutterer (1979), Csorba *et al.* (2003: 59 - 61) and Simmons (2005: 356) regard it as a distinct species, sympatric with *landeri* and somewhat larger.

COMMON NAMES:
Czech: vrápenec guinejský. English: Guinean Horseshoe Bat (Csorba *et al.*, 2003: 59 - 61, Simmons, 2005), Senegal Horseshoe Bat. French: Rhinolophe de Guinée, Rhinolophe du Sénégal. German: Guinea-Hufeisennase.

SIMILAR SPECIES:
See Csorba *et al.* (2003).

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN B2ab(i,ii,iii,v) ver 3.1 (2001) as its roost distribution is severely fragmented into approximately 20 cave/mine roosts that are critical resources where the bats roost for nearly 12 hours out of every day; these roosts are under great pressure. Its area of occupancy (AOO) is estimated to be approximately 80 km^2 based on these 20 cave/mine roosts. Its extent of occurrence (EOO), AOO, habitat, and population are all projected to continue to decline due to ongoing threats from forest loss and degradation and cave/mine loss,

degradation, and disturbance (Shapiro and Cooper-Bohannon, 2020).

Assessment History
Global
2019: EN B2ab(i,ii,iii,v) ver 3.1 (2001) (Shapiro and Cooper-Bohannon, 2020). 2008: VU B2ab(ii,iii) ver 3.1 (2001) (Fahr, 2008j; IUCN, 2009). 2004: VU B2ab(iii) ver 3.1 (2001) (Fahr, 2004g; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Major threats to *Rhinolophus guineensis* include deforestation resulting from logging operations, the conversion of land to agricultural use, and mining activities. There is also a limited threat of overhunting for the bushmeat trade (Fahr, 2008j; IUCN, 2009; Shapiro and Cooper-Bohannon, 2020). The destruction of old mine adits threatens their roosts (Shapiro and Cooper-Bohannon, 2020).

Sagot and Chaverri (2015: 1670) mention roost loss or disturbance, habitat degradation or loss, and hunting as major threats for this species.

CONSERVATION ACTIONS:
Fahr (2008j) [in IUCN (2009)] and Shapiro and Cooper-Bohannon (2020) reported *Rhinolophus guineensis* has been recorded from the Mount Nimba World Heritage Site and the "Massif du Ziama" Biosphere Reserve, both in Guinea. It has also been recorded from a few state forests ("Forets Classees") in Guinea. There is a need to conserve remaining areas of suitable habitat for this species. Further studies are needed to better determine the species range.

GENERAL DISTRIBUTION:
Rhinolophus guineensis is a West African bat that has been patchily recorded from southern Senegal, Guinea, Sierra Leone, Liberia and Côte d'Ivoire. It is a highland species recorded at elevations of 1,400 m asl and over. It may be present in Gambia in remnant patches of forest (Grubb *et al.*, 1998).

Native: Côte d'Ivoire; Guinea (Denys *et al.*, 2013: 281; Decher *et al.*, 2016: 264); Liberia (Simmons, 2005); Senegal; Sierra Leone (Csorba *et al.*, 2003).
Presence uncertain: Gambia (Grubb *et al.*, 1998).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Csorba *et al.* (2003).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Csorba *et al.* (2003).

DETAILED MORPHOLOGY:
Other
For a description of the crania, teeth, and noseleaves see Csorba *et al.* (2003).

ECHOLOCATION:
In Guinea, Fahr and Ebigbo (2003) reported the frequency of the CF-component at 85.3 - 85.4 kHz.

In Sierra Leone, one female called with a CF-component at 82.0 kHz (Weber *et al.*, 2019: 21).

HABITAT:
Monadjem *et al.* (2016y: 366) recorded this species from higher altitudes (above 900 m) in the Mount Nimba area.

Chakravarty *et al.* (2024: 7) assigned this species to the group of "highland dwelling species."

See also Csorba *et al.* (2003).

HABITS:
See Csorba *et al.* (2003).

ROOST:
Weber and Fahr (2006: 4) indicate that *R. guineensis* largely or exclusively depends on the availability of caves as day roosts in Guinea.

POPULATION:
Structure and Density
Rhinolophus guineensis is possibly a rare species overall, although little information is available on the population abundance of this bat (Fahr, 2008j; IUCN, 2009; Shapiro and Cooper-Bohannon, 2020). Global population is thought to be in decline due to forest, cave, and mine degradation and loss (Shapiro and Cooper-Bohannon, 2020). This species was the least numerous of four species of *Rhinolophus* and *Hipposideros* recorded roosting in caves and mine audits at 1,500 m asl at Mt Nimba, Guinea (Monadjem, *unpublished data* in Shapiro and Cooper-Bohannon (2020)), although other surveys in the area have found *R. guineensis* at higher relative abundances (Monadjem *et al.*, 2016y). Studies generally capture few individuals (<10) (Decher *et al.*, 2010; 2016), although Denys *et al.* (2013) found 41 individuals from two different sites on the Guinean side of Mt. Nimba.

Trend
2019: Decreasing (Shapiro and Cooper-Bohannon, 2020). 2008: Unknown (Fahr, 2008j; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Weber *et al.* (2019: 21) recorded a pregnant female on 30 March in Sierra Leone.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea, Liberia, Senegal, Sierra Leone.

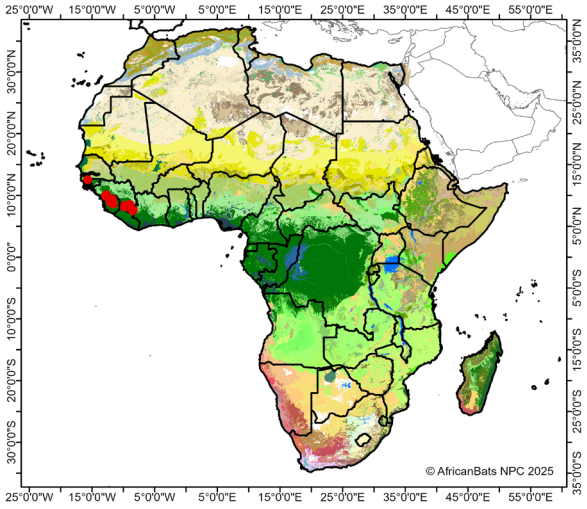

Figure 102. Distribution of *Rhinolophus guineensis*.

Rhinolophus hildebrandtii Peters, 1878

*1878. *Rhinolophus Hildebrandtii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 195, pl 1, fig 1, 1a. Type locality: Kenya: Taita district: Ndi [03 14 S 38 30 E, 2 000 m]. [Goto Description]. Syntype: NHMUK 1879.1.21.1: ad. Turni and Kock (2008: 33). Reject the holotype status for this specimen and consider this also as a possible syntype. Syntype: ZMB 5267: ad ♀, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008: 33). Syntype: ZMB 5378: ♂, skin and skull. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008: 33). Syntype: ZMB 5379: ♂, skin and skull. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008: 33). - Comments: Turni and Kock (2008: 33) reject the holotype status for the NHMUK specimen and consider this also as a syntype. - Etymology: In honour of Johannes Maria Hildebrandt (1847 - 1881), a German naturalist, explorer and linguist, who collected a large number of plants and animals in eastern Africa, Madagascar, Comoro islands and Arabia (see Pearl, 1994: 3; Taylor, 2005, Lanza *et al.*, 2015: 101). (Current Combination).
1991. *Rhinolophus hildebrantii:* Avery, Durban Mus. Novit., 16: 1. (Lapsus).
2013. *Rhinolophus hildebriandtii:* McCulloch, Barcoding of South African bat species and evaluation of their natural exposure to lyssaviruses, 122. Publication date: July 2013. (Lapsus).
2019. *R[hinolophus] hildebrandtii 1:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).
2019. *R[hinolophus] hildebrandtii 2:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): Suppl. Publication date: 22 August 2019. (Name Combination).
2020. *Rhinolophus hildebrandt:* Torquetti, Guimarães and Soto-Blanco, Sci. Total Environ., 755 (142509): 5. Publication date: 25 September 2022. (Lapsus).
? *Rhinolophus cf. hildebrandti*
? *Rhinolophus hildebrandti hildebrandti:* (Name Combination, Alternate Spelling).
? *Rhinolophus hildebrandti:* (Name Combination).
? *Rhinolophus hildebrandtii:* (Current Spelling).

TAXONOMY:
See Pearl (1994). Within the *fumigatus* species group (Csorba *et al.*, 2003: 51 - 53; Simmons, 2005: 356). See Csorba *et al.*, 2003: 52) for a review of the taxonomy.

Taylor *et al.* (2010: 297) indicate that cryptic species might be present in the southern African *R. hildebrandtii* complex. These species probably diverged during the late Neogene (Plio-Pleistocene) when more open woodlands replaced the seasonal woodland/forest habitats (Schoeman and Monadjem (2018: 4).

COMMON NAMES:
Afrikaans: Hildebrandt se saalneusvlermuis, Hildebrandt-saalneusvlermuis, Hildebrandtse Vlermuis. Chinese: 希氏菊头蝠. Czech: vrápenec Hildebrandtův. English: Hildebrandt's Horseshoe Bat. French: Rhinolophe d'Hildebrandt, Fer à cheval d'Hildebrant, Fer à cheval du Kenya. German: Hildebrandts Hufeisennase. Italian: Rinòlofo di Hildebrandt, Fèrro di cavàllo di Hildebrandt. Kiluba (DRC): Kasusu. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura de Hildebrandt. Yao (Malawi): Lichinji (applied to all largish bats).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
R. hildebrandtii was found in the earlier half of the upper Pleistocene sequence at Border Cave, KwaZulu-Natal, South Africa (Avery, 1991: 6; Taylor, 1998: 35).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs, 2008h; IUCN, 2009; Monadjem and Jacobs, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Jacobs, 2017c). 2008: LC ver 3.1 (2001) assessed as *Rhinolophus hildebrandti* (Jacobs, 2008h; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs, 2004i; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
Jacobs (2008h) [in IUCN (2009)] and Monadjem and Jacobs (2017c) reported there appear to be no major threats to *Rhinolophus hildebrantii* as a whole.

CONSERVATION ACTIONS:
Jacobs (2008h) [in IUCN (2009)] and Monadjem and Jacobs (2017c) reported there appear to be no direct conservation measures in place. In view of the species wide East African and southern African range, it seems probable that the species is present in some protected areas.

GENERAL DISTRIBUTION:
Rhinolophus hildebrandtii is largely endemic to East Africa, except for a Central African records from Rwanda and southern Democratic Republic of the Congo, and a single questionable West African record from Nigeria. In East Africa it ranges from Ethiopia and northern Sudan in the north, through Uganda, Kenya and Tanzania (including the island of Pemba [see O'Brien, 2011: 286]), into southern Africa of Zambia, Malawi, Mozambique, Zimbabwe and Botswana, being found as far south as northern South Africa. Taylor (1998: 35) mentioned Pleistocene deposits of this species reported by Avery (1991) from Border Cave, northern Maputaland, KwaZulu-Natal, South Africa. In South Africa, its distribution is mostly affected by precipitation seasonality (Babiker Salata, 2012: 49).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 946,716 km^2.

Native: Botswana (Monadjem *et al.*, 2010d: 559); Burundi; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Ansell, 1974; Monadjem *et al.*, 2010d: 559); Ethiopia (Kruskop *et al.*, 2014: 102 report the first record North of the Rift Valley); Kenya; Malawi (Ansell, 1974; Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Monadjem *et al.*, 2010d: 559); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 559; Monadjem *et al.*, 2010c: 379); Rwanda; Somalia; South Africa (Monadjem *et al.*, 2010d: 559); Sudan; Tanzania (Stanley and Goodman, 2011: 42), United Republic of; Uganda (Kityo and Kerbis, 1996: 61); Zambia (Ansell, 1969; Monadjem *et al.*, 2010d: 559); Zimbabwe (Monadjem *et al.*, 2010d: 559).

Presence uncertain: Namibia (Cotterill, 2004a: 261); Nigeria.

FUNCTIONAL MORPHOLOGY:
Aylward *et al.* (2019:) refer to Makanya and Maina (1994), who reported honeycomb ridge-like villi in the proximal part of the bat's intestine.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 9.8 Pa, aspect ratio 6.8 for a wingspan of 41 cm and a wing area of 243 cm^2 and a body mass of 24 g.

ECHOLOCATION:
Taylor *et al.* (2005), using a Pettersson D980, reported three, slightly different F_{max}: 42.3± 0.2 kHz, 43.2± 0.1 kHz, 42.4 kHz) from three different localities in Kenya for individuals of *R.* cf. *hildebrandtii*. Jacobs (1996) reported F_{max} 37 - 46 kHz for individuals at Sengwa in Zimbabwe. Aldridge and Rautenbach (1987) reported a F_{max} c. 40 kHz for individuals from Pafuri in South Africa. Jacobs *et al.* (2007a) reported a F_{peak} 33.0 ± 0.9 kHz for individuals in South Africa (detector type and localities not reported). From Mozambique Monadjem *et al.* (2010c: 379) reported that the peak echolocation frequencies ranged between 35 - 40 kHz (ANABAT, Petterson D240x). At Uzungwa Scarp Forest Reserve, Tanzania, Trentin and Rovero (2011: 56) describe the calls as starting at 28.5 kHz, increasing in 0.5 ms to 39.8 kHz, and after 5 ms decreasing to 26.7 kHz. The maximum intensity is at 35.5 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats, two calls): F_{peak}: 42.8, 42.1 kHz and duration: 57.7, 45.2 ms.

MOLECULAR BIOLOGY:
Karyotype
Both Peterson and Nagorsen (1975) and Rautenbach (1986) reported 2*n* = 58, FN = 60, BA = 4, and subtelocentric X and Y chromosomes.

HABITS:
Happold and Happold (2023: 86) mention these bats can take off from the ground and can almost hover.

PREDATORS:
Schätti (1984: 337) refers to Broadley (in lit.) who mentions a *R. hildebrandtii* specimen having been swallowed by an African housesnake (*Lamprophis fuliginosus* (Boie, 1827) [=*Boaedon fuliginosus* (Boie, 1827)]).

POPULATION:
Structure and Density
This species is quite common in Zambia (Jacobs, 2008h; IUCN, 2009; Monadjem and Jacobs, 2017c).

Trend
2016: Unknown (Monadjem and Jacobs, 2017c).
2008: Unknown (Jacobs, 2008h; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
A male with abdominal testes was collected in the West Usambara Mountains (Tanzania) on 15 July 1991 (Stanley and Goodman, 2011: 42). Trentin and Rovero (2011: 50) reported two lactating females, and six females with single youngs, netted in December 2005 at Uzungwa Scarp Forest Reserve, Tanzania.

In Malawi, young are born around June (dry season) (Happold and Happold, 1990b: 566).

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2015a: 381) found *Nycteria* sp. parasites in *R. hildebrandtii* from Kenya (see also Arnuphapprasert *et al.*, 2020: Suppl.). Lutz *et al.* (2016: 9) found eight out of 14 specimens from East Africa to be infected by *Nycteria* sp. Perkins and Schaer (2016: Suppl.) report on the presence of *Nycteria congolensis* (Garnham, 1966) on bats from the DRC and East Africa as well as of *Nycteria* sp. from Kenya and Malawi or Mozambique.

ARACHNIDA
Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides rhinolophi* Fain, 1959 on *R. hildebrandtii* from the DRC.

Sarcoptidae
Fain (1959b: 341) reports on *Nycteridocoptes eyndhoveni* Fain, 1959 collected on a bat of this species captured in Lubudi, DRC.

Spinturnicidae
Orlova *et al.* (2024: 153) mention this species as host for *Spinturnix semilunaris* de Meillon & Lavoipierre, 1944.

Trombiculidae
Stekolnikov (2018a: 116) found *Trisetica aethiopica* (Hirst, 1926). Stekolnikov and Quetglas (2019: 8) indicate this bat was captured in South Sudan.

DIPTERA
Nycteribiidae
Nycteribia scissa Speiser; *Nycteribia rotundata* Theodor; *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114).

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Rhinolophus hildebrandtii*: *Nycteribia schmidlii scotti* Falcoz, 1923, *Penicillidia (Penicillidia) fulvida* (Bigot, 1885), *Penicillidia (Penicillidia) pachymela* Speiser, 1901, *Phthiridium hoogstraali* (Theodor, 1957), *Phthiridium rhodesiense* (Theodor, 1957) and *Phthiridium scissum* (Speiser, 1900), Furthermore, *Phthiridium rhodesiense* (Theodor, 1957) has been found on *Rhinolophus hildebrandtii* clade 1.

Streblidae
Ascodipteron brevior Maa 1965, female cysts found at the base of the ears in Congo (Haeselbarth *et al.*, 1966: 106). *Brachytarsina africana* (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Raymondia intermedia* Jobling, 1936 in the Congo (Haeselbarth *et al.*, 1966: 102). *Raymondia waterstoni* Jobling, 1931 (Haeselbarth *et al.*, 1966: 104), these records may possibly also be associated with *R. smithersii* (see Shapiro *et al.*, 2016: 256). *Raymondia intermedia* Jobling, 1936 (Shapiro *et al.*, 2016: 255).

Theodor (1968) recorded *Raymondia setiloba* (Jobling, 1954) from "*R. hildebrandtii*" in the DRC, but Shapiro *et al.* (2016: 256) indicate that the identity of the host is uncertain, and therefore report it as *Rhinolophus* sp.

VIRUSES:
Coronaviridae
31.3 % (5 out of 16) of the Kenyan bats tested by Tao *et al.* (2017: 3) were positive for CoV (genus

Betacoronavirus, subgenus *Sarbecovirus*, see Markotter *et al.*, 2020: 6).

Polyomaviridae
Vidovszky *et al.* (2020: 3) referred to Polyomaviruses recovered from a *R. hildebrandtii* captured in the Leopards Hill cave in Zambia.

Rhabdoviridae
Vesiculovirus
Metselaar *et al.* (1969: 183) extracted a new virus (the "Mount Elgon Bat Virus") from the salivary glands of *R. hildebrandtii eloquens*, collected at the Kiminimi caves on the slopes of Mount Elgon, Kenya. Willoughby *et al.* (2017: Suppl.) mentions this virus as "Mount Elgon bat ledantevirus".

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burundi, Congo (Democratic Republic of the), Ethiopia, Kenya, Nigeria, South Sudan, Sudan, Tanzania, Uganda.

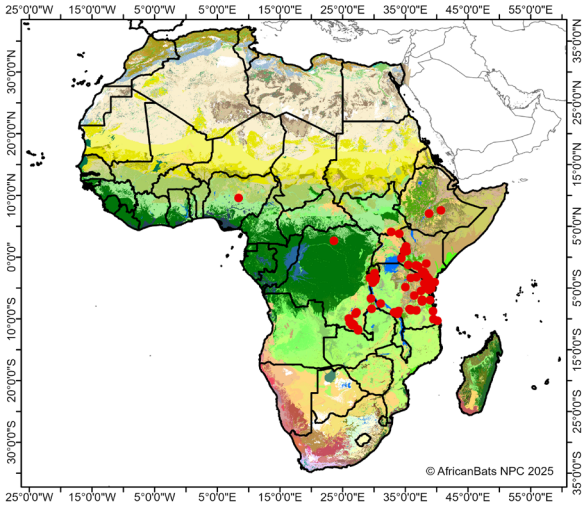

Figure 103. Distribution of *Rhinolophus hildebrandtii*.

Rhinolophus hilli Aellen, 1973

*1973. *Rhinolophus hilli* Aellen, Period. biol., 75 (1): 101. Type locality: Rwanda: Cyangugu province: Uwinka [02 29 S 29 12 E, 2 300 m]. [Goto Description]. Holotype: ZMZ 126639: ad ♀, skull and alcoholic. Collected by: U. Goepel; collection date: 25 August 1964. (Current Combination).

TAXONOMY:
Previously recognized as a synonym of *R. ruwenzorii* J. Eric Hill, 1942 but recognized as a separate species by Fahr *et al.* (2002: 108) and Simmons (2005).

COMMON NAMES:
Czech: vrápenec Hillův. English: Hill's Horseshoe Bat. French: Rhinolophe de Hill. German: Hills Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Critically Endangered (CR B1ab(iii,v)+2ab(iii,v) ver 3.1 (2001)) because its extent of occurrence appears to be less than 100 km^2 and its area of occupancy (presumably cave roosting sites) is probably less than 10 km^2 (field surveys in the Albertine rift have not found the species elsewhere), all individuals are in a single location (Nyungwe National Park), there is continuing decline in the extent and quality of its habitat, and there is believed to be an ongoing population decline related to over-harvesting for food (Fahr, 2008k; IUCN, 2009; Fahr, 2010).

R. hilli was last recorded in 1981 (see Flanders *et al.*, 2019: 109).

Assessment History
Global
2010: CE B1ab(iii,v)+2ab(iii,v) ver 3.1 (2001) (Fahr, 2010). 2008: CR B1ab(iii,v)+2ab(iii,v) ver 3.1 (2001) (Fahr, 2008k; IUCN, 2009). 2004: CR (Fahr, 2004f; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
Fahr *et al.* (2002) indicate that while there is little information available on this seemingly limited range species, it is probably threatened by habitat destruction (presumably by logging operations and the conversion of land to agricultural use) and direct exploitation (for subsistence food) in their day roosts (see Fahr, 2008k) [in IUCN (2009)]; Fahr, 2010).

CONSERVATION ACTIONS:
Fahr (2010) repeats Fahr (2008k) [in IUCN (2009)] who reported that although *Rhinolophus hilli* is present within the Nyungwe National Park, it seems additional measures are needed to conserve the habitat of this species. There is a need for bat awareness programmes for local people to prevent over-harvesting of the species. Further field surveys are also needed to locate important roosts and to learn more about the natural history of this poorly known species.

GENERAL DISTRIBUTION:
Rhinolophus hilli is known only within the Nyunwe National Park, Rwanda. It has been identified from only three close localities (approximately 8 km apart). Field surveys in surrounding areas of potentially suitable habitat have not found additional populations. It has an elevational range of between 1,750 and 2,512 m asl (Fahr *et al.*, 2002).

Native: Rwanda.

ECHOLOCATION:
Flanders *et al.* (2022: 16) mention F_{peak}: 35.4 kHz, duration: 49.5 ms and an interpulse interval of 82.25 ms.

POPULATION:
Structure and Density
There is little information available on the abundance of *Rhinolophus hilli*; colonies of this species have yet to be found but are likely to be small (Fahr *et al.*, 2002; Fahr, 2010).

Trend
2010: Decreasing (Fahr, 2010). 2008: Decreasing (Fahr, 2008k; IUCN, 2009).

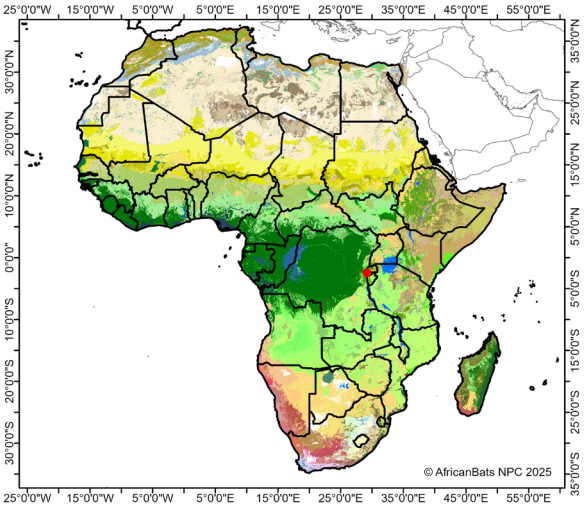

Figure 104. Distribution of *Rhinolophus hilli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Rwanda.

Rhinolophus hillorum Koopman, 1989

*1989. *Rhinolophus clivosus hillorum* Koopman, Am. Mus. Novit., 2946: 4. Publication date: 28 June 1989. Type locality: Liberia: Lofa county: ca 2 mi SW Voinjama, near Zozoma: John Hegbe farm: (the type lable mentions John's Town) [08 25 N 09 35 W, 500 m]. [Goto Description]. Holotype: AMNH 257044: ad ♀, skull and alcoholic. Collected by: Andrew S. Voros; collection date: early October; original number: 5924. Type label mentions 3 September 1983. - Etymology: In honour of the two (often confused) eminent mammalogists named John E. Hill: J. Eric (1907-1947), and J. Edwards (1928-1997) (see Koopman, 1989b: 5).
? *Rhinolophus hillorum:* (Name Combination, Current Combination).

TAXONOMY:
Considered a synonym of *clivosus* by Koopman (1993a: 164), but see Simmons (2005: 356). See Csorba *et al.* (2003: 131) for remarks on taxonomy.

COMMON NAMES:
Czech: vrápenec západoafrický. English: Upland Horseshoe bat, Hill's Horseshoe bat. French: Rhinolophe de Lofa. German: Hochland-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened since although its Extent of Occurrence is probably less than 20,000 km^2 and its habitat is declining from the loss of montane habitat, especially in northern Liberia and southern Guinea, making the species close to qualifying for Vulnerable (Jacobs *et al.*, 2010).

Assessment History
Global
2010: NT ver 3.1 (2001) (Jacobs *et al.*, 2010). 2008: VU A2c ver 3.1 (2001) (Jacobs *et al.*, 2008ad; IUCN, 2009). 2004: VU A4c; B2ab(iii) ver 3.1 (2001) (Jacobs *et al.*, 2004s; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
Colonies are threatened by general deforestation, often resulting from logging and mining operations, and overharvesting for the bushmeat trade (Jacobs *et al.*, 2008ad; IUCN, 2009; Jacobs *et al.*, 2010).

CONSERVATION ACTIONS:
Jacobs *et al.* (2010) repeats Jacobs *et al.* (2008ad) [in IUCN (2009)] who reported there appear to be no direct conservation measures in place for *Rhinolophus hillorum*. It is not known if the species is present in any protected areas, but it has been recorded from the Sapoba Forest

Reserve in Nigeria and the Bali Forest Reserve in Cameroon (Cotterill, 2002a). There is a need to identify and protect important areas for this species. Further research is needed into the species distribution, including the location of any additional colonies.

GENERAL DISTRIBUTION:
Rhinolphus hillorum is largely endemic to West and Central Africa, with a single questionable record from northern Uganda. It has been recorded from a few small, disjunct, colonies in Liberia (including Voinjama; Tokadeh; and the Wonegizi Mountains), Guinea, Nigeria (Sapoba Forest Reserve) and Cameroon (including Lake Manenguba and the Bali Forest Reserve).

Native: Cameroon; Guinea (Fahr *et al.*, 2006a: 72); Liberia; Nigeria (Tanshi *et al.*, 2022a: 317).

Presence uncertain: Uganda.

ECHOLOCATION:
Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003667_CDWBFWMLTW.WAV, https://chirovox.elte.hu/sounds/A003673_MGAGXDGXZR.WAV, https://chirovox.elte.hu/sounds/A003674_GZJEINMZUE.WAV

HABITAT:
Monadjem *et al.* (2016y: 366) recorded five specimens from forested habitats on the Liberian side of Mount Nimba, on altitudes ranging from 780 to 1,200 m.

Chakravarty *et al.* (2024: 7) considers this species to be a "highland dwelling species".

ROOST:
Monadjem *et al.* (2016y: 366) found a roost in an old mine adit at Mount Tokadeh, Liberia.

POPULATION:
Structure and Density
The species appears to have a small population, but further research is needed to confirm this (Jacobs *et al.*, 2008ad; IUCN, 2009; R,6206). 2008: Decreasing (Jacobs *et al.*, 2008ad; IUCN, 2009).

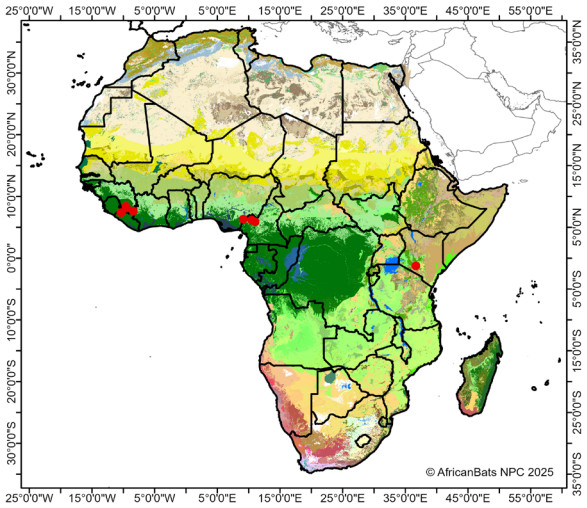

Figure 105. Distribution of *Rhinolophus hillorum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Guinea, Kenya, Liberia, Nigeria.

Rhinolophus hipposideros (André, 1797)

1792. *minor* Kerr, in: Linnaeus, Animal Kingdom, 1 (1): xvii, 91. Publication date: February 1792. Type locality: France: "France". - Comments: Preoccupied by *minor* Kerr, 1792: 97 (two pages before this) (see Simmons, 2005).

*1797. *Noctilio Hipposideros* André, Der Zoologe. Publication date: 17 April 1797. Type locality: Germany. [Goto Description].

1800. *Vespertilio hipposideros* Bechstein, Allgemeine Uebersicht Vierfüssige Thiere, 2: 629. Type locality: France: "France". - Etymology: from the masculine Greek substantive "*ἵππος*" (híppos), meaning "horse" and from the neuter Greek substantive "*σίδηρος*" (sídēros), meaning "iron", referring to the occurrence of a fleshy horseshoe-shaped expansion on the muzzle in this species as in all other species of the genus (see Lanza *et al.*, 2015: 104). (Name Combination).

1861. *Rhinolophus minimus* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 6. Publication date: 1861. Type locality: Eritrea: Kérén [ca. 15 45 N 38 20 E]. Holotype: SMNS 987: sad ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. Andersen (1904c: 455) mentions it as an immature, but full-grown specimen and 1862? as collection date. Dieterlen *et al.* (2013: 294) mention "skull and specimen in alcohol" and mention 1861 as collection date.

1870. *Rhinolophus Eggenhöffner* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 62 (1): 151. - Comments: This might be an African form, but we do not have any further information. Benda *et al.* (2023b: 290) indicate that this name is unavailable as it is only a manuscript name.

1937. *Rhinolophus hipposideros vespa* Laurent, Bull. Soc. Hist. nat. Afr. Nord, 28 (2): 157, text-fig 1 - 2. Publication date: February 1937. Type locality: Morocco: near Rabat: Oued Korifla [ca. 34 02 N 06 50 W]. [Goto Description]. Holotype: MNHN ZM-MO-1986-1071: ♂, alcoholic (skull missing). Collected by: Dr. Paul Laurent; collection date: 8 August 1927. Number 181 in Rode (1941: 238). Additional number: 919. Paratype: MNHN ZM-MO-1986-1072: ♂. Collected by: Dr. Paul Laurent; collection date: 8 August 1927. This is probably number 181a in Rode (1941: 238). Laurent (1937a: 161) mentioned two female paratypes (920 and 922), no

male. Paratype: MNHN ZM-MO-1986-1073: ♀, alcoholic (skull not removed). Collected by: Charles Alluaud; collection date: 1922. Rode (1941: 238) only mentions a male paratype, which is MNHN ZM-MO-1986-1073. Laurent (1937a: 161) mentioned two paratypes.

1978. *eggenhoffner:* Corbet, Mammals Palaearctic region, 43. - Comments: Possibly extralimital. (Lapsus).

? *Rhinolophus hipposideros:* (Name Combination, Current Combination).

TAXONOMY:

Kozhurina (2009: 72) points out that Borkhausen (1797 - Deutsche Fauna, oder kurzgefaßte Naturgeschichte der Thiere Deutschlands. Erster Theil: Säugethiere und Vögel. Frankfurt am Main: 85) was the first to give a scientific name to this species: *Noctilio Hipposideros*. However, Benda and Mlíkovský (2022: 5) and Benda *et al.* (2023b: 272) assigned the name to C.C. André, who also published the same name in 1797 (André (1797: 65), but prior to Borkhausen (17 April 1797 versus 30 September 1797).

Revised by Felten *et al.* (1977). The status of populations around the Mediterranean, on Mediterranean Islands, and on both sides of the Red Sea is unclear (see Horáček *et al.*, 2000: 101). *hipposideros* species group (Csorba *et al.*, 2003: 53 - 55; Simmons, 2005: 356 - 357). See Csorba *et al.* (2003: 54) for review of taxonomy.

Based on genetic and morphological data, Benda *et al.* (2023b: 287) distinguish two geographically exclusive phylogenetic sublineages within the species. The western lineage includes most of the European specimens and the populations from the Maghreb, whereas the eastern lineage includes the populations of Asia, including Eastern Mediterranean islands (Rhodes and Cyprus), and of Crimea. Also a single specimen from Ethiopia could be assigned to this eastern lineage. The western lineage is identified as *Rhinolophus hipposideros hipposideros* and the eastern lineage as *Rhinolophus hipposideros minimus*.

COMMON NAMES:

Albanian: Lakuriq nate hundpatkua i vogël. Arabian: Khafash abu hadwa saghir, Khaffash. Armenian: Փոքր պայտաքիթ. Azerbaijani: Kiçik nalburun. Basque: Ferra-saguzar txikia. Belarusian: Падкаванос малы. Bosnian: Mali potkovasti šišmiš. Breton: Frigribell vihan. Bulgarian: Малък подковонос. Castilian (Spain): Murciélago pequeño de herradura, Rinolofo pequeño de herradura. Catalan (Spain): Ratpenat de ferradura petit, Rat penat petit de ferradura, Ratapinyada petita de ferradura. Croatian: Mali potkovnjak, Mali potkovasti šišmiš. Czech: Vrápenec malý, wrápenec menší, vrápenec menší, malý vrápenec podkovní, vrápeník malý, vrápenec moravský. Danish: Lille hestekonæse, Dvaerghesteskonaes. Dutch: Kleine hoefijzerneus. English: Lesser Horseshoe Bat, Smaller Horseshoe Bat. Estonian: Väike-sagarnina. Finnish: Euroopanpikkuherkko. French: Petit rhinolophe, Petit rhinolophe fer à cheval, Petit Fer-à-Cheval. Frisian: Lytse hoefizernoas. Galician (Spain): Morcego de ferradura pequeño, Morcego pequeño de ferradura. Georgian: მცირე ცხვირნალა. German: Kleine Hufeisennase, Kleinhufeisennase. Greek: Μικροριινόλοφος. Hebrew: פרסף גמדי, Parsaf Gamadi. Hungarian: Kis patkósdenevér, Kis patkósorrú denevér, Rhinolophos i mikra. Irish Gaelic: Crú-ialtóg bheag. Italian: Rinolofo minore, Ferro di Cavallo Minore. Latvian: Mazais pakavdegunis. Lithuanian: Mažasis pasagnosis. Luxembourgish: Kleng Huffeisennues. Macedonian: Мал потковичар [= Mal Potkovichar]. Maltese: Rinolofu Żgħir, Farfett il-Lejl tan-Nala. Montenegrin: Mali potkovičar. Norwegian: Dverghesteskonese, Liten hesteskonese. Polish: Podkowiec mały. Portuguese: Morcego-de-ferradura-pequeno. Rhaeto-Romance: Rinolof pitschen, Nas fier-chaval pitschen. Romanian: Liliacul mic cu potcoavă, Liliac-mic-cupotcoavã. Russian: Подковонос малый [= Podkovonos malyj. Serbian: Мали потковичар [= Mali potkovičar]. Scottish Gaelic: Crudh-ialtag bheag. Slovak: Podkovár malý. Slovenian: Mali podkovnjak. Swedish: Dvärghästskonäsa. Turkish: Küçük Nalburunlu Yarasa. Ukrainian: Підковик (Підковоніс) малий [= Pidkovyk malyy]. Welsh: Ystlum pedol lleiaf.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

R. hipposideros is recorded from the Guenfouda Cave (syn. Ghar Zebouj) in eastern Morocco, dating from the beginning of the Holocene (Neolithic) period (López-García *et al.*, 2012: 51).

Dool *et al.* (2013: 4067) indicate that during the Pleistocene, *R. hipposideros* utilized multiple refugia across the Mediterranean.

Dool *et al.* (2016a: 206) indicate that *R. hipposideros* represents the oldest lineage of the genus and diverged from the other species around 16 Mya.

CONSERVATION STATUS:

Global Justification

This species has a large range. Although there have been marked and well-documented declines in some areas, the species remains widespread,

fairly common, and apparently stable in other areas. Assessed as Least Concern (LC ver 3.1 (2001)) (Jacobs *et al.*, 2008aq; IUCN, 2009; Taylor, 2016d).

Assessment History
Global
2016: LC ver 3.1 (2001) (Taylor, 2016d). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008aq; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004af; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Threats include disturbance and loss of underground habitats and attics (conversion of attics in human habitat), agricultural intensification, fragmentation and isolation of habitats, and the use of pesticides in agricultural areas (Jacobs *et al.*, 2008aq; IUCN, 2009; Taylor, 2016d).

In Austria, Reiter *et al.* (2012: 283) studied the influence of landscape fragmentation on *R. hipposideros* and found that conservation measures for colonies of lesser horseshoe bats should be undertaken within 2.5 km of the nursery roost. As these bats seem to be unable to adapt their spatial foraging behaviour by shifting from woodland to a degraded landscape, any loss of woodland near the colonial roosts will negatively influence the colony.

R. hipposideros's aerial hawking and its long-distance disperal are considered to be major risk factors in view of climatic change (Sherwin *et al.*, 2012: 174).

CONSERVATION ACTIONS:
According to Jacobs *et al.* (2008aq) [in IUCN (2009)] and supported by Taylor (2016d), *Rhinolophus hipposideros* is protected by national legislation in all European range states. There are international legal obligations for protection through Bonn Convention (Eurobats) and Bern Convention, where those apply. Included in Annex II (and IV) of EU Habitats and Species Directive and hence requiring special measures for conservation including designation of Special Areas for Conservation. Some habitat protection through Natura 2000. Recommended conservation measures include protecting maternity roosting sites, hibernation caves and foraging habitats. No specific conservation measures apply in South Asia; more research and monitoring are needed.

GENERAL DISTRIBUTION:
Generally, the type locality for this species is considered to be "France" (based on the historic assignment of the name to Bechstein, 1800. However, since Benda *et al.* (2023b) assigned the name to André, 1797, they mention (p. 271) "Germany" as type locality.

Rhinolophus hipposideros is widely distributed in the western and central Palaearctic. It is found in all the European countries (including the islands) of the Mediterranean region. In North Africa it is recorded from Morocco, Algeria, Tunisia and the eastern part of the Sinai (to Egypt); also occurs in eastern Africa. Also recorded from Anatolia and the countries of the Levant. It occurs from sea level to 2,000 m.

Native: Afghanistan; Albania; Algeria; Andorra; Armenia; Austria; Azerbaijan; Belgium; Bosnia and Herzegovina; Bulgaria; China; Croatia; Cyprus (Benda *et al.*, 2007: 71); Czech Republic; Djibouti (Pearch *et al.*, 2001: 388); Egypt (Sinai); Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147); France [Corse]; Georgia; Germany; Gibraltar; Greece [Kriti]; Holy See [Vatican City State]; Hungary; India; Iran; Ireland; Islamic Republic of; Iraq; Ireland; Israel; Italy [Sardinia, Sicily]; Jordan; Kazakhstan; Kyrgyzstan; Lebanon; Libya (Bendjeddou *et al.*, 2022: 328); Luxembourg; Macedonia, the former Yugoslav Republic of; Malta; Moldova; Monaco; Montenegro; Morocco (Benda *et al.*, 2010a: 157, El Ibrahimi and Rguibi Idrissi, 2015: 359; Dbiba *et al.*, 2025: 6); Pakistan; Palestinian Territory, Occupied (Shehab *et al.*, 2006: 161); Poland; Portugal; Romania; Russian Federation; San Marino; Saudi Arabia; Serbia; Slovakia; Slovenia; Spain [Baleares]; Sudan; Switzerland; Syrian Arab Republic; Tajikistan; Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26); Turkey; Turkmenistan; Ukraine; United Kingdom; Uzbekistan.

Regionally extinct: Liechtenstein; Netherlands.

DETAILED MORPHOLOGY:
Baculum
See Csorba *et al.* (2003: 54).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.1 Pa, aspect ratio 5.7 and tip shape index of 2.59 for a wingspan of 23 cm and a wing area of 94 cm^2 and a body mass of 7 g.

ECHOLOCATION:
Jones and Siemers (2010: 449 - 450) indicated that females emit pulses with a higher frequency

than males, and also that juveniles emit lower frequencies than adults.

Papadatou *et al.* (2008b: 132) report the following data for 5 Greek specimens: F_{start}: 96.6 ± 10.25 kHz, F_{end}: 84.8 ± 4.74 kHz, F_{peak}: 110.6 ± 3.93 kHz, bandwidth: 4.8 ± 1.61 kHz, duration 45.2 ± 6.43 ms and interpulse interval: 98.2 ± 29.10 ms. For 52 calls of bats from France, Switzerland and the UK, Walters *et al.* (2012: suppl.) report the following figures: duration: 42.47 ± 12.66 ms, F_{max}: 109.76 ± 2.35 kHz, F_{min}: 94.35 ± 3.95 kHz, bandwidth: 15.41 ± 4.26 kHz, F_{peak}: 109.58 ± 2.36 kHz.

The following data for 18 Iranian calls were reported by Benda *et al.* (2012a: 182): F_{start}: 111.2 ± 0.8 (109.9 - 112.2) kHz, F_{end}: 108.5 ± 1.4 (106.2 - 110.7) kHz, F_{peak}: 110.3 ± 0.8 (109.0 - 111.1) kHz, duration: 49.9 ± 1.5 (47.8 - 52.0) ms, interpulse interval: 41.9 ± 3.8 (36.1 - 48.7) ms.

Disca *et al.* (2014: 226) indicate that the type of call is FM-FC-FM in Morocco, with F_{peak}: 116.9 ± 0.2 kHz and duration: 39.7 ± 13.2 ms, whereas Dalhoumi *et al.* (2016b: 866) report a frequency "> 112 kHz" (111.5 - 117.5 kHz).

57 calls were recorded by Hackett *et al.* (2016: 223) from Israel: Pulse duration: 42.28 ± 12.09 ms, F_{start}: 92.54 ± 6.79 (83.9 - 109.3) kHz, F_{end}: 93.37 ± 8.61 (80 - 114.2) kHz, F_{peak}: 107.58 ± 0.49 (103.5 - 109.3) kHz.

Luo *et al.* (2019a: Supp.) reported the following data (for two calls): F_{peak}: 111.1, 109 kHz, F_{start}: 99, 98.2 kHz, F_{end}: 96.6, 96.1 kHz, and duration: 43.6, 45.7 ms.

Dool *et al.* (2016b: Suppl.) showed that there is a sexual dimorphism in the peak frequencies in Irish bats, with males call on average 4 kHz lower.

Molecular Biology:

Karyotype

Capanna *et al.* (1967) reported 2*n* = 56, FN = 60. However, Rushton (1970: 463) reported 2*n* = 58, FN = 60, a metacentric X, and a minute Y. For a female from Jordan, Qumsiyeh and Baker (1985) reported 2*n* = 58, FN = 60, BA = 4. More recently, Puerma *et al.* (2007) reported 2*n* = 54, FN = 62, BA = 10, a submetacentric X and an acrocentric Y for specimens from Spain.

Volleth *et al.* (2013: 55) and Arslan and Zima (2014: 8) indicate that three diploid chromosome numbers are present in Europe: 54, 56, and 58. The specimens with 58 chromosomes occur in Asia Minor and the Middle East, those with 56 chromosomes in the Czech Republic, Slovakia, Italy and Greece, and those with 54 chromosomes in Spain, Germany and (possibly) Switzerland.

Genetics

See Puerma *et al.* (2007).

Diet:

Andreas *et al.* (2013) using faecal analysis of *R. hipposideros* from southern Slovakia, showed that this species fed only on the small moths (<25mm) (%f = 59; %vol = 87) and this prey category was supplemented with Neuroptera (Hemerobiidae) (%f = 13.8; %vol = 1.5), nematoceran (%f = 20.7; %vol = 10.0) and brachyceran (%f = 6.9; %vol = 1.2) Diptera.

In northern Spain, Aldasoro *et al.* (2019: 9) found the following prey groups (in descending order of occurrence): Diptera (100 %), Lepidoptera (71 %), Neuroptera (48 %), Hemiptera and Trichoptera (both 12 %), Coleoptera (10 %), Aranea and Hymenoptera (6 %) and Psocoptera (3 %). Of the 55 prey species, identified by Baroja *et al.* (2019: 5-6), 25 cause significant agricultural damage and eight are pests for grapevines.

Droppings from northern Algeria were examined by Ahmim and Moali (2013: 175), who found the following prey items: Insecta (93.46 %) and Chilopoda (6.54 %). Among the Insecta, Diptera were mostly encountered (41.58 %), more specifically: Culicidae (15.59%), Chironomidae/Ceratopogonidae (9.68 %) and Tipulidae (6.45 %). Lepidoptera formed the second most important insect order (21.1 %), followed by Hemiptera (11.68 %).

Population:

Structure and Density

According to Taylor, 2016d) and Jacobs *et al.* (2008aq) [in IUCN (2009)], *Rhinolophus hipposideros*) is an infrequent species in the northern part of its range. In Europe the species forms summer colonies of 10 - 50 individuals (up to 1,500 animals), whereas it is solitary in winter or forms loose aggregations up to 500 animals per roost. Since the 1950s the northern border of the range in western and central Europe has moved to the south. In the Netherlands, northern Belgium and Germany (except for a few colonies in Bavaria, Thüringen, Sachsen and Sachsen-Anhalt) the species went extinct (Fairon *et al.*, 1982; Schofield, 1999). It disappeared from northern and western parts of Bohemia, and much of Poland where 87 % of the hibernating population was lost between 1950 and 1990 (Urbanczyk, 1994; Ohlendorf, 1997). In

Switzerland and Austria the distribution became fragmented, as colonies remained only at higher elevations (>400 m) (Stutz and Haffner, 1984; Spitzenberger, 2002), although in Switzerland at least the population has started to slowly recover over the last 10 years (increasing from 2,200 to 2,500 adults counted in maternity roosts: H. Kraettli *pers. comm.,* 2006). In Spain some colonies have disappeared due to the restoration of buildings, but there are no data on population trend (J. Juste and T. Alcalde *pers. comm.,* 2006), and in France there have been some declines in the north, although large populations in the south are thought to be more stable (EMA Workshop, 2006). In the southwest Asian part of the range it gathers in wintering colonies of up to 40 animals, although it is mainly solitary (K. Tsytsulina *pers. comm.,* 2005). In Turkey it is a commonly reported species, and the population is stable (A. Karatash *pers. comm.,* 2005). It is common in Iran although encountered less frequently than *R. ferrumequinum* (M. Sharifi *pers. comm.,* 2005). It is not known how abundant this species is in Jordan and Syria, but it may be more common than the collection reports indicate (Amr, 2000). Size and trends within Africa and South Asia are unknown.

Trend
2016: Decreasing (Taylor, 2016d). 2008: Decreasing (Jacobs *et al.*, 2008aq; IUCN, 2009).

LIFESPAN:
Lagunas-Rangel (2019: 2) reports a longevity of 29.4 years.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 120) indicate that some females might attain sexual maturity in as little as three months, whereas other females and males might need 15 months.
At birth, the young has about 34.4 % of the mother's body mass (4.2 g versus 12.3 g) (see Kurta and Kunz, 1987: 82).

MATING:
This species has a polygynandrous mating system (Webber *et al.*, 2017: Suppl.).

POSTNATAL DEVELOPMENT:
In Austria, Reiter (2004: 234) found that the average forearm length at one day of age was 17.5 mm and the average weight 2.0 g. He also found that the growth of both the forearm and weight was almost linear during the first 14 days. In some cases, a loss of weight could be observed between day 15 and 20, which occurred a few days before the first flights took place (at between 18 and 20 days of age). At the time of their first flight, the forearm was 92 % of that the adult female, and weight was 70 % of the adult's.

PARASITES:
Lainson and Naiff (2000: 128) reported *R. hipposideros* as host for *Eimeria hessei* Lavier, 1924 (Apicomplexa).

In Italy, Voyron *et al.* (2011: 193) reported the following fungal entity from *R. hipposideros* carcasses: *Mortierella gamsii* Miko, 1974.
Genov *et al.* (1992) reported the presence of the Nematode *Molinostrongylus alatus* (Ortlepp, 1932) in Moldova.

Benda *et al.* (2010b: 234) found the bat fly *Phthiridium integrum* (Theodor and Moscona, 1954) (Nycteribiidae) on *R. hipposideros* in Jordan. They also indicate that *Phthiridium bilobum* (Theodor and Moscona, 1954) was reported before from Palestine, and the fleas *Ischnopsyllus octactenus* (Kolenati, 1856) and *Rhinolophopsylla u. unipectinata* (Taschenberg, 1880) from Turkey.

From Algeria, Bendjeddou *et al.* (2013: 325) reported infestations by *Phthiridium biarticulatum* Hermann, 1804 (Diptera: Nycteribiidae) and *Cimex lectularius* (Linnaeus, 1758) (Hemiptera: Cimicidae). Another Algerian ectoparasite was reported by Bendjeddou *et al.* (2017: 15): Arachnida: *Ixodes ricinus* (Linnaeus, 1758).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ixodidae: *Ixodes ricinus* (Linnaeus, 1758), *Ixodes vespertilionis* Koch, 1844; Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia vexata* Westwood, 1835, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851.

VIRUSES:
Circoviridae
Bat Circovirus was mentioned by Nieto-Rabiela *et al.* (2019: Suppl.). Furthermore, Vidovszky *et al.* (2023: Suppl.) reported Ant associated cyclovirus 1, Bat associated cyclovirus 8, Bovine associated cyclovirus 1 and Squirrel associated cyclovirus 1 in bats from the DRC.

Coronaviridae
Alphacoronavirus
This virus was reported from Italy by Kohl and Kurth (2014: 3112).

Betacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from Bulgaria, Germany, Slovenia, Italy.

Betacoronaviruses from Ghana were assigned to the subgenus *Hibercovirus*.

Herpesviridae
Rosoleovirus
This virus was mentioned by Nieto-Rabiela *et al.* (2019: Suppl.).

Paramyxoviridae
Nieto-Rabiela *et al.* (2019: Suppl.) mention presence of Bat paramyxovirus.

Picornaviridae
Nieto-Rabiela *et al.* (2019: Suppl.) mention presence of Picornavirus.

Reoviridae
Orthoreovirus
Reported from Italy by Kohl and Kurth (2014: 3113).

Rotavirus
Rotavirus A was mentioned by Nieto-Rabiela *et al.* (2019: Suppl.).

Orthomyxoviridae
Despite sampling and testing of 6 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

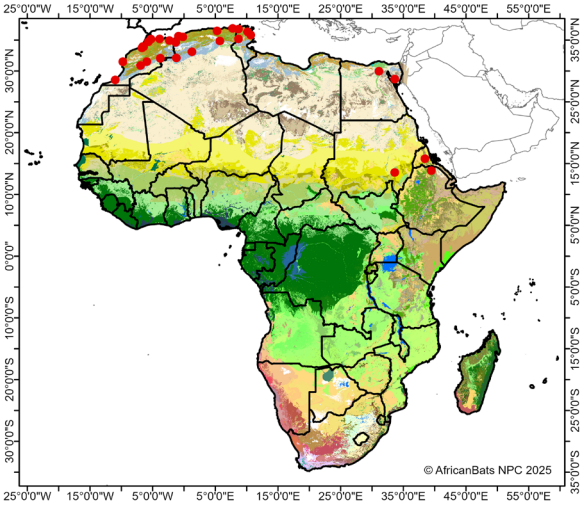

Figure 106. Distribution of *Rhinolophus hipposideros*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Egypt, Liberia.

Rhinolophus hipposideros hipposideros (André, 1797)

*1797. *Noctilio Hipposideros* André, Der Zoologe. Publication date: 17 April 1797. Type locality: Germany. [Goto Description].
1918. *[Rhinolophus hipposideros] escaleræ* K. Andersen, Ann. Mag. nat. Hist., ser 9, 2 (10): 378. Publication date: 1 October 1918. Type locality: Morocco: Mogador [=Essaouira]: Ha-ha [ca. 31 31 N 09 46 W]. [Goto Description]. Holotype: NHMUK 1910.11.24.2: ♀. Collected by: D. Manuel M. de la Escalera. Presented/Donated by: Michael Rodgers Oldfield Thomas. See Andersen (1918: 378).
? *Rhinolophus hipposideros hipposideros:* (Name Combination).

TAXONOMY:
Benda *et al.* (2023b: 290) recognized this subspecies based on genetic data.

GENERAL DISTRIBUTION:
This subspecies occurs in the Maghreb and in Europe, west of the Dnieper River, Bosporus, and the Strait of Karpathos (Benda *et al.*, 2023b: 290).

MOLECULAR BIOLOGY:
Karyotype
The karyotype of this subspecies has a 2n number of 54 - 56.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Morocco, Tunisia.

Rhinolophus hipposideros minimus Heuglin, 1861

? *Rhinolophus hipposideros minimus:* (Name Combination).

TAXONOMY:
Benda *et al.* (2023b: 290) recognized this subspecies based on genetic data.

GENERAL DISTRIBUTION:
Benda *et al.* (2023b: 290) mention that this subspecies occurs in Europe, east of the Dnieper River, including the populations of Crimea, (Caucasus), the Middle East and north-eastern Africa (Sudan, Eritrea, Djibouti, Ethiopia).

MOLECULAR BIOLOGY:
Karyotype
Benda *et al.* (2023b: 270) mention that this subspecies has a karyotype with 2n = 58.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Egypt, Eritrea, Ethiopia, Sudan.

Rhinolophus horaceki Benda and Vallo, 2012

*2012. *Rhinolophus horaceki* Benda and Vallo. Holotype: NMP 49880: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 15 May 2002; original number: pb2124. Paratype: NMP 49861: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 12 May 2002; original number: pb2104. Paratype: NMP 49879: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 15 May 2002; original number: pb2123. Paratype: NMP 49882: ad ♀, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 16 May 2002; original number: pb2127. Paratype: NMP 49915: ad ♀, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2163. (Current Combination).

TAXONOMY:
Based on cytochrome *b* sequences, Benda and Vallo (2012) were able to distinguish a new species of *Rhinolophus* from northern Libya (Cyrenaica). The cytochrome *b* shares unique base positions with the *ferrumequinum*/*clivosus* complex, but also with the *fumigatus* group.

Benda and Uvizl (2025: 297) concluded that *R. horaceki* (together with *R. sakejiensis*) doesn't belong to any of the currently recognized species groups, but represents a distinct evolutionary lineage. The two species separated from one another some 15.3 mya.

Benda *et al.* (2014c: 24) indicate that specimens of this species were reported as *R. clivosus* by Qumsiyeh and Schlitter (1982).

COMMON NAMES:
Dutch: Horacekcs hoefijzerneus. English: Horáček's Horseshoe Bat. German: Lybische Hufeisennase.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Benda *et al.* (2014c: 22) indicate that *R. horaceki* is an endemic of the Mediterranean part of Cyrenaica, streching about 360 km along the coast, and covering no more than 4,000 km^2.

ROOST:
Benda *et al.* (2014c: 22) found a group of four bats in a cave situated in the northern slope of the side valley of the western part of Wadi Al Kuf (Libya).

DIET:
The diet of this species was determined by Benda *et al.* (2014c: 26). One group of faecal pellets contained 99.8 % by volume medium-sized moths and 0.2 % small nematoceran Diptera. A second group of pellets contained 54 % of medium-size Lepidoptera, 38 % of Blattoidea, 4 % of Formicoidea, 2 % of Auchenorrhyncha and 2 % of Coleoptera.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

REPRODUCTION AND ONTOGENY:
Two pregnant females were collected by Benda *et al.* (2014c: 24) on 16 and 20 May 2002.

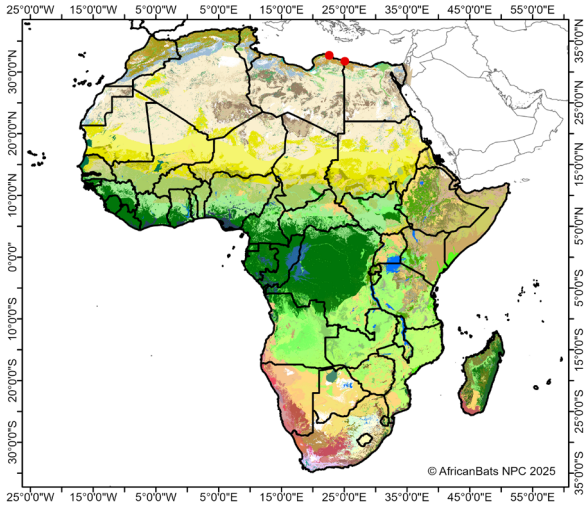

Figure 107. Distribution of *Rhinolophus horaceki*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Libya.

Rhinolophus landeri Martin, 1838

*1838. *Rhinolophus landeri* Martin, Proc. zool. Soc. Lond., 1837, V (lviii): 101. Publication date: 25 May 1838. Type locality: Equatorial Guinea: Bioko [formerly Fernando Po] [ca. 03 21 N 08 40 E]. Holotype: NHMUK 1855.12.26.250. - Etymology: Named by Martin after Richard Lemon Lander (1804 - 1834), an English explorer of western Africa (see Rosevear, 1965; Taylor, 2005; Lanza *et al.*, 2015 109). (Current Combination).

2019. *R[hinolophus] cf. landeri:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 8. Publication date: 22 August 2019. (Name Combination).

? *Rhinolophus cf. landeri TD-2019*

? *Rhinolophus landeri landeri:* (Name Combination).

TAXONOMY:
Meester *et al.* (1986) state that Rosevear (1965) and Kock (1969a) regard *guineensis* Eisentraut, 1960, from Guinea, as subspecifically distinct from *landeri*. Hayman and Hill (1971), on the other hand, consider it a synonym, while Böhme and Hutterer (1979, Csorba *et al.* (2003: 59 - 61) and Simmons (2005: 356) regard it as a distinct species, sympatric with *landeri* and somewhat larger.

Other names associated with *landeri* are *dobsoni* Thomas, 1904, which is either a synonym (Kock, 1969a) or a valid subspecies (Koopman, 1975). See Csorba *et al.* (2003: 62) for remarks on taxonomy. *lobatus* Peters, 1852 and *angolensis* Seabra, 1898 were removed by Taylor *et al.* (2018a: 22).

Patterson *et al.* (2024: 12) reject *axillaris* J.A. Allen, 1917 as a synonym of *landeri* and tentatively consider it as a valid species.

COMMON NAMES:
Afrikaans: Lander se saalneusvlermuis, Lander-saalneusvlermuis. Castilian (Spain): Murciélago de Herradura. Chinese: 兰德菊头蝠. Czech: vrápenec Landerův. English: Lander's Horseshoe Bat. French: Rhinolophe de Lander. German: Landers Hufeisennase, Kastanienrothe Kammnase, Rundlappigen Kammnase, Lander's Rundblattnase. Italian: Rinòlofo di Lànder. Kiluba (DRC): Kasusu. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura de Lander.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008an; IUCN, 2009; Monadjem *et al.*, 2017cl).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cl). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008an; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004ap; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (Monadjem *et al.*, 2016h).

MAJOR THREATS:
There appear to be no major threats to *Rhinolophus landeri* as a whole (Jacobs *et al.*, 2008an; IUCN, 2009; Monadjem *et al.*, 2017cl).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008an) reported in IUCN (2009) and Monadjem *et al.* (2017cl) that in view of the wide range of *Rhinolophus landeri* it seems probable that it is present in some protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Rhinolophus landeri has been widely reported from much of sub-Saharan Africa. It ranges from Senegal and The Gambia in the west, through most of West and Central Africa to Sudan and Ethiopia in the east. The species had been recorded as far south as eastern South Africa, but all southern and eastern African specimens are now referred to *R. lobatus* (see Taylor *et al.*, 2018a: 24). On Mount Cameroon, they have been taken at an altitude of 1,200 m asl and at 900 m asl on Mount Bintamane in Sierra Leone (Rosevear, 1965).

The specimens from Morocco are based on a series (MNHN ZM-MO-1985-910 to 918) which were collected by André Brosset and were also mentioned in Taylor *et al.* (2018a: corr. 6).

Patterson *et al.* (2024: 1) indicate that the distribution of *Rhinolophus landeri* seems to be restricted to Central and West Africa.

Native: Benin (Capo-Chichi *et al.*, 2004: 162); Burkina Faso (Kangoyé *et al.*, 2015a: 610); Cameroon; Central African Republic; Congo; Côte d'Ivoire; Equatorial Guinea (including Bioko); Ethiopia; Gabon; Gambia (Emms and Barnett, 2005: 50); Ghana; Guinea (Fahr and Ebigbo, 2003: 128; Decher *et al.*, 2016: 264); Liberia (Monadjem and Fahr, 2007: 47); Niger; Nigeria; Rwanda (Flanders *et al.* (2022: 3); Senegal; Sierra Leone; Somalia; Sudan; Togo.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Menzies (1973) [in Young (1975: 76)] indicates that, in some colonies in northern Nigeria, rufous bats get a grey fur during the moulting season, and subsequently change back to rufous.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.7 Pa, aspect ratio 6.1 for a wingspan of 29 cm and a wing area of 132 cm^2 and a body mass of 9 g.

SEXUAL DIMORPHISM:
Krutzsch (2000: 117) mentions the presence of shoulder glands in the males, consisting of tufts of long hairs in the armpits (Muñoz-Romo *et al.*, 2021: 170).

ECHOLOCATION:
In Guinea, Fahr and Ebigbo (2003) reported the frequency of the CF-component as 103.3 kHz. In Kenya, O'Shea and Vaughan (1980) using a Holgate ultrasonic sensor reported a frequency of 55 kHz for individuals at Masalani, later Taylor *et al.* (2005) using a Pettersson D980 reported a F_{max}: 110 ± 0 kHz for an individual from Bungule.

In Burkina Faso, Kangoyé *et al.* (2015a: 613) recorded one male calling at 108.5 kHz, and a female calling at 105.6 kHz.

In Sierra Leone, two males called at 102.0 (101.5 - 102.5) kHz (Weber *et al.*, 2019: 21).

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 109 kHz and duration: 43.1 ms.

In Benin, the bat's call was categorized as a FMu-CF-FMd (Frequency Modulation upward - Constant frequency - Frequency modulation downward) sonotype by Roemer *et al.* (2021: Suppl.).

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 12 calls of 2 bats: F_{peak}: 103.2 ± 0.5 (102.8 - 103.8) kHz, F_{min}: 85.0 ± 1.4 (83.2 - 86.6) kHz, F_{max}: 104.6 ± 0.8 (103.9 - 105.3) kHz, duration: 75.0 ± 16.5 (53.7 - 88.7) ms.

MOLECULAR BIOLOGY:
Karyotype
2*n* = 58, FN = 60, BA = 4, and a submetacentric X chromosome (Rautenbach *et al.*, 1993). Koubínová *et al.* (2010b) agree with Rautenbach *et al.* (1993), and reported for a female from Senegal 2*n*= 58, and a Fna= 64, which contained four pairs of biarmed autosomes three pairs of which were medium to small sized meta- or submetacentrics and one was a medium sized subtelocentric, the remaining 24 pairs were a gradated series of acrocentrics.

HABITAT:
Monadjem *et al.* (2016y: 366) recorded this species in the Mount Nimba area in forested habitats between 550 and 1,000 m.

HABITS:
Happold and Happold (2023: 88) indicate that these bats can take off from the ground and can briefly hover.

PREDATORS:
Based on Fenton *et al.* (1981), Gual-Suárez and Medellín (2021: Suppl.) reported that this species accounted for 0.5 % of the food items taken by *Nycteris grandis*.

POPULATION:
Structure and Density
This species is rather common locally, colonies can consist of hundreds of individuals (Jacobs *et al.*, 2008an; IUCN, 2009; Monadjem *et al.*, 2017cl).

Trend
2016: Unknown (Monadjem *et al.*, 2017cl). 2008:- Unknown (Jacobs *et al.*, 2008an; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Menzies (1973: 937 - 941) reported that in Nigeria the male's testes reached their maximum size in November. The size was about 50% larger than in July, when the minimum size was reached. He was also able to find spermatozoa in July, November and December (most). Most of the females he collected in March were pregnant, whereas those collected in May were lactating. A few lactating bats were still found in July.

For Malawi, Happold and Happold (1990b: 566) reported that young are born early in the wet season.

Orr and Zuk (2014: 902) refer to Racey (1982) [who in turn refers to Menzies (1973)] and indicated that in *R. landeri* it can take up to two months before the blastocyst gets implanted.

PARASITES:
PROTOZOA
Adam and Landau (1973a: 5) report on the presence of a protozoan parasite of the genus *Polychromophilus* (Haemoproteidae) in *R. landeri*. About 50 % of the specimens from Congo they examined, were found to be infected. Gametocytes were found year-round. The bats were also infested by the nycteribiids *Penicillidia fulvida* Bigot, 1885 and *Nycteribia schmidlii scotti* Falcoz, 1923, of which the prior was a major carrier of *Polychromophilus* sporozoites. Schaer *et al.* (2013a: 17416) also found a *Nycteria* parasite (possibly *N. congolensis* or *N. gabonensis*) in one out of two West African bats they examined. Arnuphapprasert *et al.* (2020: Suppl.) reported on GenBank data for *Nycteria* from bats from Guinea and Sierra Leone.
Polychromophilus ? murinus was reported by Garnham (1973: 237), based on a record by Adam and Landau.

Espinosa-Álvarez *et al.* (2018: Suppl.), Cai *et al.* (2019: Suppl.) and Sato and Mafie (2022: 2) reported *Trypanosoma livingstonei* from three bats from Mozambique. Four out of eight Ugandan bats were also infected by this species (Babyesiza *et al.*, 2025: 4).

In Cameroon, Tsague *et al.* (2024: Suppl.) mentioned the presence of either *Trypanosoma* cf. *livingstonei* or *Trypanosoma* sp.

Schaer *et al.* (2015a: 381) found *Nycteria* sp, in a bat from Guinea and *Nycteria* cf. *congolensis* in a *R. landeri* from Sierra Leone. Perkins and Schaer (2016: Suppl.) reported on *Nycteria congolensis* (Garnham, 1966) from Sierra Leone, and *Nycteria* sp. from Côte d'Ivoire or Guinea. Rosskopf *et al.* (2018: 31) also found *Nycteria* parasites in bats from Gabon. These parasites were also found by Tsague *et al.* (2021: 3) in two out of 10 bats from the Centre province in Cameroon.

Justine (1989b: 537, 544) described two new stomach parasites: *Capillaria landauae* and *Capillaria brosseti* (Nematoda) from *R. landeri* from Makokou (Gabon).

Werb *et al.* (2024: 476) reported a putative new *Plasmodium* from a bat from Sierra Leone.

Polyctenidae
Androctenes horvathi Jordan, 1912 recorded from Congo (Haeselbarth *et al.*, 1966: 17).

ARACHNIDA
Ixodidae
Orlova *et al.* (2024: 155) reported a new host-parasite association for this species with *Ixodes simplex* Neumann, 1906.

Myobiidae;
Bochkov and Fain (2003: 41) referred to *Neomyobia guineensis* Fain, 1972 on bats from Guinea-Bissau.

DIPTERA
Streblidae
Ascodipteron lophotes Monticelli 1898 from Kenya (Haeselbarth *et al.*, 1966: 106, but Maa (1965) suggests that these records need verification). *Brachytarsina africana* (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Penicillidia*

pachymela Speiser, 1901, from Somalia, Sudan, Kenya, Tanzania, the Congo, Guinea and the Cameroon Mts (Haeselbarth *et al.*, 1966: 114). *Raymondia intermedia* Jobling, 1936 in Sierra Leone (Haeselbarth *et al.*, 1966: 102), Kenya (Haeselbarth *et al.*, 1966: 102, host referred to as *R. axillaris*), see also Shapiro *et al.* (2016: 255). *Raymondia simplex* Jobling, 1955 at Kasongo, Congo (Haeselbarth *et al.*, 1966: 104; Shapiro *et al.*, 2016: 256). *Raymondia waterstoni* Jobling, 1931 (Shapiro *et al.*, 2016: 256).

Nycteribiidae
Verrett *et al.* (2022: 8) reported *Penicillidia fulvida* (Bigot, 1885) from Kenyan *Rhinolophus* cf. *landeri*.

Dick *et al.* (2023: 78) mentioned that *Penicillidia (Penicillidia) pachymela* Speiser, 1901 has been found on *Rhinolophus landeri* and both *Nycteribia schmidlii scotti* Falcoz, 1923, *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) on *Rhinolophus* cf. *landeri*.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Rhinolophus landeri*: Astroviruses and Coronaviruses. In a more restricted study (3 localities), Kamau *et al.* (2022: 5) also reported the presence of viruses of these two families, but also retroviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Seven out of 58 (12.1 %) Kenyan bats tested positive for CoV (Tao *et al.*, 2017: Suppl.).

Meyer *et al.* (2024: 4) found a single Ghanaian bat to be infected by CoV 2b viruses.

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen they examined from Ghana tested negative for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*. In South Africa, however, Mortlock *et al.* (2015: 1841) reported that the only *R. landeri* specimen they examined, tested positive for *Paramyxovirus* sequences.

Picornaviridae
Hepatovirus
Zeghbib *et al.* (2019: Suppl) reported this virus from a Ghanaian bat.

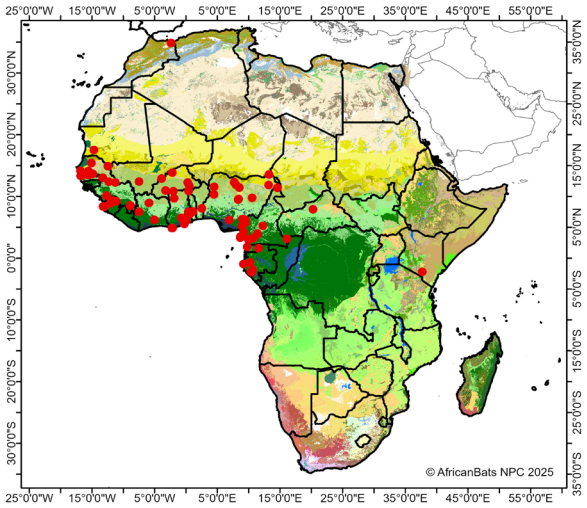

Figure 108. Distribution of *Rhinolophus landeri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Mali, Mauritania, Morocco, Nigeria, Senegal, Sierra Leone, The Gambia, Togo.

Rhinolophus lobatus Peters, 1852

1852. *Rhinolophus lobatus* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 41, pl 9; pl 13, figs 16 - 17. Publication date: 1852. Type locality: Mozambique: S bank Zambesi River, Tette: Sena [17 28 S 35 01 E]. [Goto Description]. Syntype: ZMB 24922: ♂, complete skeleton. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 24927: ♀, complete skeleton. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 2496: ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 375: ♀, skin only. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). - Comments: Brown and Dunlop (1997: 1) mention the type locality as "Africa orientalis, Sena, Tette" (=Sena, Mozambique) restricted by Moreau *et al.* (1946: 399). For coordinates: see Ansell and Dowsett (1988: 33). Taylor *et al.* (2018a: 22) situate Sena at -15.679 S, 33.809 E [=15 40 44 S 33 48 32 E]. This is in the Tete province, but north of Tete and 57 km north of the Zambezi River, whereas they also mention the locality to be on the south bank of the Zambezi River. According to Google maps these coordinates point to Muchena, which is on the Revuboe River. We believe the type locality is the same as "Vila de Sena", which is located at 17 26 30 S 35 01 38 E in the Sofala province, at the south bank of the Zambezi River.

1898. *Rhinolophus angolensis* Seabra, J. Sci. mat. phys. nat., ser 2, 5: 250. Type locality: Angola: Hanha [12 15 S 13 45 E]. [Goto Description].

? *Rhinolophus landeri lobatus:* (Name Combination).

TAXONOMY:



Figure 109. *Rhinolophus lobatus*, Zanzibar Island.

Used to be included in *R. landeri* Martin, 1838, but Taylor *et al.* (2018a: 22) found molecular differences which led them to recognize the taxon as a separate species. They also transferred *angolensis* Seabra, 1898, although this taxon might turn out to be a separate species. Taylor *et al.* (2019b: 535) indicated that the above analyses was based on a contaminated cyt-*b* sequence of *R. landeri*, but a new analyses with a correct sequence led to an identical result.

COMMON NAMES:
English: Lobed Horseshoe Bat, Peters's Horseshoe Bat. German: Peters Hufeisennase.

CONSERVATION STATUS:
Global Justification

Assessment History
Regional
South Africa (as *R. landeri*): 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016h). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

GENERAL DISTRIBUTION:
For southern African "*R. landeri*", Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,008,924 km^2. Taylor *et al.* (2018a: 25) suggest that all savannah populations in southern and eastern Africa might belong to *R. lobatus*.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 560); Burundi; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259Monadjem *et al.*, 2010d: 560); Kenya; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 560); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 560; Monadjem *et al.*, 2010c: 379); Namibia; Rwanda; South Africa (Monadjem *et al.*, 2010d: 560); Tanzania (including Unguja [=Zanzibar] [O'Brien, 2011: 286]); Uganda; Zambia (Ansell, 1969; Ansell, 1978; Monadjem *et al.*, 2010d: 560); Zimbabwe (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 560) [All as *R. landeri*].

However, as most of the underlying specimens have not been re-examined, some records from the northeastern DRC and northern Uganda might actually represent *R. landeri*. Grunwald *et al.* (2025: 292) also indicate that the geographic ranges of *R. landeri* and *R. lobatus* remain uncertain.

ECHOLOCATION:
In South Africa, Aldridge and Rautenbach (1987) reported (as *R. landeri*) a maximum frequency of 110 kHz for individuals from Pafuri, while Jacobs *et al.* (2007a) reported a peak frequency of 107.3 (± 2.1) kHz (detector type and locality not reported). Monadjem *et al.* (2010c: 379) reported from Mozambique that the peak echolocation frequencies for a single female was102.2 kHz (ANABAT), while a single male was recorded at 104 kHz (Pettersson S240x).

Four specimens from Chihalatan and Malashane (Mozambique) had peak frequency of 106.8 ± 0.4 kHz (Taylor *et al.*, 2018a: 24).

ROOST:
For *Rhinolophus* cf. *lobatus*, Jackson *et al.* (2023: 5) reported three roosts in buildings (Taita-Taveta county, Kenya), which were all shared with two other species of bats.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
HAEMOSPORIDA
Texeira and Camargo [in Lima *et al.* (2013: 13)] described *Trypanosoma livingstonei* from a "*R. landeri*" specimen collected in Mozambique (see also Barbosa *et al.*, 2016: 215).

DIPTERA
Streblidae
Raymondia aspera Maa, 1968 was reported from "*R. landeri*" in Mozambique (Shapiro *et al.*, 2016: 254).

VIRUSES:
Astroviridae
None of the nine Mozambican bats tested by Hoarau *et al.* (2018: 2) was positive for Astroviridae.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera of two "*R. landeri*" specimens from then Limpopo Province, South Africa, neither was positive (0/2).

Hoarau *et al.* (2021: Suppl.) reported Mozambican bats testing positive for viruses belonging to this family.

Joffrin *et al.* (2020: 4) reported on an Alphacoronavirus in a bat from Mozambique.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Congo (Democratic Republic of the), Kenya, Malawi, Mozambique, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe.

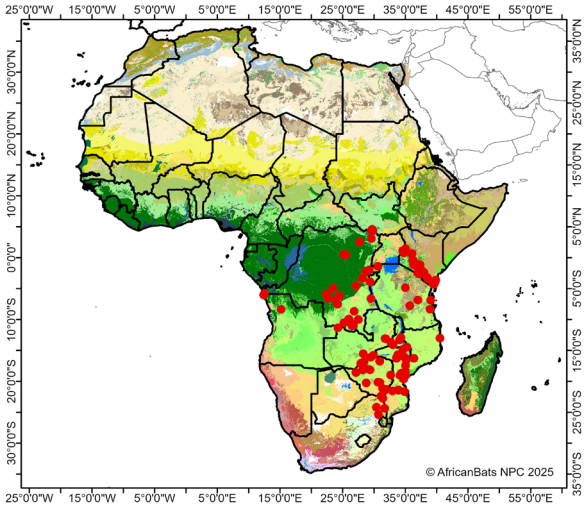

Figure 110. Distribution of *Rhinolophus lobatus*.

Rhinolophus mabuensis Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012

*2012. *Rhinolophus mabuensis* Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, PLoS ONE, 7(9): 17. Publication date: 12 September 2012. Type locality: Mozambique: Mt. Mabu [161702S 362353E, 1043 m]. Holotype: DNSM 10842: ad ♀, skull and alcoholic. Collected by: Michael Curran and Mirjam Kopp; collection date: 13 October 2008. Baculum prepared Taylor *et al.* (2012c: 17). Paratype: DNSM 11485: ad ♀, skull and alcoholic. Collected by: J. Bayliss; collection date: 5 September 2009. - Etymology: Taylor *et al.* (2012c: 17) selected the specific epithet to draw attention to the serious threats to the unique biodiversity isolated on the montane forest islands in northern Mozambique – notably Mts Mabu and Inago. None of these landforms lie within formally protected areas, and all are undergoing major habitat degradation and destruction from ever-increasing human activities - hunting, fires, timber harvesting and expanding agriculture. - ZooBank: C205928E-D72C-40D5-9647-FDC9391CB1A6. (Current Combination).

TAXONOMY:
Based on mitochondrial and nuclear DNA sequences and morphological and morphometric data, Taylor *et al.* (2012c) found that the *Rhinolophus hildebrandtii* group includes more species than previously recognized.

The closest relative of this species is *Rhinolophus hildebrandtii* from East Africa and it separated from this species approximately 1 - 2 mya (Bayliss *et al.* (2024: 10).

COMMON NAMES:
English: Mount Mabu Horseshoe Bat. German: Mt Mabu Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Endangered B2ab(iii) ver 3.1 (2001) as the species is found only in montane forest on Mt Mabu is 80 km² in extent. Assuming lesser extent on Mt Inago, and even if the species range includes Mt Mulanje which is 650 km² in extent (although much of this would be degraded habitat), it is reasonable to expect that the area of occupancy (AOO) is <500 km². Since the species is known from potentially only three or four isolated montane forests, and since Bayliss *et al.*, 2014) provide evidence of alarming continuing decline in the extent and quality of forest habitat on Mt. Mabu, the species qualifies as Endangered (Taylor, 2019b).

Assessment History
Global
2016: EN B2ab(iii) (ver 3.1 2001) (Taylor, 2019b).

Regional
None known.

MAJOR THREATS:
Taylor (2019b) report that the habitat of the species at Mt Mabu is undergoing major degradation and destruction from ever increasing human activities: hunting, fires, timber harvesting and expanding agriculture (Bayliss *et al.*, 2014). Similar problems, along with widespread afforestation of lower and mid slopes, have been reported from Mt Mulanje which may harbour populations of this species (Curran *et al.*, 2012).

CONSERVATION ACTIONS:
Pernet *et al.* (2014) highlighted the biodiversity importance of Mt Mabu (at least 10 new species

from there have been recently described including *R. mabuensis*). The government of Mozambique has agreed to protect the forest but no formal gazetting of this decision has been taken.

Taylor (2019b) report that it is also not clear whether populations from Mt Mulanje constitute *R. mabuensis*, or *R. hilderbrandtii sensu stricto*, which occurs further north in Tanzania. Montane forests on Mt Mulanje form part of a national park but the size of this park has decreased in recent years. The Mount Mulanje Conservation Trust has been set up to project the national park.

GENERAL DISTRIBUTION:
Known only from two mountains in northern Mozambique but quite possibly extending to nearby Mts. Namuli, Chiperone, Mulanje and the Malawi Rift (Taylor *et al.*, 2012c: 17).

Accurate delimitation of this species' range is subject to further collecting and reappraisal of existing museum material, previously referred to as *R. hildebrandtii*.

Native: Mozambique (Taylor *et al.*, 2012c: 17).

POPULATION:
Structure and Density
There is no information about population size or population trend for this species (Taylor, 2019b).

Trend
2016: Unknown (Taylor, 2019b).

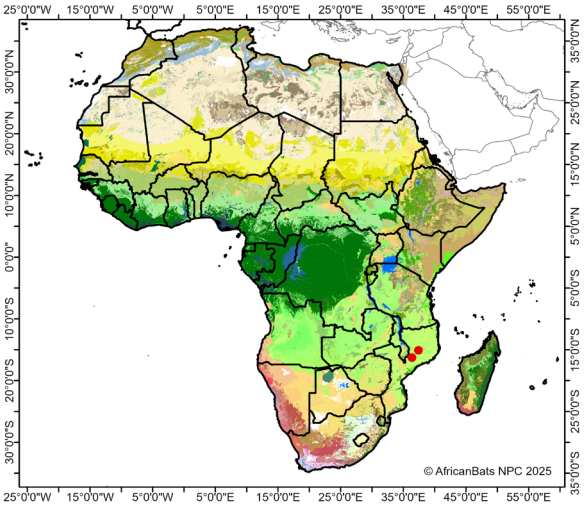

Figure 111. Distribution of *Rhinolophus mabuensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Mozambique.

Rhinolophus maclaudi Pousargues, 1898

*1898. *Rhinolophus Maclaudi* Pousargues, Bull. Mus. natn. Hist. nat., Paris, sér 1, 3 (8): 358, f 1, 2 (for 1897). Publication date: 22 January 1898. Type locality: Guinea: Conakry Island [09 31 N 13 43 W]. [Goto Description]. Holotype: MNHN ZM-MO-1897-981: ♀, skull and alcoholic. Collected by: Dr. C. MacLaud. Number 177 in Rode (1941: 237). - Comments: Grubb *et al.* (1998: 78) mention 1898 as year of publication. - Etymology: Named in honour of dr. Maclaud, collector of the holotype (Pousargues, 1897: 361). (Current Combination).

? *Rhinolophus maclaudi:* (Current Spelling).

TAXONOMY:
R. maclaudi is an ecomorphological outlier having long-ears, which traditionally placed it in the *R. philippinensis* group (Andersen, 1905c). Csorba *et al.* (2003: xvii, 63 - 64) state that it is located well inside the Africa clade, in the *maclaudi*-group, and are followed by Simmons (2005: 358). Koopman (1993a: 167) included *ruwenzorii* and *hilli*, but this is revised by Fahr *et al.* (2002), who recognizes them as distinct species (followed by Csorba *et al.*, 2003 and Simmons, 2005).

COMMON NAMES:
Czech: vrápenec Maclaudův. English: MacLaud's Horseshoe Bat. French: Rhinolophe de MacLaud. German: Maclauds Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN B2ab(iii) ver 3.1 (2001)) because its area of occupancy (cave roosts) is probably less than 500 km², its distribution is severely fragmented through habitat degradation, and the extent of its habitat in the Fouta Djallon Highlands is declining (Fahr, 2008l; IUCN, 2009).

Assessment History
Global
2008: EN B2ab(iii) ver 3.1 (2001) (Fahr, 2008l; IUCN, 2009). 2004: EN B1ab(iii) ver 3.1 (2001) (Fahr, 2004e); IUCN, 2004. 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The relatively limited range of *Rhinolophus maclaudi* is quite densely populated, and it is threatened by habitat loss and degradation of remaining patches of forest, and by

overharvesting for the bush meat trade (Fahr *et al.*, 2002).

Sagot and Chaverri (2015: 1670) mention habitat degradation or loss, and hunting as major threats for this species.

CONSERVATION ACTIONS:
Fahr (2008l) [in IUCN (2009)] reported that there appear to be no direct conservation measures in place. It is not known if *Rhinolophus maclaudi* is present in any protected areas. Protection of habitat, further research, and awareness education urgently required.

GENERAL DISTRIBUTION:
Rhinolophus maclaudi is known from a very few localities in eastern Guinea. Fahr *et al.* (2002) report that "apart from the type locality, supposedly Conakry Island, all records are located along the lower, southern slope of the Fouta Djallon region between Kindia and Mamou near the border with Sierra Leone". However, recent surveys have revealed additional localities in the Fouta Djallon Highlands, ranging as far north as the Gessorewoul River in Prefecture Mali (Weber and Fahr, 2007).

Fahr (2007a: 104) re-identified specimens reported from Liberia by Simmons (2005: 358) as *R. ziama*. Specimens from Nigeria reported by Koopman *et al.* (1995: 6, 19), Happold (1987: 60 - 61), and Csorba *et al.* (2003: 64) were re-identified Fahr *et al.* (2002: 99) as *R. hildebrandtii*.

Native: Guinea.
Presence uncertain: Liberia (Simmons (2005: 358); Nigeria (Koopman *et al.*, 1995: 6, 19; Happold, 1987: 60 - 61; Csorba *et al.*, 2003: 64).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Csorba *et al.* (2003: 63) indicate that *R. maclaudi* is a very large species with enormous ears (40.0 - 44.0 mm) and a broad horseshoe, covering almost the whole muzzle. There is also a distinct ridge running on its surface nearly parallel to the outer ridge. There is no secondary horseshoe. The sella is very broad with a broadly rounded summit and parallel margined above. The lancet is long, narrow and cuneate.

ROOST:
For Guinea, Weber and Fahr (2006: 4) indicate that *R. maclaudi* largely or exclusively depends on the availability of caves as day roosts.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species. The species roosts singly or in small groups (Fahr *et al.*, 2002).

Trend
2008: Decreasing (Fahr, 2008l; IUCN, 2009).

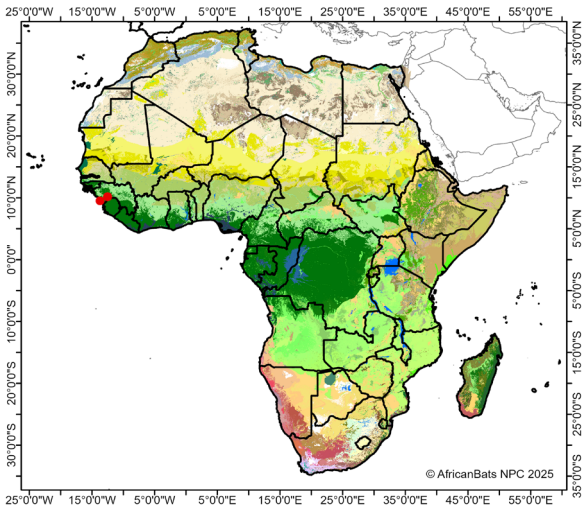

Figure 112. Distribution of *Rhinolophus maclaudi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea.

Rhinolophus maendeleo Kock, Csorba and Howell, 2000

*2000. *Rhinolophus maendeleo* Kock, Csorba and Howell, Senckenb. biol., 80 (1/2): 233, 234, figs 1, 4, 7. Publication date: 22 December 2000. Type locality: Tanzania: Tanga district: 2.5 km W of Tanga, Mkulumuzi River Gorge: Amboni Cave Forest [05 05 S 39 02 E, 0 - 80 m]. [Goto Description]. Holotype: SMF 79643: ad ♂, skull and alcoholic. Collected by: L. Stubblefield; collection date: 25 February 1992; original number: KMH 7673. Paratype: SMF 66960: ad ♀. Collected by: H. Grossmann; collection date: 29 August 1985; original number: KMH 3216. - Etymology: From the Swaihili "*maendeleo*" for progress; a noun in apposition. Named in allusion to the increasing knowledge of the Tanzanian bat fauna (see Kock *et al.* (2000). (Current Combination).

TAXONOMY:
adami species group (Csorba *et al.*, 2003: 5 - 7; Simmons, 2005: 359). See Csorba *et al.* (2003: 6) for remarks on taxonomy.

COMMON NAMES:
Czech: vrápenec tanganjický. English: Maendeleo Horseshoe Bat. French: Rhinolophe de Tanga. German: Tanzania-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) is very little information on its extent of occurrence, status and ecological requirements (Jacobs *et al.*, 2008ae; IUCN, 2009; Cooper-Bohannon, 2020).

Assessment History
Global
2018: DD ver 3.1 (2001) (Cooper-Bohannon, 2020). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008ae; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004r; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are unknown (Jacobs *et al.*, 2008ae; IUCN, 2009), but disturbance or destruction of cave sites or habitat destruction of forest reserves this species has been recorded in would pose a threat (Cooper-Bohannon, 2020). Cooper-Bohannon (2020) also, the forests in which the species occurs are rapidly being degraded and clear-cut to make way for slash-and-burn agriculture.

CONSERVATION ACTIONS:
Relatively little is known about this species and further surveys are needed to better understand its distribution, ecological requirements, threats, population size and trend (Cooper-Bohannon, 2020). While the species is present in the Mazumbai Forest Reserve, further habitat protection is likely needed (Jacobs *et al.* (2008ae) in IUCN (2009)). Cave assessments, including baseline data such as population size, time of year the caves are occupied, if caves are maternity roosts, etc. and would help to inform future conservation action (Cooper-Bohannon, 2020).

GENERAL DISTRIBUTION:
Rhinolophus maendeleo is a poorly known species that has only been recorded from two localities in Tanzania at elevations of up to 1,900 m asl, the type locality of 'Amboni Cave Forest, Mkulumuzi River Gorge, 2.5 km W of Tanga, Tanga District' (Anciaux de Faveaux, 1958) and Mazumbai Forest Reserve in the Usambara Mountains. It has recently been recorded from a single locality in Mozambique. Additional surveys are needed to better determine the range of this recently described species.

Native: Mozambique (Monadjem *et al.*, 2010d: 560; Monadjem *et al.*, 2010c: 379); Tanzania (Kock *et al.*, 2000; Csorba *et al.*, 2003: 6).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Csorba *et al.* (2003: 6) indicate that the skull of *R. maendeleo* has an open foramen infraorbitale (without bony bar).

DETAILED MORPHOLOGY:
Baculum
See Csorba *et al.* (2003: 6).

POPULATION:
Structure and Density
Rhinolophus maendeleo is currently known only from two specimens, and there is no information on population sizes or trends (Jacobs *et al.*, 2008ae; IUCN, 2009; Cooper-Bohannon, 2020).

Trend
2018: Unknown (Cooper-Bohannon, 2020). 2008: Unknown (Jacobs *et al.*, 2008ae; IUCN, 2009).

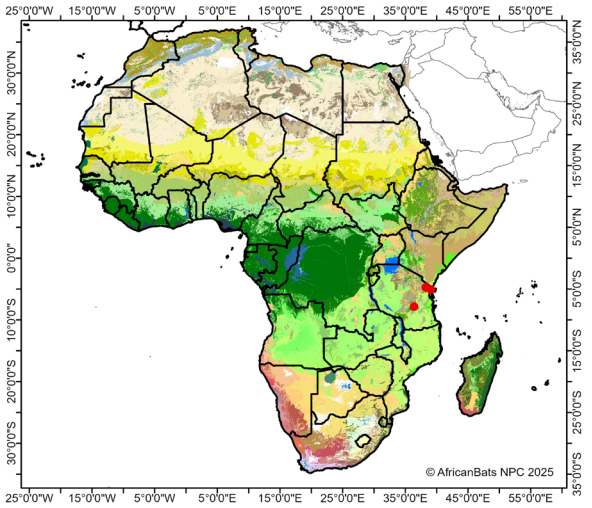

Figure 113. Distribution of *Rhinolophus maendeleo*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Tanzania.

†*Rhinolophus maghrebensis* Gunnell, Eiting and Geraads, 2011

*2011. *Rhinolophus maghrebensis* Gunnell, Eiting and Geraads, N. Jb. Geol. Paläont. Abh., 260 (1): 56, figs 3A, 7A. Publication date: January 2011. Type locality: Morocco: Ahl al Oughlam [ca. 33 35 N 07 30 W]. Holotype: INSAP AaO 4655. Right maxilla with P4-M3. Paratype: INSAP AaO 4673. Left dentary p4-m3. - Etymology: Name taken from *Maghreb* ("countries of the setting sun"), the Arabic name for north-western African countries (Morocco, Algeria, Tunisia) (see Gunnell *et al.*, 2011: 56). (Current Combination).

2013. *Rhinolophus maghrebiensis:* Stoetzel, Palaeog., Palaeoclim., Palaeoecol., 392: 373. Publication date: 29 September 2013. (Lapsus).

TAXONOMY:
Gunnell *et al.* (2011: 56) describe it as a large species of the *Rhinolophus ferrumequinum* phenotypic group - larger than extant African *Rhinolophus* species *R. alticolus, R. blasii, R. euryale, R. denti, R. landeri, R. mehelyi, R. hipposideros*, and *R. simulator*, smaller than *R. hildebrandtii*.

Rhinolophus mehelyi Matschie, 1901

*1901. *Rhinolophus mehelyi* Matschie, Sber. Ges. naturf. Freunde Berlin, 225. Type locality: Romania: Ilfov province: Bucharest [44 26 N 26 06 E]. - Etymology: In honour of Lajos Méhely (1862 - 1952) (see Kozhurina, 2002: 16). (Current Combination).

1904. *E[uryalus] barbarus* K. Andersen and Matschie, Sber. Ges. naturf. Freunde Berlin, 79. Type locality: Morocco: Tangiers [35 48 N 05 50 W]. [Goto Description]. Holotype: ZMB 12967: ♂, skull and alcoholic. Collected by: Kurt Floericke; collection date: 12 March 1898. See Turni and Kock (2008). Paratype: MHNG |TS525|: ♂, skull and alcoholic. Former ZMB 12968, exchanged in 1909; see Turni and Kock (2008: 28). Paratype: MHNG |TS526|: ♂, skull and alcoholic. Former ZMB 12972, exchanged in 1909; see Turni and Kock (2008: 28). Paratype: ZMB 12969: ♂, skull and alcoholic. Collected by: Kurt Floericke. See Turni and Kock (2008: 28). Paratype: ZMB 12970: ♂, skull and alcoholic. Collected by: Kurt Floericke. See Turni and Kock (2008: 28). Paratype: ZMB 12971: ♂, skull and alcoholic. Collected by: Kurt Floericke. See Turni and Kock (2008: 28). Paratype: ZMB 12972: Collected by: Kurt Floericke; collection date: 12 March 1898. Paratype: ZMB 12973: alcoholic (skull missing). Collected by: Dr. Lühe; collection date: 12 March 1898. From cave near Tebourba; see Turni and Kock (2008: 28). Paratype: ZMB 12974: ♂, alcoholic, skull and skeleton. Collected by: Dr. Lühe; collection date: 12 March 1898. From cave near Terbourba, see Turni and Kock (2008: 28) [lost]. Paratype: ZMB 12975: alcoholic (skull missing). Collected by: Dr. Lühe; collection date: 12 March 1898. From cave near Tebourba; see Turni and Kock (2008: 28).

1904. *E[uryalus] meridionalis* K. Andersen and Matschie, Sber. Ges. naturf. Freunde Berlin, 79. Type locality: Algeria: "Algeria". Holotype: ZMB 12976: ♀, skull and alcoholic. Collected by: Verreaux; collection date: undated. See Turni and Kock (2008: 26). Paratype: ZMB 3052: ♀. Collected by: Verreaux; collection date: undated. Number of paratype is 3052, not 12977 as mentioned by Andersen and Matschie (1904: 83): see Turni and Kock (2008: 29).

1955. *Rhinolophus euryale tuneti* Deleuil and Labbé, Bull. Soc. Sci. nat. Tunisie, 8: 52, 53. Type locality: Tunisia: Cap Bon: El Haouaria cave [37 03 N 11 01 E]. [Goto Description]. Neotype: USNM 498999: ad ♂, skin and skull. Collected by: Tom Vaughan and Pamela Vaughan; collection date: 4 May 1975; original number: TPV 3244. Fisher and Ludwig (2015: 54) mention that a type specimen was not designated by Deleuil and Labbe (1955a), and that the type series has been lost. They also indicate that Cockrum (1976: 868) incorrectly gave the wrong number when assigning the neotype (USNM 498998). - Comments: Horáček *et al.* (2000: 102) consider it a valid subspecies. Dalhoumi *et al.* (2011: 267) indicate that Deleuil and Labbe (1955a) based their description on a specimen belonging to *R. mehelyi* (type) and two belonging to *R. blasii* (paratypes), as was already suggested by Aellen and Strinati (1970: 231) and Cockrum (1976: 685).

1993. *tunetae:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 167. (Lapsus).

1995. *tunetai:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 81. (Lapsus).

2018. *Rh[inolophus] mehleyi:* Khelfaoui, Kebaci and Benyacoub, Bull. Soc. zool. France, 143 (2): 67. (Lapsus).

? *Rhinolophus euryale barbarus:* (Name Combination).

? *Rhinolophus mehelyi mehelyi:* (Name Combination).

? *Rhinolophus mehelyi tuneti:* (Name Combination).

TAXONOMY:
Revised by DeBlase (1972). *euryale* species group (Csorba *et al.*, 2003: 17 - 18; Simmons, 2005: 359). See Csorba *et al.* (2003: 17 - 18) for remarks on taxonomy.

Based on the measurements given by Andersen and Matschie (1904), Puechmaille *et al.* (2012: 216) suggest that *R. barbarus* Andersen et Matschie, 1904 and *R. meridionalis* Andersen et Matschie, 1904 are both synonyms of *R. mehelyi* Matschie, 1901 rather than of *R. euryale* Blasius, 1853.

Based on mitochondrial data, Najafi *et al.* (2019: 103, 106) estimated that *R. mehelyi* separated from *R. euryale* some 4.14 (3.17 - 5.09) mya. They also suggest that the African and southern-European haplotypes if *R. mehelyi* belong to one taxon, which is different from the Iranian haplotypes, and seem to support the division in subspecies (*mehelyi* and *tuneti*). However, further analyses of nuclear DNA is required to confirm this. Both groups became isolated some 1.18 (0.68 - 1.61) mya.

COMMON NAMES:
Albanian: Lakuriq nate hundëpatkua i Mehely-it. Arabian: Khaffash. Armenian: Մեհելիի պայտաքիթ. Azerbaijani: Eynəkli nalburun. Basque: Mehelyi ferra-saguzar. Belarusian: Падкаванос Мегеля. Bosnian: Meheljev potkovasti šišmiš. Breton: Frigribell Méhely. Bulgarian: Подковонос на Мехели. Castilian (Spain): Murciélago mediano de herradura, Rinolofo mediano de herradura. Catalan (Spain):

Ratpenat de ferradura mitjà, Rat penat mitjá de ferradura. Croatian: Meheljev potkovnjak. Czech: Vrápenec Mehelyův. Danish: Mehelys hestekonæse. Dutch: Mehely's hoefijzerneus, Mehely-hoefijzerneus. English: Mehely's Horseshoe Bat, Mediterranean Horseshoe Bat. Estonian: Meheli sagarnina. Finnish: Täpläherkko. French: Rhinolophe de Mehély, Rhinolophe des forêts, Rhinolophe de Roumanie. Frisian: Mehely's hoefizernoas. Galician (Spain): Morcego de ferradura mediano. Georgian: მეჰელის ცხვირნალა. German: Mehely-Hufeisennase. Greek: Ρινόλοφος του Mehely. Hebrew: פרסף חיוור, Parsaf Hiver. Hungarian: Méhely-patkósdenevér, Rhinolophos i mehelios. Irish Gaelic: Crú-ialtóg Mehely. Italian: Rinolofo di Méhely, Ferro di cavallo di Méhely. Latvian: Meheļa pakavdegunis. Lithuanian: Mehelio pasagnosis. Luxembourgish: Méhelÿ-Huffeisennues. Macedonian: Мехелов потковичар. Maltese: Rinolofu ta' Mehely. Montenegrin: Mehelijev potkovičar. Norwegian: Middelhavshesteskonese. Polish: Podkowiec średni. Portuguese: Morcego-de-ferradura-mourisco. Rhaeto-Romance: Rinolof da Méhely. Romanian: Liliacul cu potcoavă a lui Mehely, Liliac-românesc. Russian: Подковонос Мегели (очковый). Serbian: Тамнооки потковичар [= Tamnooki potkovičar]. Scottish Gaelic: Crudh-ialtag Mehelyi. Slovak: Podkovár Mehélyho. Slovenian: Mehelyjev podkovnjak. Swedish: Kusthästskonäsa. Turkish: Mehely Nalburunlu Yarasası. Ukrainian: Підковик (Підковоніс) Мегеля, Підковик масковий (= Pidkovyk maskovyy). Welsh: Ystlum pedol Mehely.

Conservation status:

Global Justification

The species is declining throughout its range, which is becoming increasingly fragmented. The rate of decline has been estimated as 10 % in the last 10 years in Andalucia (Spain). Elsewhere, declines have not been quantified but appear to have been considerable, with some colonies having been reduced to a fraction of their former size. Overall, declines throughout the global range are thought likely to exceed 30 % over 3 generations (27 years) over a time window including both the past and the future. The species is going extinct in France and is declining in Morocco due to disturbance in caves. The species only roosts in caves and does not use artificial roosts. Hence the species is listed as Vulnerable (VU A4c ver 3.1 (2001)) (Hutson *et al.*, 2008n; IUCN, 2009; Alcaldé *et al.*, 2016).

Assessment History

Global

2016: VU A4c ver 3.1 (2001) (Alcaldé *et al.*, 2016). 2008: VU A4c ver 3.1 (2001) (Hutson *et al.*, 2008n; IUCN, 2009). 1996: VU A2c ver 2.3 (1994) (Baillie and Groombridge, 1996).

Regional

None known.

Major threats:

Rhinolophus mehelyi is affected by disturbance and loss of underground habitats, changes in foraging habitats, and destruction of caves by tourism. Mortality due to collision with cars is a problem in some areas (e.g., Portugal). The reasons for the declines are not fully understood (Hutson *et al.*, 2008n; IUCN, 2009; Alcaldé *et al.*, 2016).

According to Sherwin *et al.* (2012: 174), climatic change will have an important impact due to the following risk factors: its small range, roosting in caves or trees, its water stress and aerial hawking feeding style. Piccioli Cappelli *et al.* (2021: 10) identified this species (together with *Nyctalus lasiopterus* as running the highest risk of extinction due to climate change in Europe and North-west Africa.

Roost loss or disturbance, and habitat degradation or loss are considered the major threats for this species by Sagot and Chaverri (2015: 1670).

Conservation actions:

Hutson *et al.* (2008n) [in IUCN (2009)] and Alcaldé *et al.* (2016) reported that *Rhinolophus mehelyi* is protected by national legislation in all European range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention where those apply. It is included in Annex II (and IV) of EU Habitats and Species Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. There is some habitat protection through Natura 2000 (some roosts are already protected by national legislation). An EU-LIFE funded project aims to ensure the long-term conservation of the large populations of cave and forest-dwelling bats, including this species, in Spain. There are no specific conservation measures in place in North Africa. Research is required on the causes of the declines across the range.

General distribution:

Rhinolophus mehelyi is largely restricted to the Mediterranean. It has a discontinuous distribution from north Africa (Morocco, Algeria, Tunisia and Egypt) and southern Europe (southern Portugal and Spain, possibly one occurrence in France, a few places in Italy and the Balkans) through Asia

Minor, Anatolia, to Transcaucasia, Iran and Afghanistan (where its exact roost location is not known: Srinivasulu et al., in press). It is patchily distributed in some large and vulnerable colonies. It occurs up to 2,000 m in High and Saharan Atlas mountains, although it is typically found at lower altitudes in other parts of its range (e.g., in Spain it tends to occur below 700 m).

Puechmaille (2023: 915) indicates that the records from Egypt are all for specimens collected until the 1950s.

Native: Afghanistan; Algeria (Horáček *et al.*, 2000: 102); Armenia; Azerbaijan; Bosnia and Herzegovina; Bulgaria; Cyprus; Egypt; Georgia; Gibraltar; Greece; Iran, Islamic Republic of; Iraq; Israel; Italy (Sardinia, Sicily); Jordan; Libyan Arab Jamahiriya; Macedonia, the former Yugoslav Republic of; Mediterranean islands; Moldova; Montenegro; Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 359; Dbiba *et al.*, 2025: 6); Palestinian Territory, Occupied; Portugal; Romania; Russian Federation; Serbia; Slovenia; Spain; Syrian Arab Republic; Tunisia (Dalhoumi *et al.*, 2016b: 867; 2019b: 26); Turkey; Yugoslavia.

Regionally extinct: Croatia.

Presence uncertain: France.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Salsamendi *et al.* (2005)] mention a wing loading value of 9.3 Pa, aspect ratio 6.7 and tip shape index of 2.54 for a wingspan of 32 cm and a wing area of 160 cm^2 and a body mass of 15 g.

ECHOLOCATION:
Jones and Siemers (2010: 450) indicate that juveniles emit lower frequencies than adults, and that the CF-frequency is positively related to the body condition (mass/forearm length). Puechmaille *et al.* (2014b: 4) demonstrated that the body length and weight for bats caught during the mating season showed a strong positive correlation (which was significant) with the peak frequency in both sexes: larger and heavier bats call at higher frequencies. Females clearly show a preference for higher calling males, and the latter have a larger offspring. Puechmaille *et al.* (2014b: 6) also found that the distribution of the echolocation frequencies was not normally distributed in adults, but left-skewed (meaning that there are more individuals calling at higher frequencies). Furthermore (p. 7), they indicate [referring to Jones and Ransome (1993)] that the peak frequency in horseshoe bats increases with about 0.45 kHz during the first year and an average reduction of 0.09 kHz per year occurs over their lifetime.

For 16 Greek specimens, Papadatou *et al.* (2008b: 132) report a start frequency of 96.2 ± 7.06 kHz, a terminating frequency of 90.3 ± 2.16 kHz, a peak frequency of 109.5 ± 1.44 kHz, and a bandwidth of 5.1 ± 2.62 kHz. The duration of the call is 35.9 ± 12.04 ms, and the interpulse interval is 62.5 ± 23.92 ms.
Walters *et al.* (2012: suppl.) present the following figures for 41 calls from Bulgarian bats: duration: 27.73 ± 7.12 ms, F_{max}: 108.59 ± 1.51 kHz, F_{min}: 92.61 ± 4.73 kHz, bandwidth: 15.98 ± 4.44 kHz, F_{peak}: 107.78 ± 2.74 kHz. Tunisian bats emitted sounds at 106.11 ± 1.31 kHz (111.5 - 117.5 kHz; Dalhoumi *et al.*, 2016b: 866).

Luo *et al.* (2019a: Supp.) reported the following data: F_{peak}: 109.5 kHz, F_{start}: 96.2 kHz, F_{end}: 90.3 kHz, and duration: 35.9 ms.

Schuchmann *et al.* (2012: 161) found that both sexes were able to recognize the sex of conspecifics from their echolocation calls.

MOLECULAR BIOLOGY:
Karyotype
Đulić and Soldatovic (1969) and Rushton (1970 463) reported 2*n* = 58, FN = 64, a submetacentric X chromosome, and an acrocentric Y chromosome. While Baker *et al.* (1974; 1975) reported FN = 60 and BA = 4. Volleth *et al.* (2002: 483) and Volleth and Eick (2012: 166) report 2*n* = 58 and a segment number [= autosomal segments + X] of 44. Arslan and Zima (2014: 8) indicate that different numbers of bi-armed autosomes have been reported, leading to FNa values between 60 and 64.

Đulić and Soldatovic (1969: 5) also reported the type of the autosomes as 4 metacentric, 2 small-sized and 24 acrocentric.

HABITAT:
In south-western Spain, Russo *et al.* (2005: 327) found that *R. meheyli* least preferred open habitats but was frequently found in a semi-natural oak savanna habitat. Salsamendi *et al.* (2012a: 122) pointed out that this was in an area where both *R. mehelyi* and *R. euryale* occurred, and they reported that *R. mehelyi*, in another area, always foraged in woodlands, preferably in cluttered spaces, but also in less-cluttered/more-open ones, and was avoiding open spaces. They also indicated that the bats foraged generally less than 500 m from water bodies. The bats were using linear landscape elements (tree lines and riparian forests) to travel from their roosts to their feeding areas. Salsamendi *et al.* (2012a: 129)

also indicated that habitat types used by males and females in south-western Spain were different: males foraged in riparian forest and broad-leaved woodlands, whereas females foraged in denser, scrubland and eucalypt plantations.

HABITS:
Kameneva (1976) [in Pervushina *et al.* (2012: 750)] found that among captive *R. mehelyi* individuals, conflicts took place during foraging flights, although they were primarily friendly or neutral to one another when resting during the day.

ROOST:
Based on data from Sardinia, Russo *et al.* (2014: 9) rule out that *R. euryale* and *R. mehelyi* compete for roosting sites.

DIET:
In the Iberian peninsula, Salsamendi *et al.* (2009: 282) report that Lepidoptera form the most important prey category for this species (from 51.3 to 100.0 volume percent; 90.9 to 100.0 occurrence percentage), followed by Neuroptera, Diptera, Coleoptera, Hemiptera and undefined items. In Iran, Lepidoptera also form the dominant food item, followed by scarabaeid beetles and muscid dipterans (see Benda *et al.*, 2012a: 247).

In the southwestern Iberian peninsula, Arrizabalaga-Escudero *et al.* (2018: Suppl.) identified the following food items from faecal samples of *R. mehelyi* (food items marked with an asterisk were also found in faecal samples of *R. euryale*): Coleoptera (Cerambycidae: *Arhopalus ferus* (Mulsant, 1839)*); Diptera (Tachinidae: unidentified*; Anthomyiidae: *Hylemya* sp.; Muscidae: *Neomyia cornicina* (Fabricius, 1781); Calliphoridae: *Pollenia vagabunda* (Meigen, 1826)); Lepidoptera (Blastobasidae: *Blastobasis phycidella* (Zeller, 1839); Cosmopterigidae: *Eteobalea intermediella* (Riedl, 1966); Crambidae: *Calamotropha paludella* (Hübner, 1824)*; *Ostrinia nubilalis* (Hübner, 1796)*; *Udea ferrugalis* (Hübner, 1796); Erebidae: *Catocala nymphagoga* (Esper, 1787)*; Gelechiidae: *Teleiopsis* sp.*; Geometridae: *Camptogramma bilineata* (Linnaeus, 1758)*; *Ennomos quercaria* (Hübner, 1813)*; *Pachycnemia hippocastanaria* (Hübner, 1799)*; *Rhoptria asperaria* (Hübner, 1817)*; Lasiocampidae: *Malacosoma neustria* (Linnaeus, 1758); Lecithoceridae: *Eurodachtha canigella* (Caradja, 1920); Noctuidae: *Agrotis segetum/trux**; *Agrotis ipsilon* (Hufnagel, 1766)*; *Autographa gamma/pulchrina**; *Calophasia platyptera* (Esper, [1788])*; *Heliothis incarnata* Freyer, 1838; *Mythimna albipuncta* (Denis & Schiffermüller, 1775)*; *Mythimna vitellina* (Hübner, 1808); *Mythimna loreyi/sicula**; *Peridroma saucia* (Hübner, 1808)*; *Polyphaenis sericata* (Esper, 1787)*; *Sesamia nonagrioides* (Lefèbvre, 1827)*; Praydidae: *Prays fraxinella* Bjerkander, 1784*; Pterophoridae: *Crombrugghia laetus* (Zeller, 1847); *Emmelina monodactyla* (Linnaeus, 1758); *Stenoptilia zophodactyla* Duponchel, 1840; Pyralidae: *Pempelia palumbella* (Denis & Schiffermüller, 1775)*; Tortricidae: *Archips xylosteana* (Linnaeus, 1758); *Cnephasia* sp. 1*; *Cnephasia* sp. 2*; Yponomeutidae: *Zelleria oleastrella* (Millière, 1864); Neuroptera (Hemerobiidae: *Wesmaelius nervosus* (Fabricius, 1793); Chrysopidae: *Chrysoperla* sp.*; Myrmeleontidae: *Distoleon tetragrammicus* (Fabricius, 1798)*). Of the 64 prey taxa, 32 (representing over 75 % of all food items) were consumed by both *R. mehelyi* and *R. euryale*.

Benda *et al.* (2014c: 33) analysed 22 faecal pellets from Wadi Darnah (Libya) and found these to consist primarily of Blattoidea (99.1 % by volume) and 0.9 % of Lepidoptera.

POPULATION:
Structure and Density
Hutson *et al.* (2008n) [in IUCN (2009)] and Alcaldé *et al.* (2016) indicate that *Rhinolophus mehelyi* is an infrequent species, which is reported to have declined in all parts of its range for which data are available. In Andalucia (Spain), the rate of decline has been estimated at 10 % over the last ten years. The species is close to extinction in France (Rodrigues and Palmeirim, 1999), Romania (Botnariuc and Tatole, 2005), and north-east Spain (J. Juste and T. Alcalde *pers. comm.,* 2006). In France, only one individual was recorded in 2004 (S. Aulagnier *pers. comm.,* 2006), and in Romania the population was estimated at 5,000 in the 1950s, but now numbers approximately 100 (Dumitrescu *et al.*, 1962-3, Botnariuc and Tatole, 2005). It is also declining in southern Spain (Franco and Rodrigues de los Santos, 2001), Portugal (Rodrigues *et al.*, 2003), the Russian Federation (K. Tsytsulina *pers. comm.,* 2005), Georgia, and Morocco (SW Asia Workshop 2005). In Iran mixed-species colonies including *R. mehelyi*, which in the 1970s were estimated to be over 10,000 individuals, now only number a few hundred individuals (M. Sharifi *pers. obs.,* 2005). Summer nursery colonies typically number 30 - 500 individuals (although colonies of up to 3,000 individuals have been recorded, separated in smaller groups within the same cave). Winter clusters consist of up to 5,000 animals.

Trend
2016: Decreasing (Alcaldé *et al.*, 2016). 2008: Decreasing (Hutson *et al.*, 2008n; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Benda *et al.* (2014c: 30) captured a lactating female on 15 May at Wadi Darnah (Libya).

MATING:
Puechmaille *et al.* (2011b: 40-41) found that during the mating season, females prefer males with higher frequency calls, indicating that this high frequency is probably a signal of good body condition.

POSTNATAL DEVELOPMENT:
In western Iran, Sharifi (2004: 155) determined that Fa and body mass followed a linear pattern of growth until day 14 (resp. 1.55 mm/day and 0.58 g/day) and subsequently decreased to reach a stable level. The length of the gap of the metacarpal-phalangeal joint showed an increase up to 10 days and decreased until it had closed at over 55 days. At about four weeks of age, the young started to fly.

PARASITES:
Beaucournu and Kock (1996) report the presence of the flea *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921 on specimens from Algeria.

Benda *et al.* (2014c: 33) recorded the following parasites from Libyan *R. mehelyi*: Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921, Nycteribiidae: *Phthiridium biarticulatum* (Hermann, 1864), Streblidae: *Brachytarsina flavipennis* Macquart, 1851

Aellen (1955b) reported on the occurrence of the following nycteribid and streblid flies on bats from Morocco and Algeria: *Nycteribia (Nycteribia) latreillei* (Leach, 1817), *Nycteribia (Acrocholidia) vexata* Westwood, 1835, *Penicillidia dufouri* (Westwood, 1835), *Penicillidia conspicua* Speiser, 1901, and *Nycteribosca kollari* (Frauenfeld, 1855).

The following ectoparasites were found on Algerian bats by Bendjeddou *et al.* (2017: 15) and Khelfaoui *et al.* (2018: 67): Nycteribiidae: *Nycteribia (Nycteribia) pedicularia* Latreille, 1805 and *Phthiridium biarticulatum* Hermann, 1804; Streblidae: *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851; and Arachnida: *Spinturnix myoti* (Kolenati, 1856) and *Eyndhovenia euryalis* (G. Canestrini, 1885).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia vexata* Westwood, 1835, *Penicillidia conspicua* Speiser, 1901, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Eyndhovenia euryalis euryalis* (Canestrini, 1884), *Eyndhovenia euryalis oudemansi* (Eyndhoven, 1941); Streblidae: *Brachytarsina flavipennis* Masquart, 1851; and Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921.

Other nycteribiid flies reported by Júnior *et al.* (2020: Suppl.) (not necessarily from Africa) include: *Basilia italica* Theodor, 1954, *Basilia nana* Theodor, 1954, *Basilia nattereri* (Kolenati, 1857), *Nycteribia kolenatii* Theodor and Moscona, 1954, *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularis* (Latreille, 1805), *Nycteribia vexata* Westwood, 1835, *Phthiridium biarticulatum* Hermann, 1804.

From Iran, Sharifi *et al.* (2013: 181) mention the presence of the following ectoparasites: *Eyndhovenia* sp. (Acari: Spinturnicidae; on 89.65 % of the 87 bats examined, with 13.79 ind/bat, primarily on wing and tail membranes), *Penicillidia* sp. (Diptera: Nycteribiidae; 66.66 %, 2.31, mainly on fur) and one species from Streblidae (Diptera; 11.49 %, 1.80, on all parts of the body).

In Azerbaijan, Duszynski (2002: 6) mentions *Eimeria mehelyi* Musaev and Gauzer, 1971 (Apicomplexa) as parasite.

Sándor *et al.* (2021a: 4) report the argasid ticks *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) and *Carios vespertilionis* Latreille, 1802.

VIRUSES:
Coronaviridae - Coronaviruses
Luis *et al.* (2013: suppl.) mention the presence of a SARS coronavirus-related virus.

Alphacoronavirus
This virus was reported from Germany by Kohl and Kurth (2014: 3112).

Betacoronavirus
Kohl and Kurth (2014: 3112) report this virus from Bulgaria and Germany.

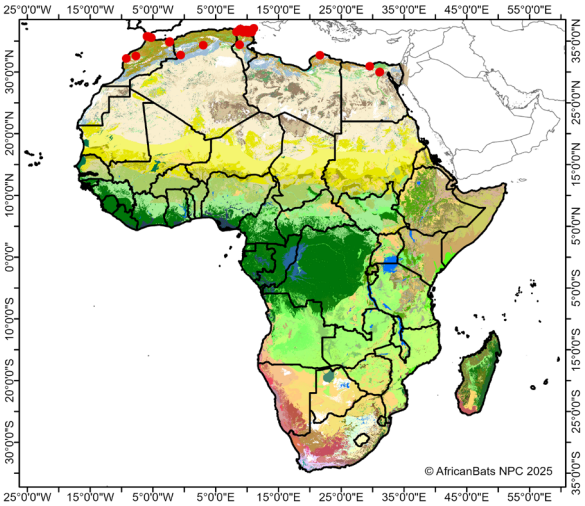

Figure 114. Distribution of *Rhinolophus mehelyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Egypt, Libya, Morocco, Tunisia.

†***Rhinolophus mellali*** Lavocat, 1961

*1961. *Rhinolophus ferrumequinum mellali* Lavocat, Notes Mém. Serv. Mines Carte geol. Maroc, 155: xxx. Type locality: Morocco: Beni Mellal. - Comments: The holotype consists of a left mandibular fragment with I, C, P_2-M_1 (Marandat, 1994: 60).
? *Rhinolophus mellali:* (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Early late Miocene to Early Pliocene (Chornelia and Hughes, 2022: 12)..

GENERAL DISTRIBUTION:
Northern Africa (Gunnell *et al.*, 2011: 70).

Rhinolophus mossambicus Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012

*2012. *Rhinolophus mossambicus* Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, PLoS ONE, 7(9): 19. Publication date: 12 September 2012. Type locality: Mozambique: Nissa Game Reserve: Maputo Camp [121056S 373300E, 489 m]. Holotype: DNSM 8578: ♂, skull and alcoholic. Collected by: Dr. Ara Monadjem; collection date: 1 July 2006. Baculum; skull and mandible in good condition (Taylor *et al.*, 2012c: 19). Paratype: DNSM 11276: ad ♀, skull and alcoholic. Paratype: DNSM 8577: ad ♀, skull and alcoholic. Paratype: DNSM 8579: ad ♂, skull and alcoholic. Baculum. Paratype: DNSM 8580: ad ♂, skull and alcoholic. Baculum. - Etymology: The name denotes the country of origin (Mozambique) of the type specimen of this species (Taylor *et al.*, 2012c: 20). - ZooBank: 0D97DC39-F9CD-415E-A7AE-4DCF70C807B4. (Current Combination).

TAXONOMY:
Based on mitochondrial and nuclear DNA sequences and morphological and morphometric data, Taylor *et al.* (2012c) found that the *Rhinolophus hildebrandtii* group includes more species than previously recognized.

Carr *et al.* (2017) performed some additional analyses, which confirmed that *R. mossambicus* forms a well-defined clade based on mtDNA, but based on nuclear DNA, however, this taxon groups with *R. fumigatus* from Namibia.

COMMON NAMES:
English: Mozambican Horseshoe Bat. German: Mossambique-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Schoeman (2017) listed as Least Concern because it is relatively widespread in Mozambique and eastern Zimbabwe. Its extent of occurrence is >20,000 km^2 and its area of occupancy (cave roosting sites) is probably >2,000 km^2. Although its population is probably decreasing through bushmeat hunting and guano mining, there is no evidence that the decrease has been rapid enough to warrant Near Threatened or threatened status.

Assessment History
Global
2016: LC ver. 3.1 (2001) (Schoeman, 2017).

Regional
None known.

MAJOR THREATS:
Schoeman (2017) report that this species is collected for bushmeat in Mozambique (particularly in the Inhassoro province). Additionally, the local communities disturb the roosts of this species with guano mining activities.

CONSERVATION ACTIONS:
R. mossambicus has been recorded from Niassa Game Reserve and Gorongosa National Park. Additional surveys are needed to learn more about the distribution, natural history and threats to this species. Existing cave roosts need to be protected from guano mining and hunting for bushmeat (S.M. Goodman and M.C. Schoeman unpublished data in Schoeman (2017). Other potential threats include habitat loss (due to charcoal collecting and logging) and fire (Schoeman, 2017).

GENERAL DISTRIBUTION:
Based on genetic data, the species is known from five localities in Mozambique from altitudes of 1,500 m - Chinizuia Forest, Gerhard's Cave, Gorongosa Caves, Namapa, Niassa Game Reserve and one locality, Lutope-Ngolangola Confluence in NW Zimbabwe. These scattered records across the subregion suggest that *R. mossambicus* is widespread across the savanna biome of Zimbabwe and Mozambique (Taylor *et al.*, 2012c: 20).

ECHOLOCATION:
In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 2 calls: Interpulse interval: 97.9 ± 8.6 (91.8 - 104.0) ms; F_{max}: 38.5 ± 2.1 (37.0 - 40.0) kHz; Start slope: -0.1 ± 0.0 (-0.1 - -0.1) kHz/ms; End slope: -3.0 ± 1.3 (-2.0 - -3.9) kHz/ms; Ledge duration: 0.4 ± 0.0 (0.3 - 0.4) ms.

POPULATION:
Structure and Density
There is no information on population size. Museum specimens have been collected from seven sites in Mozambique, and one locality in Zimbabwe (Monadjem *et al.*, 2010c, 2010d; Taylor *et al.*, 2012c; S.M. Goodman and M.C. Schoeman, *unpublished data* in Schoeman (2017)). Population sizes at roost sites were estimated between 50 – 400 (Monadjem *et al.*, 2010d; S.M. Goodman and M.C. Schoeman *unpublished data* in Schoeman (2017)). Environmental niche models suggest additional roost sites may be present, but the localities are unknown (Taylor *et al.*, 2012c).

Trend
2016: Decreasing (Schoeman, 2017).

PARASITES:
DIPTERA
Streblidae
Raymondia aspera Maa, 1968 (Shapiro *et al.*, 2016: 254). *Raymondia waterstoni* Jobling, 1931 (Shapiro *et al.*, 2016: 256).

VIRUSES:
Astroviridae
None of the 20 Mozambican bats tested by Hoarau *et al.* (2018: 2) was positive for this group of viruses.

Coronaviridae
Joffrin *et al.* (2020: 4) reported an Alphacoronavirus from a Mozambican bat.

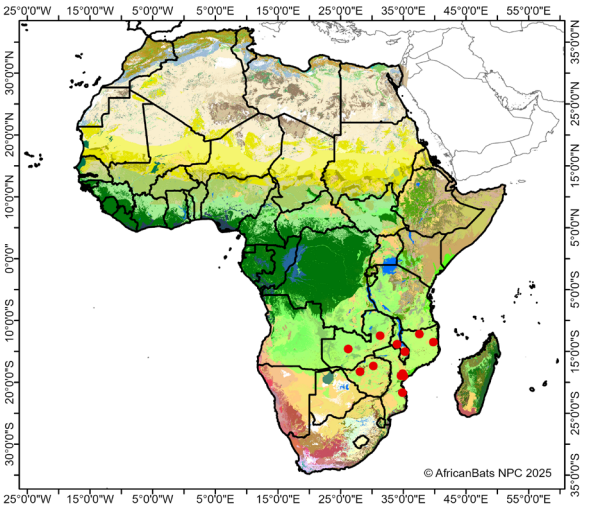

Figure 115. Distribution of *Rhinolophus mossambicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Malawi, Mozambique, Zambia, Zimbabwe.

Rhinolophus namuli Curran, Kopp, Ruedi and Bayliss, 2022

2009. *Rhinolophus sp.:* Timberlake, Dowsett-Lemaire, Bayliss, Alves, Baena, Bento, Cook, Francisco, Harris, Smith and de Sousa, Mt Namuli, Mozambique: Biodiversity and Conservation. Publication date: February 2009. (Name Combination).
2010. *Rhinolophus cf. maendeleo:* Monadjem, Schoeman, Reside, Pio, Stoffberg, Bayliss, Cotterill, Curran, Kopp and Taylor, Acta Chiropt., 12 (2): 379. - Comments: In part: Mount Namuli (Curran *et al.*, 2022: 26).
2010. *Rhinolophus maendeleo:* Monadjem, Taylor, Cotterill and Schoeman, Bats of Southern and Central Africa, 222. - Comments: In part: Mount Namuli (see Curran *et al.*, 2022: 26). (Name Combination).
2019. *R[hinolophus] cf. denti/simulator:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 7. Publication date: 22 August 2019. (Name Combination).

*2022. *Rhinolophus namuli* Curran, Kopp, Ruedi and Bayliss, Acta Chiropt., 24 (1): 26, figs 4, 5b,d,g, 6, 7, 8a-d,g. Publication date: 16 July 2022. Type locality: Mozambique: Zambezia Province: Mount Namuli: ca. 10 km north-west of Gurue [15.369250°S, 37.061361°E, 1650 m]. Holotype: MHNG 1971.068: ad ♂, skull and alcoholic. Collection date: 21 November 2008; original number: MZ 120. Paratype: MHNG 1971.067: ad ♀, skull and alcoholic. Collection date: 20 November 2008; original number: MZ 261. Paratype: MHNG 1971.069: ad ♂, skull and alcoholic. Collection date: 21 November 2008; original number: MZ 257. - Etymology: The name refers to the type locality (Mount Namuli), and is a noun in apposition (Curran *et al.*, 2022: 28). - ZooBank: 7A9806D9-CCC6-41A2-B898-6DCDEFFFBB51.

? *Rhinolophus cf. denti/simulator TD-2019*

COMMON NAMES:
English: Namuli Horseshoe Bat. German: Mt. Namuli Hufeisennase.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
This species is currently known from a limited number of specimens from Mozambique, Malawi and Tanzania, where it occurs at between 1,220 and 1,650 m of altitude (Curran *et al.*, 2022: 28).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^1/_2$, $C^1/_1$, $PM^2/_2$, $M^3/_3$ = 30.

ECHOLOCATION:
R. namuli has a F_{peak} of 76.9 kHz and a bandwidth between 75.9 and 78.0 kHz (Curran *et al.*, 2022: 30).

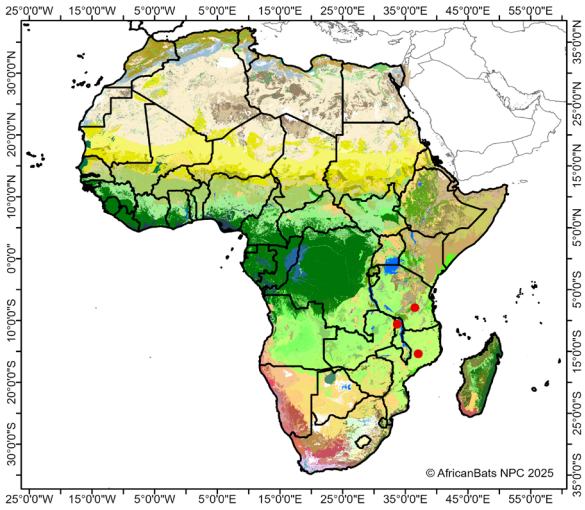

Figure 116. Distribution of *Rhinolophus namuli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Malawi, Mozambique, Tanzania.

Rhinolophus ruwenzorii J. Eric Hill, 1942

*1942. *Rhinolophus ruwenzorii* J. Eric Hill, Am. Mus. Novit., 1180: 1, fig 1. Publication date: 28 July 1942. Type locality: Congo (Democratic Republic of the): Kivu province: W slope of Mount Ruwenzori: Buhatu valley [00 22 N 29 44 E,, 7 500 ft]. [Goto Description]. Holotype: AMNH 82394: ad ♀, skull and alcoholic. Collected by: James Paul Chapin, Dewitt L. Sage, Frank P. Mathews and The Ruwenzori-Kivu Expedition; collection date: 24 December 1926. - Comments: Fahr *et al.* (2002: 99) mention "S-side of Butahu Valley, 2286 m, W slope Rwenzori Mts., Congo (K.)." as type locality. - Etymology: Referring to the Ruwenzori mountains, where the type specimen was collected. (Current Combination).

*2013. *Rhinolophus kahuzi* Fahr and Kerbis Peterhans, in: Kerbis Peterhans, Fahr, Huhndorf, Kaleme, Plumptre, Marks and Kizungu, Bonn. Zool. Bull., 62 (2): 192, 194, figs 5, 6. Publication date: November 2013. Type locality: Congo (Democratic Republic of the): Western slope of Mt. Kahuzi [02 15 09 S 28 40 09 E, 2 600 m]. Holotype: FMNH 219793: ad ♂, skull and alcoholic. Collected by: R. Kizungu; collection date: 28 July 2007; original number: JCK 5406. - Etymology: The name refers to the type locality and is used as a noun in apposition (see Kerbis Peterhans *et al.*, 2013: 194).

? *Rhinolophus maclaudi ruwenzorii:* (Name Combination).

TAXONOMY:
Included in *maclaudi* by Koopman (1993a: 167), see Smith and Hood (1980: 170); but see Fahr *et al.* (2002), Csorba *et al.* (2003: 65 - 66) and Simmons (2005: 362).

Demos *et al.* (2019a: 7) pointed out that *kahuzi* is genetically identical to three *ruwenzorii* sequences they compared it with, both mitochondrial and nuclear data indicate that *Rhinolophus kahuzi* is a synonym of *Rhinolophus ruwenzorii* (p. 11).

COMMON NAMES:
Czech: vrápenec ruwenzorijský. English: Ruwenzori Horseshoe bat. French: Rhinolophe

du Ruwenzori. German: Ruwenzori-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Assessed as Endangered (EN B2ab(ii,iii,v) ver 3.1 (2001)) as its area of occupancy (AOO) is 48 km^2 and the population is severely fragmented. The species occurs in highly threatened cave/mine roosts, which are critical resources for day roost. The extent and quality of this species habitat are projected to continue to decline due to ongoing threats from forest loss and degradation and cave/mine loss, degradation, and disturbance (Fahr, 2008m; IUCN, 2009). Further, most specimens were collected over 50 years ago and only a few specimens have been collected in the past 20 years (Fahr and Cooper-Bohannon, 2020).

Assessment History
Global
2019: EN B2ab(ii,iii,v) ver 3.1 (2001) (Fahr and Cooper-Bohannon, 2020). 2008: VU B1a+2b(ii,iii,iv,v) ver 3.1 (2001) (Fahr, 2008m; IUCN, 2009). 2004: VU A4c; B1ab(iii) ver 3.1 (2001) (Fahr, 2004d; IUCN, 2004); and assessed as *R. hilli* by Fahr (2004f).

Regional
None known.

MAJOR THREATS:
Rhinolophus ruwenzorii is threatened by the deforestation of its mesic miombo woodland, gallery forest and montane habitat, generally through logging and mining activities, and the conversion of forest to farmland. It is dependent on cave habitats for roosting, and it is likely that disturbance of these sites could be an important threat to the species. It may also be threatened by overharvesting for subsistence food; while this needs to be fully confirmed, populations are vulnerable to direct exploitation (Fahr, 2008m; IUCN, 2009; Fahr and Cooper-Bohannon, 2020).

CONSERVATION ACTIONS:
Fahr (2008m) [in IUCN (2009)] reported that *Rhinolophus ruwenzorii* has been recorded from five protected areas, such as the Mount Ruwenzori National Park. Fahr and Cooper-Bohannon (2020) suggest that a conservation priority for this species would be to work locally to reduce levels of deforestation within the Albertine Rift region as a whole. There is a need to initiate and develop public awareness programmes in the region, and to reduce the disturbance of roosting localities. Further field surveys are needed to locate additional population of this species, and to confirm its presence at sites which have not been visited for over half a century. Other research needs are to better understand the species' distribution, population size and trend, ecology and threats.

GENERAL DISTRIBUTION:
Rhinolophus ruwenzorii is restricted to the mountains of the Albertine Rift, where it has been recorded from the countries of the eastern Democratic Republic of the Congo, western Uganda, and Rwanda, at elevations of 1,666 to 2,666 m asl. The distribution includes the Ruwenzori Mountains, Kivu Region and Kibali-Ituri-Forest, Bwindi-Impenetrable Forest and Mutura in northwestern Rwanda (Fahr *et al.*, 2002). Eastern Democratic Republic of the Congo, Western Uganda.

Native: Congo (The Democratic Republic of the) Kityo and Kerbis (1996: 60); Rwanda (Fahr *et al.*, 2002); Uganda Kityo and Kerbis (1996: 60).

POPULATION:
Structure and Density
This species is known only from 36 specimens collected from 15 localities, these total only eight distinct locations(Fahr, 2008m; IUCN, 2009; Fahr, 2013j; Kerbis Peterhans *et al.*, 2013). Fahr and Cooper-Bohannon (2020) note that little is known about this species as most specimens were captured half a century ago, and few specimens have been collected in the past 20 years, it is likely the species may have been extirpated from some of the historic sites.

Trend
2019: Decreasing (Fahr and Cooper-Bohannon, 2020). 2008: Decreasing (Fahr, 2008m; IUCN, 2009).

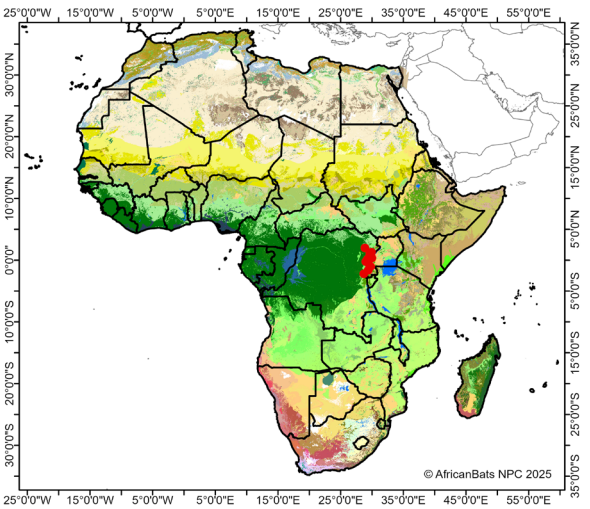

Figure 117. Distribution of *Rhinolophus ruwenzorii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Congo (Democratic Republic of the), Rwanda, Uganda.

Rhinolophus sakejiensis Cotterill, 2002

*2002. *Rhinolophus sakejiensis* Cotterill, J. Zool., Lond., 256: 166, figs 2a, 3, 4a, 5a, 6a, 7a. Type locality: Zambia: Mwinilunga district; Ikelenge Pedicle: btw Sakeji/Zambezi rivs,c.11 km NNE source Zambezi: Kavunda [11 17 S 24 21 E, 1 388 m]. [Goto Description]. Holotype: NHMZ 29153: ad ♂, skull and alcoholic. Collected by: Fenton Peter David ("Woody") Cotterill; collection date: 11 October 1990; original number: FWC 1090. Baculum extracted. Paratype: HZM 1.32236: ad ♂, skull and alcoholic. Collected by: Fenton Peter David ("Woody") Cotterill; collection date: 11 October 1990; original number: FWC 1092. Baculum extracted. Paratype: NHMZ 29154: sad ♂, skull and alcoholic. Collected by: Fenton Peter David ("Woody") Cotterill; collection date: 11 October 1990; original number: FWC 1091. Baculum extracted. (Current Combination).

2025. *Rhinolophus sakajiensis:* Benda and Uvizl, Mammalia, 89 (3): Suppl. Publication date: 27 January 2025. (Lapsus).

TAXONOMY:
Cotterill (2002b: 5) considers it a member of the *ferrumequinum* species group, and is followed by Simmons (2005: 362). However, based on cyt *b* analyses, Benda and Uvizl (2025: 297) conclude that *sakejiensis* doesn't belong to any of the recognised species groups, but represents a distinct evolutionary lineage, along with *Rhinolophus horaceki*.

See Csorba *et al.* (2003: 132 - 133) for further remarks on taxonomy.

COMMON NAMES:
Czech: vrápenec sakežianský. English: Sakeji Horseshoe bat. French: Rhinolophe de Sakeji. German: Sakeji-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since it has only recently been discovered, and there is still very little information on its extent of occurrence, ecological requirements and threats (Cotterill, 2008a; IUCN, 2009; Cotterill, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) (Cotterill, 2019a). 2008: DD ver 3.1 (2001) (Cotterill, 2008a; IUCN, 2009). 2004: DD ver 3.1 (2001) (IUCN, 2004; Cotterill, 2004c).

Regional
None known.

MAJOR THREATS:
The threats to *Rhinolophus sakejiensis* are not well known, but it is presumably threatened by the loss of roosting sites resulting from logging and the conversion of suitable habitat to agricultural use (Cotterill, 2008a; IUCN, 2009; Cotterill, 2019a).

CONSERVATION ACTIONS:
Cotterill (2008a) [in IUCN (2009)] and Cotterill (2019a) reported that it is not known if *Rhinolophus sakejiensis* is present in any protected areas. Further surveys are needed to better determine the extent of the distribution of this species, to gather more information on the species natural history, and to review the threats to this species.

GENERAL DISTRIBUTION:
Rhinolophus sakejiensis is known only from the type locality of Kavunda, between the Sakeji and Zambezi rivers: c. 11 km north-north-east of the source of the Zambezi River in the Ikelenge Pedicle, Mwinilunga District of north-west Zambia (Cotterill, 2002a). Recently, Benda *et al.* (2022: 302) reported a fourth specimen from another Zambian locality, approximately 4 km WNW of the type localiy. It is likely that the species is also present within similar suitable habitat in Angola and the Congo basin (Cotterill, 2002a).

Native: Zambia (Monadjem *et al.*, 2010d: 560).

POPULATION:
Structure and Density
Rhinolophus sakejiensis is currently known only from the type collection of three bats, taken from a cluster of six roosting bats (Cotterill, 2008a; IUCN, 2009; Cotterill, 2019a).

Trend
2018: Unknown (Cotterill, 2019a). 2008: Unknown (Cotterill, 2008a; IUCN, 2009).

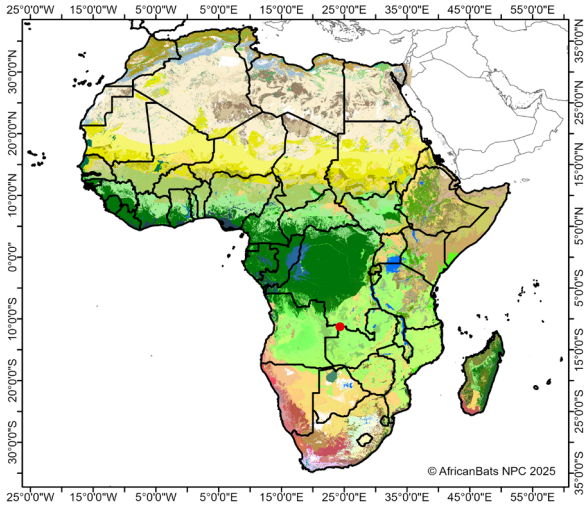

Figure 118. Distribution of *Rhinolophus sakejiensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Zambia.

Rhinolophus silvestris Aellen, 1959

*1959. *Rhinolophus silvestris* Aellen, Archs Sci. Genève, 12 (2): 228. Type locality: Gabon: Lastourville: N'Dumbu cave [ca. 00 50 S 12 03 E]. [Goto Description]. Holotype: MHNG 965.040: ad ♂, skull and alcoholic. Collected by: Pierre Strinati and Villy Aellen; collection date: 4 August 1957. - Etymology: From the Latin for forest dweller (see Flannery, 1995a: 321). (Current Combination).
2016. *Rhinolophus sylvestris:* Karadjian, Hassanin, Saintpierre, Gembu Tungaluna, Ariey, Ayala, Landau and Duval, PNAS, 113 (35): 9835. Publication date: 30 August 2016. (Lapsus).
? *Rhinolophus clivosus silvestris:* (Name Combination).

TAXONOMY:
Considered a subspecies of *clivosus* by Hayman and Hill (1971: 23), but Barratt *et al.* (1995: 386), Cotterill (2002a), Csorba *et al.* (2003: 46 - 48) and Simmons (2005: 363), which indicate the relationships of *Rhinolophus deckeni* and *R. silvestris* are unclear, with the forms possibly being conspecific. Considered part of the *ferrumequinum* species group (Cotterill, 2002a; Csorba *et al.*, 2003: 46 - 48; Simmons, 2005: 363).

COMMON NAMES:
English: Forest Horseshoe Bat. French: Rhinolophe sylvestre. German: Wald-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Cotterill, 2008b; IUCN, 2009; Cotterill, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Cotterill, 2019b). 2008: DD ver 3.1 (2001) (Cotterill, 2008b; IUCN, 2009). 2004: VU B2ab(iii) ver 3.1 (2001) (Cotterill, 2004g; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Rhinolophus silvestris is considered to be threatened by habitat loss through conversion of land to agricultural use and logging operations. Additional threats include general disturbance of cave roost sites and overharvesting of the species for the bushmeat trade (Cotterill, 2008b; IUCN, 2009; Cotterill, 2019b).

CONSERVATION ACTIONS:
Cotterill (2008b) [in IUCN (2009)] and Cotterill (2019b) reported that *Rhinolophus silvestris* does not appear to have been recorded from any protected areas. An additional examination of the taxonomic relationship between this species and *Rhinolophus deckeni* is needed. Further field surveys are needed to better determine the distribution, natural history and the extent of threats to this little-known bat.

GENERAL DISTRIBUTION:
Rhinolophus silvestris a poorly known species has only been recorded from three localities in Gabon (Benga; Belinga; and the type locality of

Dumbu Cave, Latoursville), and a single site in Congo (Meya-Nzouari).

Native: Congo (Bates *et al.*, 2013: 335); Gabon.

POPULATION:
Structure and Density
Rhinolophus silvestris is usually found in small colonies of fewer than 20 bats. It is believed to be in overall decline (Cotterill, 2008b; IUCN, 2009; Cotterill, 2019b).

Trend
2018: Decreasing (Cotterill, 2019b). 2008: Decreasing (Cotterill, 2008b; IUCN, 2009).

PARASITES:
Adam and Landau (1973a: 5) report on the presence of a protozoan parasite of the genus *Polychromophilus* (Haemoproteidae) in *R. clivosus sylvestris*. About 50 % of the specimens from Congo they examined, were found to be infected. Gametocytes were found year-round. The bats were also infested by the nycteribiids *Penicillidia fulvida* Bigot, 1885 and *Nycteribia schmidlii scotti* Falcoz, 1923, of which the prior was a major carrier of *Polychromophilus* sporozoites.

The Haemosporidan *Nycteria gabonensis* Rosin, Landay & Hugot, 1978 was reported by Landau *et al.* (2012: 142), Perkins and Schaer (2016: Suppl.) and Karadjian *et al.* (2016: 9835) from the Republic of Congo and Gabon.

Justine (1989a: 334; 1989b: 553) described two new stomach parasites: *Capillaria chabaudi* and *Capillaria gabonensis* (Nematoda) from *R. silvestris* from Belinga (Gabon).

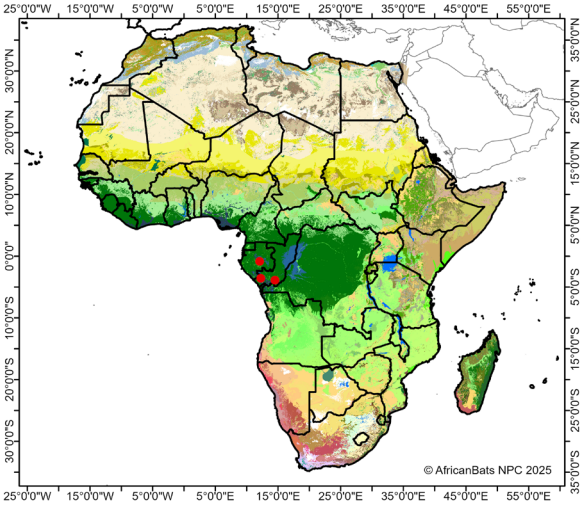

Figure 119. Distribution of *Rhinolophus silvestris*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo, Gabon.

Rhinolophus simulator K. Andersen, 1904

*1904. *Rhinolophus simulator* K. Andersen, Ann. Mag. nat. Hist., ser 7, 14 (83): 384. Publication date: 1 November 1904. Type locality: Zimbabwe: Mashonaland: Mazoe [17 30 S 31 03 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1902.2.7.10: ad ♂, skull and alcoholic. Collected by: James Johnston ffolliot Darling Esq. - Etymology: From the masculine Latin substantive *simulàtor*, meaning "simulator", as *R. simulator*, according its descriptor, "[...] by quite superficial inspection, could be taken for a curiously small and long-tailed form of [*R. capensis*]." (see Lanza *et al.*, 2015: 115). (Current Combination).

1914. *Rhinolophus bembanicus* Senna, Annuario Mus. Zool. R. Univ. Napoli, (2) 4: no 9, p 1, 2, text-fig 1, 2. Publication date: 27 March 1914. Type locality: Zambia: Lake Bengueolo [=Lake Bangweulu] [11 05 00 S 29 45 00 E, 2000 ft]. - Comments: Ansell and Dowsett (1988: 34) indicate that *bembanicus* might represent a separable species, but the type specimen no longer exists.
Gippoliti (2024: 8) also indicated that the assignment to *R. simulator* by Koopman (1975) is doubtful as it is unlikely that anyone studied the type before its destruction in WWII.

1946. *Rhinolophus swinnyi rhodesiae* Roberts, Ann. Transv. Mus., 20 (4): 304. Type locality: Zimbabwe: Limpopo valley: Bezwe river: a tributary of the Wanetsi (? Nuanetsi) River [ca. 21 22 S 30 45 E]. [Goto Description]. Holotype: TM 1325: ad ♀. Collected by: Austin Roberts; collection date: 19 August 1913. - Etymology: The name refers to Southern Rhodesia (currently Zimbabwe), the country where the type specimen was collected.

2010. *Rhinolophus rhodesiae:* Monadjem, Taylor, Cotterill and Schoeman, Bats of Southern and Central Africa, 594. (Name Combination).

2018. *Rhinolophus gorongosae* Taylor, MacDonald, Goodman, Kearney, Cotterill, Stoffberg, Monadjem, Schoeman, Guyton, Naskrecki and Richards, Zool. J. Linn. Soc., 184 (1): 1249, 1262, figs 6, 8, 9, 10, 12. Publication date: 24 April 2018. Type locality: Mozambique: Sofala province: Gorongosa National Park: Bunga Inselberg [18 35 56 S 34 20 35 E, 212 m]. Holotype: DNSM 14820: ad ♂, skull and alcoholic. Collected by: Jennifer ("Jen") Anna Guyton; collection date: 25 April 2015; original number: JAG 196. Paratype: DNSM 14815: ♀. Collected by: Jennifer ("Jen") Anna Guyton; collection date: 24-25 April 2015; original number: JAG 188. Paratype: DNSM 14816: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 24-25 April 2015. Paratype: DNSM 14817: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 24-25 April 2015. Paratype: DNSM 14818: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 24-25 April 2015. Paratype: DNSM 14819: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 24-25 April 2015. Paratype: DNSM 14828: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 2 May 2015. Paratype: DNSM 14843: ♀. Collected by: Jennifer ("Jen") Anna Guyton; collection date: 5 November 2015; original number: JAG 228. Paratype: DNSM 14865: Collected by: Jennifer ("Jen") Anna Guyton; collection date: 22 July 2015. - Etymology: The name refers to the Gorongosa district (Mozambique) and the Gorongose National Park, where the type specimen was collected (Taylor *et al.* (2018a: 14).

2018. *Rhinolophus rhodisiae:* Hoarau, Le Minter, Joffrin, Schoeman, Lagadec, Ramasindrazana, Dos Santos, Goodman, Gudo, Mavingui, Lebarbenchon, Virology J., 15: Suppl. Publication date: 30 June 2018. (Lapsus).
2019. *R[hinolophus] simulator 2:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol., 19 (166): 8. Publication date: 22 August 2019. (Name Combination).
2019. *Rhinolophus simulator 1:* Demos, Webala, Goodman, Kerbis Peterhans, Bartonjo and Patterson, BMC Evol. Biol.,
19 (166): 8. Publication date: 22 August 2019. (Name Combination).
? *Rhinolophus cf. simulator SJP-2016*
? *Rhinolophus simulator complex sp. 1 TD-2019*
? *Rhinolophus simulator complex sp. 2 TD-2019*
? *Rhinolophus simulator simulator:* (Name Combination).

TAXONOMY:



Figure 120. *Rhinolophus simulator* from Madimatle Cave, South Africa.

Included *alticolus* and *bembanicus* (see Koopman, 1975: 387; Hayman and Hill, 1971: 25; Koopman, 1993a: 169; Simmons, 2005: 363). Considered part of the *capensis* species group (Csorba *et al.*, 2003: 10 - 12; Simmons, 2005: 363).

Demos *et al.* (2019a: 11) resequenced the cyt-*b* of some of the *Rhinolophus gorongosae* specimens used by Taylor *et al.* (2018a) in the description of the species and found that this diverged only between 1 and 1.4 % from that of *R. simulator* and *R. rhodesiae*. This "strongly suggests" that the genetic arguments for the newly described *R. gorongosae* and for raising *R. swinnyi rhodesiae* to full species were based on sequencing errors. *R. gorongosae* and *R. rhodesiae* are no longer recognized as a valid species by Simmons and Cirranello (2023b).

COMMON NAMES:

Afrikaans: Bosveldsaalneusvlermuis, Bosveldvlermuis. Chinese: 布什维尔德菊头蝠. English: Bushveld Horseshoe Bat. French: Rhinolophe de brousse, Rhinolophe du Veld, Rhinolophe du Bushveld. German: Buschveld-Hufeisennase, Buschland-Rundblattnase. Italian: Rinòlofo sirnulatóre, Fèrro di cavàllo simulatóre. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura das savanas.

ETYMOLOGY OF COMMON NAME:

The colloquial name refers to its occurrence in savanna woodland in the subregion (see Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

R. simulator may be present in the late Holocene at Nkupe, South Africa (Avery, 1991: 6).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ao; IUCN, 2009; Monadjem *et al.*, 2017cm).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cm). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008ao; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004al; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016l). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

Rhinolophus simulator is threatened in parts of its range by cave disturbance and the loss of habitat resulting from the conversion of land to agricultural use and mining operations (Jacobs *et al.*, 2008ao; IUCN, 2009; Monadjem *et al.*, 2017cm).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008ao) [in IUCN (2009)] and Monadjem *et al.* (2017cm) reported that there appear to be no direct conservation measures in place. In view of the species East African and southern African distribution, it seems likely that it is present in some protected areas.

GENERAL DISTRIBUTION:

Rhinolophus simulator is widely distributed in sub-Saharan Africa. There are records in West

Africa from the Wonegizi Mountains and Mount Nimba (Guinea and Liberia), and from central Nigeria. In Central Africa it has been reported from Cameroon. In East Africa there are many more records, with the species being reported from as far north as Ethiopia and southern Sudan, ranging southwards through Uganda, Kenya and Tanzania to Zambia, Malawi, Mozambique, Zimbabwe, eastern South Africa, Swaziland and southern Botswana. In South Africa, its distribution is strongly associated with the amount of precipitation in the warmest quarter of the year (Babiker Salata, 2012: 49).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 855,537 km^2.

Native: Botswana (Skinner and Smithers, 1990; Csorba *et al.*, 2003: 12; Monadjem *et al.*, 2010d: 560); Cameroon (Rosevear, 1965; Csorba *et al.*, 2003: 12); Côte d'Ivoire; Eswatini (Monadjem, 2005: 6; Monadjem *et al.*, 2010d: 561, Monadjem *et al.*, 2021: 5); Ethiopia (Hill and Morris, 1971; Largen *et al.*, 1974; Csorba *et al.*, 2003: 12); Guinea (Brosset, 1985; Csorba *et al.*, 2003: 12: Denys *et al.*, 2013: 282); Kenya (Koopman, 1975; Aggundey and Schlitter, 1984; Csorba *et al.*, 2003: 12); Liberia; Malawi (Ansell and Dowsett, 1988; Happold *et al.*, 1988; Happold and Happold, 1997b: 818; Csorba *et al.*, 2003: 12; Monadjem *et al.*, 2010d: 560); Mozambique (Smithers and Lobão Tello, 1976: 561; Csorba *et al.*, 2003: 12; Monadjem *et al.*, 2010c: 380); Nigeria (Rosevear, 1965 Happold, 1987; Csorba *et al.*, 2003: 12); South Africa (Ellerman *et al.*, 1953; Taylor, 1998; Rautenbach *et al.*, 1984; Maree and Grant, 1997; Csorba *et al.*, 2003: 11; Monadjem *et al.*, 2010d: 561); Sudan (Koopman, 1975; Csorba *et al.*, 2003: 12); Tanzania (Aellen, 1957; Csorba *et al.*, 2003: 12; Stanley and Goodman, 2011: 42; Stanley and Goodman, 2011: 42); Uganda; Zambia (Ansell, 1967; Ansell, 1969; Ansell, 1973; Ansell, 1978; Csorba *et al.*, 2003: 12; Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 561) ; Zimbabwe (Smithers and Wilson, 1979; Csorba *et al.*, 2003: 12; Monadjem *et al.*, 2010d: 561).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Mutumi *et al.* (2021) discuss the geographic variation of the skulls of *R. simulator* and *R.* cf. *simulator* in southern Africa and found that the skulls of these two lineages appear to be under different selection pressures. In *R.* cf. *simulator* the differences are primarily in the nasal dome region, whereas in *R. simulator* they are in the cranium and the mandible.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Jacobs *et al.* (2007a)] mention a wing loading value of 5.8 Pa, aspect ratio 5.5 for a wingspan of 27 cm and a wing area of 132 cm^2 and a body mass of 8 g.

ECHOLOCATION:
Jacobs (1996) and Fenton and Bell (1981) reported a F_{max}: 78 kHz for an individual from Sengwa in Zimbabwe. Monadjem *et al.* (2007a), using an Anabat detector, reported a F_{max}: 84.1 ± 0.36 kHz for individuals from various localities in Swaziland. Additional parameters from the same country were given by Monadjem *et al.* (2017c: 179): F_{min}: 72.1 ± 2.97 (68.6 - 76.0) kHz, F_{knee}: 83.8 ± 0.18 (83.6 - 84.1) kHz, F_c: 83.4 ± 0.20 (83.7 - 84.2) kHz, and duration: 16.8 ± 4.70 (12.0 - 25.9) ms.

For individuals in South Africa, Taylor (1999b), using a Pettersson D980, reported a F_{max} at Shongweni of 82.7 ± 0.4 kHz, while Jacobs *et al.* (2007a) reported a F_{peak}: 80.6 ± 1.0 kHz (detector type and locality not indicated). Taylor (2000) reported a constant frequency component at 83 kHz.

Mutumi and Jacobs (2013: 108) investigated the peak frequency over the entire distribution range and found that this frequency was not correlated to body size or vegetation index, but in one location (where the mean annual rainfall and temperatures where the highest), they found that the peak frequency was significantly lower. They suggest that this lower frequency was linked with an increased detection range due to the more humid conditions. The resting call frequency was studied by Mutumi *et al.* (2016), who concluded that the acoustic divergence was best predicted by latitude, geography and climate-induced differences in atmospheric attenuation.

Taylor *et al.* (2013b: 19) reported 9 calls from Waterberg, South Africa with the following characteristics: F_{max}: 82.0 ± 0.58 (81.1 - 82.9) kHz, F_{min}: 79.3 ± 1.42 (75.9 - 80.6) kHz, F_{knee}: 80.5 ± 0.46 (79.8 - 81.2) kHz, F_{char}: 81.5 ± 0.47 (80.9 - 82.1) kHz, duration: 12.4 ± 1.71 (9.6 - 14.4) ms. An additional 16 calls from Swaziland had the following parameters: F_{max}: 84.0 ± 0.34 (83.2 - 84.4) kHz, F_{min}: 78.6 ± 3.77 (71.5 - 82.3) kHz, F_{knee}: 83.1 ± 0.83 (80.3 - 83.7) kHz, F_{char}: 83.4 ± 1.20 (79.2 - 84.1) kHz, duration: 13.1 ± 3.66 (7.0 - 18.9) ms.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg range (RSA): F_{min}: 76 - 81 kHz, F_{peak}: 79 - 84 kHz, F_{knee}: 80 - 84 kHz, slope: 70 - 368 OPS, duration: 7 - 19 ms.

20 calls from Mapungubwe National Park (RSA) recorded by Parker and Bernard (2018: 57) had the following characteristics: F_{char}: 79.70 ± 1.02 kHz, F_{max}: 79.86 ± 0.99 kHz, F_{min}: 75.43 ± 4.93 kHz, F_{knee}: 79.71 ± 1.01 kHz, duration: 37.79 ± 9.97 ms, with 7.46 ± 3.46 calls/sec.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 79.16 ± 3.49 kHz, F_{max}: 80.75 ± 3.60 kHz, F_{min}: 68.39 ± 3.40 kHz.

For one bat from southern KwaZulu-Natal or Eastern Cape (RSA), Moir (2020: 29) and Moir *et al.* (2021a: 371) reported: F_{max}: 82.31 ± 0.10 (82.11 - 82.31) kHz, F_{min}: 77.24 ± 0.08 (77.24 - 77.39) kHz, F_{char}: 81.06 ± 0.08 (80.90 - 81.06) kHz, F_{knee}: 81.12 ± 0.09 (80.93 - 81.12) kHz, and duration: 11.20 ± 0.87 (9.47 - 11.20) ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 69 calls of 10 bats: F_{max}: 79.65 ± 8.63 kHz, F_{min}: 67.51 ± 23.43 kHz, F_{knee}: 78.73 ± 9.07 kHz, F_{char}: 78.77 ± 9.37 kHz, slope: -5663.39 ± 16,360.82 OPS, duration: 13.54 ± 13.02 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 11.83 ± 5.77 ms, F_{min}: 77.86 ± 2.07 kHz, F_{max}: 79.93 ± 0.44 kHz, F_{knee}: 79.26 ± 0.45 and F_{char}: 79.31 ± 0.48 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 41 *Rhinolophus simulator* calls from the Kruger Park (RSA): F_{min}: 67.4 ± 3.4 (56.7 - 76.6) kHz, duration: 15.7 ± 4.6 (5.4 - 24.2) ms, F_{max}: 80.7 ± 60.4 (3.6 - 83.1) kHz, F_{knee}: 79.3 ± 3.5 (59.7 - 82.2) kHz, F_{char}: 79.2 ± 3.5 (59.5 - 82.0) kHz.

37 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 75 - 80 kHz, F_{max}: 83 - 84 kHz, F_{char}: 80 - 82 kHz, F_{knee}: 79 - 81 kHz and duration 9 - 14 ms.

For 33 calls from 5 *Rhinolophus simulator* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 79.95 ± 0.92 kHz, F_{knee}: 79.18 ± 0.78 kHz, F_{min}: 70.90 ± 4.62 kHz, F_{max}: 81.28 ± 1.06 kHz, Bandwidth: 10.38 ± 4.70 kHz, Duration: 28.79 ± 9.16 ms.

The following values were reported by Taylor-Boyd *et al.* (2025: 116) for 9 calls from Zambia: Interpulse interval: 98.9 ± 13.8 (81.2 - 122.0) ms; F_{max}: 77.9 ± 1.6 (75.7 - 79.9) kHz; Start slope: -0.1 ± 0.0 (-0.1 - -0.2) kHz/ms; End slope: -2.4 ± 1.2 (-1.1 - -4.5) kHz/ms; Ledge duration: 0.7 ± 0.9 (0.3 - 3.1) ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 32 calls of 1 *R.* cf. *simulator*: F_{peak}: 70.7 ± 0.2 (70.1 - 71.1) kHz, F_{min}: 58.7 ± 2.3 (55.2 - 61.5) kHz, F_{max}: 71.4 ± 0.5 (70.8 - 72.1) kHz, duration: 32.4 ± 4.6 (27.7 - 39.7) ms.

Jacobs (2016: 119) indicates that the second harmonic of this bat coincides with the third harmonic of *R. capensis*.

Molecular Biology:

Karyotype

Rautenbach (1986) reported 2*n* = 58, FN = 60, BA = 4, and submetacentric X and Y chromosomes.

Roost:

Taylor *et al.* (1999: 70) reported a colony of 50 - 60 bats roosting in the Shongweni Dam tunnel (RSA), but Happold and Happold (2023: 89) mention some colonies in the RSA can contain 150 to 300 individuals. In a tunnel near Pietermaritzburg, which contained about 150 animals, the females migrated to maternity roosts in spring, whereas the males remained in the original roost.

Diet:

From Sudwala (RSA), Jacobs (2000: 201) reported the following proportions of prey: Lepidoptera (57.6 ± 34.9), Coleoptera (18.3 ± 23.0), Isoptera (19.4 ± 29.8), Hymenoptera (1.5 ± 4.1), Diptera (2.2 ± 4.2), Hemiptera (0.2 ± 1.1), Mandotea (0.2 ± 0.7), and unknown (0.6 ± 2.5).

Weier *et al.* (2019c: 6) examined droppings from this species in the Levubu region (Limpopo, RSA) and found DNA sequences of *Nezara viridula* (Linnaeus, 1758) (Hemiptera).

Predators:

Mikula *et al.* (2016: Supplemental data) and Malan *et al.* (2022: 167) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Population:

Structure and Density

Rhinolophus simulator can be locally common. Colonies may consist of a couple of hundred individuals, although these are often quite fragmented because of the species association with caves for breeding (Jacobs *et al.*, 2008ao; IUCN, 2009; Monadjem *et al.*, 2017cm).

Trend
2016: Decreasing (Monadjem *et al.*, 2017cm).
2008: Decreasing (Jacobs *et al.*, 2008ao; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] reported that births take place around mid November. In Malawi, the births took place early in the wet season after a gestation period of 90 to 130 days (Happold and Happold, 1990b: 566; Happold and Happold, 2023: 89).

PARASITES:
BACTERIA
Dietrich *et al.* (2016a: 4) found *Rickettsia* in the faeces of bats from South Africa. Federici *et al.* (2022: 5) [referring to Dietrich *et al.* (2016a)] mentions Proteobacteria *Burkholderia, Helicobacter* and *Bartonella*.

Clément *et al.* (2019a: 5) reported on 27 *R. simulator* specimens of which 2 were infected by *Trypanosoma livingstonei*_A and *T. livingstoneii*_C.

DIPTERA
Streblidae
Brachytarsina africana (Walker, 1849) has a wide distribution in sub Saharan Africa (Haeselbarth *et al.*, 1966: 100). *Raymondia hardyi* Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254). *Raymondia waterstoni* Jobling, 1931 (Haeselbarth *et al.*, 1966: 104; Shapiro *et al.*, 2016: 256).

HEMIPTERA
Polyctenidae
Adroctenes horvathi Jordan, 1912 was reported from South Africa by Szentiványi *et al.* (2022: 5).

VIRUSES:
Astroviridae
None of the 31 Mozambican "*Rhinolophus rhodesiae*" bats tested by Hoarau *et al.* (2018: 2) was positive for this group of viruses.

Coronaviridae
Joffrin *et al.* (2020: 4) reported an Alphacoronavirus found in Mozambican "*Rhinolophus rhodesiae*" bats.

Paramyxoviridae
Hoarau *et al.* (2021: Suppl.) mentioned the presence of viruses belonging to this family in "*Rhinolophus rhodesiae*".

Polyomaviridae
Carr *et al.* (2017) reported two new viruses from *R. blasii* from Zambia: *Rhinolophus simulator polyomavirus 4* and *Rhinolophus simulator polyomavirus1*, besides the two already known: *Rhinolophus simulator polyomavirus 2* and *Rhinolophus simulator polyomavirus 3*

Reoviridae
Sasaki *et al.* (2016: 2489) retrieved a VP7 type Rotavirus from a Zambian *R. simulator*: RVA/Bat-wt/ZMB/LUS12-14/2012/G3P[3] (LUS12-14).

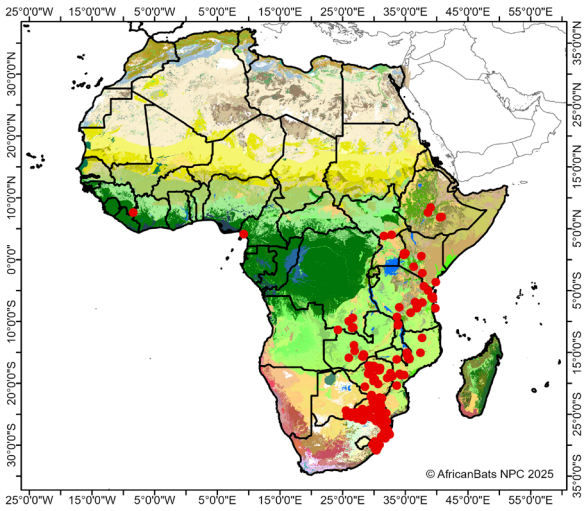

Figure 121. Distribution of *Rhinolophus simulator*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Cameroon, Congo (Democratic Republic of the), Eswatini, Ethiopia, Guinea, Kenya, Malawi, Mozambique, South Africa, South Sudan, Tanzania, Zambia, Zimbabwe.

Rhinolophus smithersi Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, 2012

*2012. *Rhinolophus smithersi* Taylor, Stoffberg, Monadjem, Schoeman, Bayliss and Cotterill, PLoS ONE, 7(9): 19. Publication date: 12 September 2012. Type locality: Zimbabwe: Sebungwe: Gokwe Communal Land: Ngolangola Gorge at confluence with Lutope River [181705S 280500E, 1000 m]. Holotype: NHMZ 33647: ♀, skull and alcoholic. Collected by: Fenton Peter David ("Woody") Cotterill and Peter John Taylor; collection date: 26 October 2000; original number: FWC 4764. Skull and mandible in good condition (Taylor *et al.*, 2012c: 19). Paratype: NHMZ 33652: ♂, skull and alcoholic. Collected by: Fenton Peter David ("Woody") Cotterill and Peter John Taylor; collection date: 26 October 2000; original number: FWC 4769. - Etymology: Taylor *et al.* (2012c: 19) selected the specific epithet in recognition of the late Reay Henry Noble Smithers (1907–1987), former Director of the National Museums of Zimbabwe, prodigious collector and researcher of mammals including bats, and author of important regional texts on the mammalogy of Botswana, Zimbabwe and Mozambique, notably his definitive monograph – The Mammals of the Southern African Subregion subsequently updated and revised. The species name combines the surname Smithers and genitive singular

case-ending ‘‘i’’ indicative of masculine gender. - ZooBank: E78B0F44-7534-4991-975A-F176CB668DDE. (Current Combination).

2015. *[Rhinolophus] smthersi:* Kaipf, Rudolphi and Meinig, NABU - Biodiversity Assessment in Kafa, Ethiopia, 13.

TAXONOMY:
Based on mitochondrial and nuclear DNA sequences and morphological and morphometric data, Taylor *et al.* (2012c) found that the *Rhinolophus hildebrandtii* group includes more species than previously recognized.

Benda *et al.* (2024) does not recognize *Rhinolophus smithersi* as a separate species and assigned the specimens to *Rhinolophus hildebrandtii*.

COMMON NAMES:
English: Smithers's Horseshoe Bat. German: Smithers Hufeisennase.

CONSERVATION STATUS:
Global Justification
Taylor (2017) reports that the species does not trigger any thresholds for any threatened categories under any of the criteria. Recent collecting has shown that, although essentially limited to one province of South Africa (with an isolated small Zimbabwean population), the species is quite widespread, so areas of occupancy and extent of occurrence exceed the thresholds for Vulnerable under criterion B. There is no evidence for declines in the species or its habitat. However, colony sizes are very small, and the species appears to have a scattered occurrence in the landscape (e.g., it is rarely collected with harp traps or recorded with bat detectors during surveys of the Soutpansberg). Since it is limited by availability of roosting sites, and possibly suitable water sources, it is hard to believe that the entire population of the species could be much more than 1,000 individuals, so it could potentially be Vulnerable under criterion D1. Until the population size can be confirmed to be below 1,000, however, the species is assessed as Near Threatened (nearly meets VU D1).

Assessment History
Global
2016: NT D1 ver 3.1 (2001) (Taylor, 2017).

Regional
South Africa: 2016: NT D1 ver 3.1 (2001) (Taylor *et al.*, 2016b).

MAJOR THREATS:
Taylor (2017) report that there are no known major threats to this species at present as much of its range occurs throughout the Soutpansberg, Blouberg and Waterberg ranges of Limpopo where human impacts and habitat transformation are not yet severe. The threat of extensive planned coal, platinum, natural gas (fracking) and other mining developments over much of the Limpopo Valley and the foothills of the Soutpansberg and Waterberg mountains and the Mahabeng Plateau, could impact heavily on populations, e.g., through roosting and foraging habitat loss, noise, air and water pollution and water abstraction leading to degradation of riparian habitats. Suppression of fire together with over-grazing of cattle and game and climate change has resulted in serious bush encroachment of savannas across much of its range (e.g., the western Soutpansberg) which has been shown to have a negative effect on biodiversity generally. In the eastern Soutpansberg, afforestation and alien plant invasions have considerably altered natural habitats. Limpopo is extremely drought-prone and water-stressed and with projected climate change, since the species seems to be dependent on water sources for drinking, extreme droughts in the area have had potentially devastating effects on wildlife generally.

CONSERVATION ACTIONS:
Taylor (2017) report that not counting the Zimbabwean population, the entire South African range of the species is included within two UNESCO Biosphere Reserves, the Vhembe and Waterberg Biosphere Reserves. Defining and refining core and buffer areas is a critical part of the ongoing management of these Reserves. Roosting sites of bats should be included as a layer in determining the location of such zones within biosphere reserves. This means that important bat underground (natural and man-made) roosts (including those of *R. smithersi*) should be included wherever possible in core or buffer areas where developments (including mining) would have to be regulated. Such conservation zonation plans (including Strategic Environmental Frameworks, EMFs) would inform planning by Provincial Nature Conservation (including the protected areas expansion strategy) and municipal Integrated Development Plans (IDPs), thereby affording protection to roosting sites.

GENERAL DISTRIBUTION:
Known from Lutope-Ngolangola Gorge south of the Zambezi Escarpment in NW Zimbabwe and also from Pafuri in the Limpopo Valley in the foothills of the Soutpansberg Mountains of northern Limpopo Province, South Africa but

likely more widespread across savanna woodlands of the Limpopo and Zambezi valleys, and their escarpments (the Gwembe horst, and the Soutpansberg and Waterberg Mountains, respectively) (Taylor *et al.*, 2012c: 19).

Accurate delimitation of this species' range is subject to further collecting and reappraisal of existing museum material, previously referred to as *R. hildebrandtii*.

Native: South Africa (Taylor *et al.*, 2012c: 19); Zimbabwe (Taylor *et al.*, 2012c: 19); Malawi (tentatively, all of the material previously assigned to *R. hildebrandtii*, but Meredith Happold (pers. comm., 24/02/2019) indicated that two species might be involved).

Kaipf *et al.* (2015: 22) report "*Rhinolophus smithersi* or a new species" from God's Bridge in Ethiopia.

ECHOLOCATION:
For 7 calls from specimens from Blouberg, South Africa, Taylor *et al.* (2013b: 18) recorded the following parameters: F_{max}: 45.2 ± 0.17 (44.9 - 45.4) kHz, F_{min}: 40.6 ± 1.28 (38.1 - 41.7) kHz, F_{knee}: 44.7 ± 0.13 (44.5 - 44.8) kHz, F_{char}: 44.6 ± 0.13 (44.3 - 44.7) kHz, duration: 34.9 ± 6.69 (26.0 - 46.9) ms. 13 calls from Waterberg resulted in the following parameters: F_{max}: 47.8 ± 0.31 (47.0 - 48.4) kHz, F_{min}: 45.7 ± 0.91 (44.1 - 44.7) kHz, F_{knee}: 47.2 ± 0.31 (46.3 - 47.7) kHz, F_{char}: 47.3 ± 0.29 (46.4 - 47.7) kHz, duration: 18.2 ± 4.52 (10.9 - 24.8) ms, and 10 calls from Soutpansberg: F_{max}: 46.0 ± 0.12 (45.9 - 46.2) kHz, F_{min}: 44.8 ± 0.20 (44.4 - 45.0) kHz, F_{knee}: 45.2 ± 0.07 (45.2 - 45.4) kHz, F_{char}: 45.5 ± 0.05 (45.5 - 45.6) kHz, duration: 12.0 ± 2.22 (9.6 - 16.5) ms. 19 calls recorded at the Mapungubwe National Park (RSA) by Parker and Bernard (2018: 57) had the following characteristics: F_{char}: 47.23 ± 1.62 kHz, F_{max}: 47.47 ± 1.50 kHz, F_{min}: 43.27 ± 2.65 kHz, F_{knee}: 47.26 ± 1.54 kHz, duration: 44.74 ± 22.83 ms, with 8.02 ± 3.70 calls/sec.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 65 calls of 3 bats: F_{max}: 47.26 ± 5.09 kHz, F_{min}: 39.78 ± 14.96 kHz, F_{knee}: 46.45 ± 5.57 kHz, F_{char}: 46.34 ± 5.66 kHz, slope: -195.04 ± 1520.38 OPS, duration: 16.36 ± 11.26 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 23 *Rhinolophus smithersi* calls from the Kruger Park (RSA): F_{min}: 45.5 ± 1.1 (43.2 47.4) kHz, Duration: 21.0 ± 9.1 (9.4 49.7) ms, F_{max}: 47.8 ± 0.5 (46.2 48.8) kHz, F_{knee}: 47.2 ± 0.6 (45.6 48.3) kHz, F_{char}: 47.1 ± 0.5 (45.7 48.1) kHz,

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 47.23 ± 1.62 kHz, F_{max}: 47.47 ± 1.50 kHz, F_{min}: 43.27 ± 2.65 kHz.

46 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 44 - 47 kHz, F_{max}: 47 - 48 kHz, F_{char}: 46 - 47 kHz, F_{knee}: 44 - 45 kHz and duration 10 - 25 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 47.23 ± 1.62 kHz, F_{max}: 47.47 ± 1.50 kHz and F_{min}: 43.27 ± 2.65 kHz.

POPULATION:
Structure and Density
Rhinolophus smithersi has colony sizes very small but more precise information about population size is missing (Taylor, 2017).

Trend
2016: Stable (Taylor, 2017).

PARASITES:
DIPTERA
Streblidae
Ascodipteron brevior Maa, 1965, female cysts found at the base of the ears from Namibia and South Africa (Haeselbarth *et al.*, 1966: 106 host referred to as *R. hildebrandtii*). *Raymondia hardyi* Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254; based on a record by Theodor (1968), who mentioned "*R. hildebrandtii*" as host).

Nycteribiidae
Nycteribia scissa rhodesiensis Theodor, 1957 from Zimbabwe and Malawi (Haeselbarth *et al.*, 1966: 108, host as *R. hildebrandtii*). *Nycteribia rotundata* Theodor, 1957 from Mazoe, Zimbabwe (Haeselbarth *et al.*, 1966: 110, host referred to as *R. hildebrandtii*). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114, host referred to as *R. hildebrandtii*).

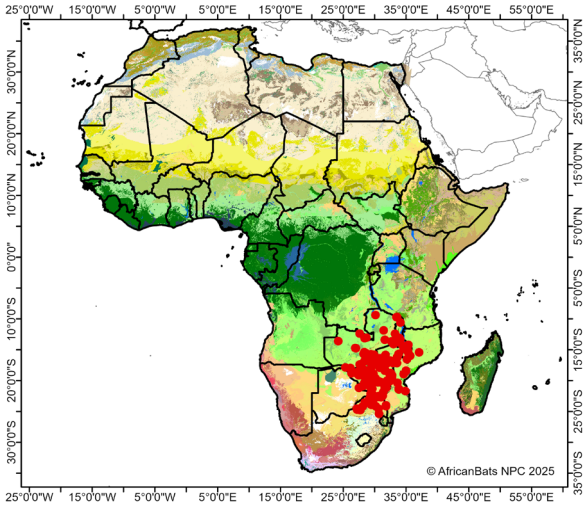

Figure 122. Distribution of *Rhinolophus smithersi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Malawi, Mozambique, South Africa, Zambia, Zimbabwe.

Rhinolophus swinnyi Gough, 1908

*1908. *Rhinolophus swinnyi* Gough, Ann. Transv. Mus., 1: 71, 2 text-f. Publication date: April 1908. Type locality: South Africa: Cape province: Ngqeleni district: W Pondoland: "Ngqeleni district" [30 40 S 29 02 E]. [Goto Description]. Holotype: TM 1021: ad ♂, skin and skull. Collected by: H.H. Swinny; collection date: 22 February 1908; original number: 153. Paratype: TM 1022: ad ♂, skin and skull. Collected by: H.H. Swinny; collection date: 23 February 1908; original number: 154. Notes: skull found lying loose- may not belong to this specimen [signed A. Roberts]). - Comments: Meester *et al.* (1986: 41) mentioned the type locality as "Ngqeleni district, west of Port St. Johns, Transkei". (Current Combination).

1913. *Rhinolophus swinnyi piriensis* Hewitt, Records Albany Mus., 2: 402. Publication date: 6 February 1913. Type locality: South Africa: E Cape province: near King William's Town: Pirie [32 43 S 27 18 E].

TAXONOMY:
Koopman (1966, 1982) suggests that this species may be conspecific with *denti*. *capensis* species group (Csorba *et al.*, 2003: 12 - 14; Simmons, 2005: 364). See Csorba *et al.* (2003: 11) for remarks on taxonomy.

Taylor *et al.* (2024: 7) found that *Rhinolophus swinnyi* from the eastern slopes of the Maloti-Drakensberg (South Africa) became separated from *Rhinolophus capensis* from the Fynbos and Succulent Karoo biomes of the CFB and southern Escarpment about 5.57 (2.87 - 8.7) Mya.

Taylor *et al.* (2024: 11) also indicated that *Rhinolophus swinnyi* can easily be distinguished from similar sized *Rhiniolophus rhodesiae* by their echolocation frequency, baculum size and shape.

COMMON NAMES:
Afrikaans: Swinny se saalneusvlermuis, Swinny-saalneusvlermuis, Swinnyse Vlermuis. Czech: vrápenec mosambický. English: Swinny's Horseshoe Bat. French: Rhinolophe de Swinny. German: Swinnys Hufeisennase. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego ferradura de Swinny.

ETYMOLOGY OF COMMON NAME:
Named after H.H. Swinny, who collected the original specimens from the Nqqueleni district, Eastern Cape (Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Although *Rhinolophus swinnyi* is known mainly from sparse records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large overall population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Cotterill, 2008c; IUCN, 2009; Monadjem and Cotterill, 2017b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Cotterill, 2017b). 2008: LC ver 3.1 (2001) (Cotterill, 2008c; IUCN, 2009). 2004: NT ver 3.1 (2001) (Cotterill, 2004h; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: VU C2a(i) ver 3.1 (2001) (Jacobs *et al.*, 2016h). 2004: EN C2a(i) ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
Populations may be locally threatened by deforestation, largely resulting from logging operations, local use of timber and firewood, and general conversion of land to agricultural use (Cotterill, 2008c; IUCN, 2009; Monadjem and Cotterill, 2017b).

CONSERVATION ACTIONS:
Cotterill (2008c) [in IUCN (2009)] and Monadjem and Cotterill (2017b) reported that *Rhinolophus swinnyi* is present in some protected areas (e.g., Kruger National Park, South Africa). Further studies are needed into the taxonomic status of this species, the distribution and possible threats.

GENERAL DISTRIBUTION:
Rhinolophus swinnyi has been recorded from eastern parts of South Africa, much of Zimbabwe, northwestern Mozambique, with additional scattered records further north in Malawi, Zambia, Democratic Republic of the Congo and Tanzania (including the island of Unguja [=Zanzibar]) (Skinner and Chimimba, 2005; O'Brien, 2011: 286). It may be present in Angola, but this needs confirmation. In South Africa, its distribution is mainly affected by temperature seasonality (Babiker Salata, 2012: 49).

Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,054,284 km^2.

Native: Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Happold *et al.*, 1988; Kock and Howell, 1988; Csorba *et al.*, 2003: 14; Monadjem *et al.*, 2010d: 561); Malawi (Happold and Happold, 1997b: 818; Csorba *et al.*, 2003: 14); Mozambique (Smithers and Lobão Tello, 1976; Skinner and Smithers, 1990; Csorba *et al.*, 2003: 14; Monadjem *et al.*, 2010d: 561; Monadjem *et al.*, 2010c: 380); South Africa (Maree and Grant, 1997; Rautenbach and Espie, 1982; Kock and Howell, 1988; Taylor, 1998; Csorba *et al.*, 2003: 13; Monadjem *et al.*, 2010d: 561); Tanzania (Skinner and Smithers, 1990; Kock and Howell, 1988; Csorba *et al.*, 2003: 14); Zambia (Ansell, 1969; Ansell, 1978; Csorba *et al.*, 2003: 14; Monadjem *et al.*, 2010d: 561); Zimbabwe (Cotterill, 1996a; Cotterill, 2004a: 261; Csorba *et al.*, 2003: 14; Monadjem *et al.*, 2010d: 561).
Presence uncertain: Angola

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 123. Clockwise from top lateral, ventral and dorsal skull images of TM 1021, holotype of *Rhinolophus swinnyi* Gough, 1908.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.3 Pa, aspect ratio 6.6 for a wingspan of 27 cm and a wing area of 109 cm^2 and a body mass of 7 g.

ECHOLOCATION:
Aldridge and Rautenbach (1987) reported a maximum frequency of 115 kHz for individuals from Pafuri in South Africa. Jacobs *et al.* (2007a) reported a slightly different peak frequency of 107.0 ± 0.8 kHz for individuals from South Africa. Monadjem *et al.* (2010c: 380) reported from Mozambique that the peak echolocation frequencies ranged between 99 - 103 kHz (Petterson D240x).

Taylor *et al.* (2018a: 25) mention a mean frequency of 106.6 ± 0.4 kHz for 10 specimens from the Eastern Cape Province and 105.6 ± 0.76 kHz from KwaZulu-Natal. From the same area, Moir (2020: 29) and Moir *et al.* (2021a: 371) reported the following parameters for 811 calls of 29 bats: F_{max}: 107.29 ± 1.11 (105.29 - 109.61) kHz, F_{min}: 95.93 ± 3.98 (88.12 - 104.39) kHz, F_{char}: 105.4 ± 0.91 (103.56 - 107.61) kHz, F_{knee}: 105.79 ± 1.18 (103.02 - 108.41) kHz, and duration: 13.11 ± 5.44 (5.78 - 30.09) ms.

Mutumi *et al.* (2016) found that acoustic divergence in RF was best predicted by latitude, geography and climate-induced differences in atmospheric attenuation.

Jacobs (2016: 119) indicates that the second harmonic of this bat coincides with the third harmonic of *R. capensis*, which possibly might illustrate "harmonic hopping".

MOLECULAR BIOLOGY:
Karyotype
Rautenbach (1986) reported 2*n* = 58, FN = 62, BA = 6, a subtelocentric X chromosome and a metacentric Y chromosome.

ROOST:
Happold and Happold (2023: 91) mention that, in Zimbabwe; these bats roost in caves, where a single cave can contain no more than five animals, scattered throughout the cave.

POPULATION:
Structure and Density
In parts of its range *Rhinolophus swinnyi* is considered to be uncommon, however, Taylor (2000) records that it is fairly common in Zimbabwe. It generally forms small colonies of fewer than ten animals (Cotterill, 2008c; IUCN, 2009; Monadjem and Cotterill, 2017b).

Trend
2016: Unknown (Monadjem and Cotterill, 2017b).
2008: Unknown (Cotterill, 2008c; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In Malawi, Happold and Happold (2023: 91) found three out of four females were pregnant at the beginning of the wet season (November), whereas the fourth was lactating.

PARASITES:
DIPTERA
Streblidae
Raymondia waterstoni Jobling, 1931 (Shapiro *et al.*, 2016: 256).

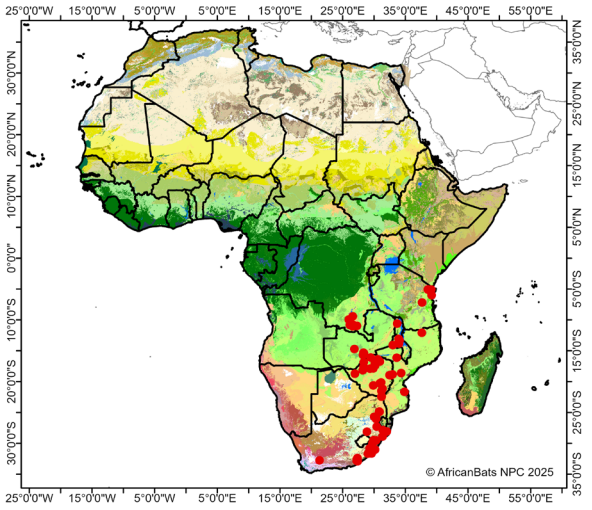

Figure 124. Distribution of *Rhinolophus swinnyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Malawi, Mozambique, South Africa, Tanzania, Zambia, Zimbabwe.

Rhinolophus webalai Patterson, Dick, Bartonjo and Demos, 2024

*2024. *Rhinolophus webalai* Patterson, Dick, Bartonjo and Demos, in: Patterson et al., J. Mamm., xxx (x): 7, figs 6, 7d, S7, S8. Publication date: 13 September 2024. Type locality: Kenya: Malindi district: Malindi Marine Park, KWS Headquarters [03 15 17 S 040 07 55 E, 5 m]. Holotype: FMNH 215894: ad ♂, skull and alcoholic. Collected by: Bruce D. Patterson, Paul W. Webala and Carl W. Dick; collection date: 10 May 2006; original number: BDP 4600. - Etymology: In honour of Dr. Paul Waswa Webala, one of Africa's foremost bat biologists in recognition of his important contributions as a field biologist, conservation scientist, prolific author, and mentor to Africa's next generation (Patterson *et al.*, 2024: 7).

COMMON NAMES:
English: Webala's Horseshoe Bat. German: Webala-Hufeisennase.

CONSERVATION STATUS:
Patterson *et al.* (2024: 12) suggest a listing as "Least Concern" based on the extensive distribution and varied ecological and roosting associations.

GENERAL DISTRIBUTION:
This species occurs in Kenya and South Sudan, and possibly in Uganda and N Tanzania (Patterson *et al.*, 2024: 10)

DETAILED MORPHOLOGY:
Baculum:
The baculum of this species is a simple, straight rod-like shaft with a smoothly flaring and slightly notched base when viewed dorsally. It is 2.05 to 2.49 (2.25) mm long and 0.685 to 0.885 (0.78) mm wide (Patterson *et al.*, 2024: 10).

SEXUAL DIMORPHISM:
Patterson *et al.* (2024: 10) indicate that most of the males had rust-coloured axillary tufts.

ECHOLOCATION:
Echolocation calls of *R. webalai* are dominated by a long constant-frequency signal (109.73 ± 1.17

[105.53 - 110.70] kHz, which is flanked initially and terminally by brief frequency-modulated elements; the terminal element has a great frequency span, resulting in a very broad bandwidth (30.17 ± 3.83 [19.31 - 35.58] kHz) for a high duty-cycle bat. The fundamental (first) harmonic is conspicuous (Patterson *et al.*, 2024: 9, 10). Other parameters are: F_{start}: 110.41 ± 1.26 (105.93 - 111.71) kHz, F_{end}: 80.23 ± 3.62 (75.47 - 89.53) kHz, duration: 58.87 ± 9.37 (47.60 - 85.00) ms, call interval: 177.55 ± 36.45 (113.30 - 293.30) ms.

PARASITES:
DIPTERA
Nycteribiidae
In their original description, Patterson *et al.* (2024: 10) already reported the presence of Penicilidia fulvida (Bigot, 1885).

Streblidae
Patterson *et al.* (2024: 10) also reported the presence of *Raymondia planiceps* Jobling, 1930.

ANTHROPOPHILOUS:
The holotype was found inside of an abandoned building (Patterson *et al.*, 2024: 7).

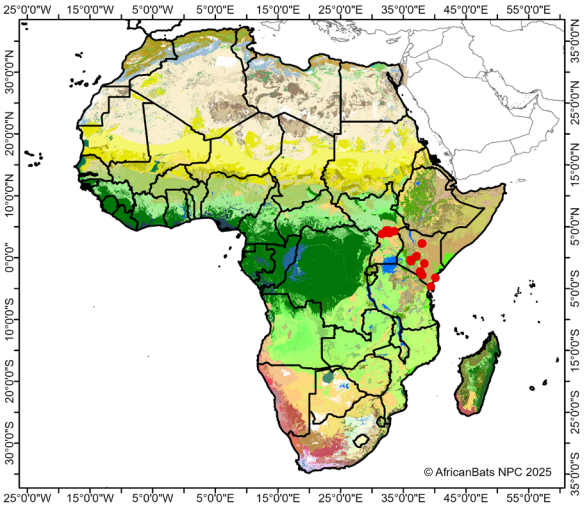

Figure 125. Distribution of *Rhinolophus webalai*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, South Sudan.

Rhinolophus willardi Kerbis Peterhans and Fahr, 2013

*2013. *Rhinolophus willardi* Kerbis Peterhans and Fahr, in: Kerbis Peterhans, Fahr, Huhndorf, Kaleme, Plumptre, Marks and Kizungu, Bonn. Zool. Bull., 62 (2): 190, figs 3, 4, 6. Publication date: November 2013. Type locality: Congo (Democratic Republic of the): Misotschi-Kabogo highlands [05 06 19 S 29 03 56 E, 1 880 m]. Holotype: FMNH 195182: ad ♂, skull and alcoholic. Collected by: A.J. Plumptre and E.A. Mulungu; collection date: 17 February 2007; original number: DCM 1680. Paratype: FMNH 195082: ad ♀, skin and skeleton and skull. Collected by: Ben D. Marks; collection date: 14 February 2007; original number: MHH 837. From 4 km SW of the village Talama, "Camp 2", 4°59'29''S, 29°04'49''E, 1950 m. Paratype: FMNH 195083: ad ♀, skin and skeleton and skull. Collected by: Ben D. Marks; collection date: 14 February 2007; original number: MHH 838. Paratype: FMNH 195084: ad ♀, skin and skeleton and skull. Collected by: Prince Kiswele Kaleme; collection date: 16 February 2007; original number: PK 754. Paratype: FMNH 198083: ad ♀, complete skeleton. Collected by: Ben D. Marks; collection date: 14 February 2007; original number: MHH 838. From 4 km SW of the village Talama, "Camp 2", 4°59'29''S, 29°04'49''E, 1950 m. Paratype: FMNH 198084: ad ♀, complete skeleton. Collected by: Ben D. Marks; collection date: 16 February 2007; original number: PK 754. From 4 km SW of the village Talama, "Camp 2", 4°59'29''S, 29°04'49''E, 1950 m. - Etymology: In honour of Dr. David Willard (Collection Manager, Division of Birds, FMNH) in recognition of his unparalleled 35+ years of service to the Field Museum of Natural History (see Kerbis Peterhans *et al.*, 2013: 191). (Current Combination).

COMMON NAMES:
English: Willards horseshoe bat. German: Willards Hufeisennase.

Regional
None known.

CONSERVATION STATUS:
Global Justification
Assessed as Endangered (EN B1ab(i,iii,v) ver 3.1 (2001)) because its extent of occurrence (EOO) is 3,588 km^2, and all individuals are from a single unprotected region (forest patches within the Misotschi-Kabogo highlands) where there is continuing decline in the extent and quality of its habitat (Monadjem, 2020b).

Assessment History
Global
2016: EN B1ab(i,iii,v) ver 3.1 (2001) (Monadjem, 2020b).

MAJOR THREATS:
This species is known only from one (1) location (two nearby capture sites) in unprotected forest patches the Misotschi-Kabogo highlands (Kerbis Peterhans *et al.*, 2013). This area is destabilized by regional conflict which is contributing to unregulated forest clearing, habitat degradation and loss (Monadjem, 2020b). The species likely roosts in caves and mines, which are heavily disturbed within the region.

CONSERVATION ACTIONS:
Monadjem (2020b) report that this species is in urgent need of conservation attention since it is

only known from one location in unprotected forest patches in the Misotschi-Kabogo highlands, a region destabilized by conflict. Research is needed into the species distribution, population size and trends, habitat, ecology, and threats.

HABITAT:
Chakravarty *et al.* (2024: 7) assigned this species to the group of "highland dwelling species."

POPULATION:
Structure and Density
Currently there is no information on the species population size, but it is suspected to be decreasing due to unregulated forest clearing within its limited range (Monadjem, 2020b). Further, cave roosting bats are heavily hunted and the roosts disturbed in the region.

Trend
2016: Decreasing (Monadjem, 2020b).

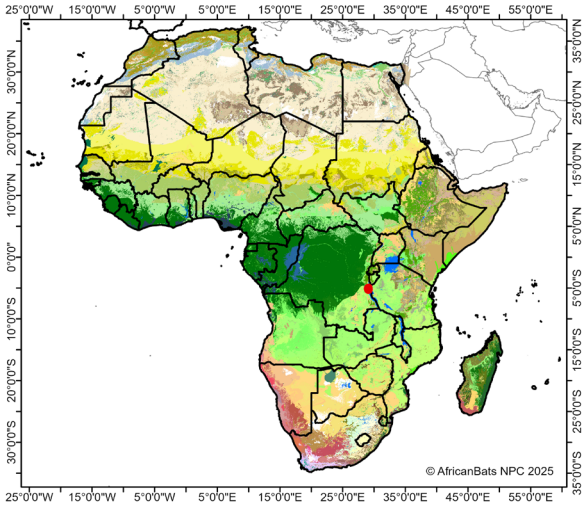

Figure 126. Distribution of *Rhinolophus willardi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

Rhinolophus ziama Fahr, Vierhaus, Hutterer and Kock, 2002

*2002. *Rhinolophus ziama* Fahr, Vierhaus, Hutterer and Kock, Myotis, 40: 102, 109, figs 1 - 7. Type locality: Guinea: Guinée Forestière: border "Réserve Biosphère de la Massif du Ziama": Sérédou, W edge of: near Park Station [ca. 08 23 N 09 17 W]. [Goto Description]. Holotype: ZFMK MAM-1999.0934: ad ♂, alcoholic, skull and skeleton. Collected by: Henning Vierhaus; collection date: 12 August 1992; original number: HV 2590. Paratype: AMNH 265708: ad ♂, skull and alcoholic. Collected by: Dr. Robert W. Dickerman; collection date: 4 March 1990; original number: 2144. 7 mi ?, 1 mi E Ziggida, Lofa county, Wonegizi Mts., Liberia: see Fahr *et al.* (2002: 109). - Etymology: In reference to the protected area near the type locality, the "Réserve de la Biosphère du Massif de Ziama", and as a noun in apposition (Fahr *et al.*, 2002: 110). (Current Combination).

TAXONOMY:
maclaudi species group (Fahr *et al.*, 2002; Simmons, 2005: 365).

COMMON NAMES:
Czech: vrápenec liberijský. English: Ziama Horseshoe Bat (first use Simmons, 2005: 365). French: Rhinolophe du Ziama. German: Ziama-Hufeisennase.

CONSERVATION STATUS:
Global Justification
Rhinolophus ziama is listed as Endangered (EN B2ab(iii) ver 3.1 (2001)) as it is only known from three locations in Guinea, Liberia, and Sierra Leone where its area of occupancy (AOO) is 150-300 km^2. The global population for this species is projected to continue to decline as the quality, area, and extent of its forest and cave habitats continues to be lost and/or degraded (Fahr, 2008n; IUCN, 2009; Cooper-Bohannon and Monadjem, 2020)..

Assessment History
Global
2019: EN B2ab(iii) ver 3.1 (2001) (Cooper-Bohannon and Monadjem, 2020). 2008: EN B1ab(iii) ver 3.1 (2001) (Fahr, 2008n; IUCN, 2009). 2004: EN B1ab(iii) ver 3.1 (2001) (Fahr, 2004c; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
Rhinolophus ziama is threatened by past and continued deforestation of its roosts and foraging habitats, largely through logging and mining operations as well as inundation of forest for the generation of hydroelectric power, and conversion of land to agricultural use. It is also considered possible that the species could be threatened by overharvesting for subsistence food in the future (Fahr, 2008n; IUCN, 2009; Fahr, 2013k; Cooper-Bohannon and Monadjem, 2020).

CONSERVATION ACTIONS:
Fahr (2008n) [in IUCN (2009)] and Cooper-Bohannon and Monadjem (2020) reported that it is not known if the species is present in any protected areas. There is a need to protect suitable areas of forest habitat for this species, and to initiate appropriate bat conservation

awareness programmes among local people. In addition, further studies are needed into the distribution, abundance, natural history, and threats to this species.

GENERAL DISTRIBUTION:
Rhinolophus ziama is a West African bat, known from two localities in the Guinea Highlands (c. 600 m asl) of southeast Guinea (Ziama Forest) and north-west Liberia (Wonegizi Mountains) (Fahr *et al.*, 2002). Surrounding areas have been surveyed but the species has not been found elsewhere.

Native: Guinea; Liberia; Sierra Leone (Decher *et al.*, 2010; Norris *et al.*, 2015: 83)..

POPULATION:
Structure and Density
Rhinolophus ziama is known only from five specimens (Fahr *et al.*, 2002; Decher *et al.*, 2010). The global population is thought to be declining due to ongoing loss and degradation of forests and cave/mine habitats (Cooper-Bohannon and Monadjem, 2020).

Trend
2019: Decreasing (Cooper-Bohannon and Monadjem, 2020). 2008: Decreasing (Fahr, 2008n; IUCN, 2009).

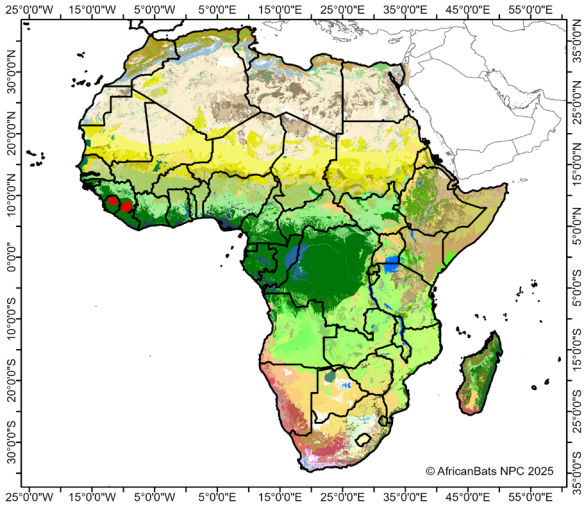

Figure 127. Distribution of *Rhinolophus ziama*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea, Liberia, Sierra Leone.

Family RHINONYCTERIDAE J. E. Gray, 1866

*1866. *Rhinonycteridae* J. E. Gray, Proc. zool. Soc. Lond., 81.
1866. *Rhinonycterina* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 81. Publication date: May 1866. - Comments: Proposed as tribe (?). Type genus: *Rhinonicteris* J. Gray, 1866, and originally included the genus *Rhinonicteris* J. Gray, 1847. Retained as subtribe by Koopman (1994: 68) (see Jackson and Groves, 2015: 251).
*2009. *Triaenopini* Benda and Vallo, Folia Zool., 58 (Mon 1): 2, 33. - Comments: Type genus: *Traenops* Dobson, 1871. Proposed as tribe and originally included the genera *Triaenops* Dobson, 1871 and *Paratriaenops* Benda and Vallo, 2009. Synonymized with *Rhinonycteridae* by Foley *et al.* (2014: 319) (see Jackson and Groves, 2015: 251).
? *Rhinonicteridae* (Alternate Spelling).

TAXONOMY:
Based on the phylogram, the timetree, and a unique retrotransposon insertion, Foley *et al.* (2014: 313) elevated the subtribe Rhinonycterina Gray, 1866 to family level: Rhinonycteridae. They also found (p. 318) that the monophyletic grouping of this family is supported by a unique shared indel in the *THY* gene fragment.

The validity of this family was also confirmed by Amador *et al.* (2016: 3, 6).

Currently (Simmons and Cirranello, 2024a) recognized extant genera of Rhinonycteridae: ***Cloeotis*** Thomas, 1901; ***Paratriaenops*** Benda and Vallo, 2009; *Rhinonicteris* Gray, 1847, ***Triaenops*** Dobson, 1871.
Additionally, there are extinct genera: †*Archerops* Hand and Kirsch, 2003; †*Brachipposideros* Sigé, 1968; †*Brevipalatus* Hand and Archer, 2005,

COMMON NAMES:
English: **Trident bats** (Armstrong *et al.*, 2016: 116).

SIMILAR SPECIES:
Key characters for the genera:
Cloeotis – Head and body length is 33 – 50 mm, tail length is 22 – 33 mm (tail completely enclosed by interfemoral membrane and is longer than the femur), and forearm length is 30 – 39 mm. Posterior component of noseleaf with three tall tapering projections. Two upper premolars on each side, M^3 not reduced (four ridges) (Nowak, 1994: 118, Happold, 2013al: 357).
Paratriaenops – Head and body length is 35 – 62 mm, tail length is 20 – 34 mm (tail completely enclosed by interfemoral membrane), and the forearm length is about 49 – 61 mm. Posterior component of noseleaf with three tall tapering projections. Two upper premolars on each side, M^3 not greatly reduced (three ridges).

Rhinonicteris – Head and body length is 45 – 53 mm, tail length is 24 – 28 mm, forearm length is 47 – 50 mm. The complex upper portion of the nose-leaf surmounts the nostrils like a crown. The crown-like portion of the leaf is extensively honeycombed and sculptured (Nowak, 1994: 116).

Triaenops – Head and body length is 35 – 62 mm, tail length is 20 – 34 mm (tail completely enclosed by interfemoral membrane), and forearm length is 45 – 61 mm. Posterior component of noseleaf with three tall tapering projections as in *Cloeotis*. Cranially, *Triaenops* differs from genera in its raised and inflated rostrum and relatively much larger cochleae but resembles *Rhinonycters* in the structure of the anterorbital region and zygoma and in the curiously thickened premaxillae, two upper premolars on each side, M^3 not greatly reduced (three ridges) (Nowak, 1994: 115, Happold, 2013al: 357).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Chornelia and Hughes (2022: 18) suggest that the origin of the Madagascan Rhinonycteridae is Sudanian + Somalia + Ethiopia, where they split off from *Paratriaenops*.

MOLECULAR BIOLOGY:
Karyotype
The family's karyotype 2*n* value varies between 36 and 40 (Sotero-Caio *et al.*, 2017: 5).

PARASITES:
BACTERIA
Esteves *et al.* (2022: 1) indicate that the Rhinonycteridae - together with the Nycteridae - are the bat families that are most heavily infected by (*Leptospira* bacteria.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

†Genus ***Brachipposideros*** Sigé, 1968

*1968. *Brachipposideros* Sigé, Paleovert., 1 (3): 83.

†Genus ***Brevipalatus*** Hand and Archer, 2005

*2005. *Brevipalatus* Hand and Archer, Palaeontology, 48 (2): 372.

Genus ***Cloeotis*** Thomas, 1901

*1901. *Clœotis* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 28. Publication date: 1 July 1901 [Goto Description]. - Comments: Type species: *Clœotis percivali* Thomas, 1901. - Etymology: From the Greek "*κλοτός*", meaning collar and "*οὐς*" or "*ὠτός*", meaning ear, referring to Thomas' statement that "the whole ear is very like a man's 'stand-up' collar with angles in front rounded off." (see Palmer, 1904: 191). Alternatively, "*cloeotis*" might simply mean short-eared.

1941. *Cleotis:* Winge, The interrelationships of the mammalian genera. I. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata, 301. (Lapsus).

? *Cloeotis:* (Current Spelling).

TAXONOMY:
Reviewed by Hill (1982b).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Cloeotis*: ***percivali*** Thomas 1901.

COMMON NAMES:
Czech: jihoafričtí cíponosi. English: Short-eared Trident Bats, Short-eared Bats, African Trident Bats, African Trident-nosed Bats, Trident-nosed Bats. French: Cléothes. German: Kleinohr-Dreizackblattnase. Italian: Cloeòtidi.

Cloeotis percivali (Thomas, 1901)

*1901. *Clœotis Percivali* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 28. Publication date: 1 July 1901. Type locality: Kenya: Coast province: N of Mombassa: Takaungu [03 42 S 39 51 E, 20 m]. [Goto Description]. Holotype: NHMUK 1901.5.1.11: ♂. Collection date: 15 February 1901. Presented/Donated by: Arthur Blayney Percival. -

Etymology: In honour of Arthur Blayney Percival, game ranger in the former British East Africa, and collector of the type specimen (see Lanza *et al.*, 2015: 133). (Current Combination).

1917. *Clœotis percivali australis* Roberts, Ann. Transv. Mus., 5: 264-5. Publication date: 16 May 1917. Type locality: South Africa: W Transvaal province: Rustenburg district: Mooimeisiesfontein [25 01 S 27 37 E]. [Goto Description]. Holotype: TM 1670: ad ♀, skin and skull. Collected by: W. Powell; collection date: 28 May 1915. Paratype: TM 1669: ad ♀, skin and skull. Collected by: W. Powell; collection date: 26 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1671: ad ♀, skin and skull. Collected by: W. Powell; collection date: 27 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1672: ad ♀, skin and skull. Collected by: W. Powell; collection date: 28 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1673: ad ♀, skin and skull. Collected by: W. Powell; collection date: 28 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1674: ad ♂, skin and skull. Collected by: W. Powell; collection date: 26 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1675: ad ♂, skin and skull. Collected by: W. Powell; collection date: 26 May 1915. Roberts (1917b: 265) called this a "Metatype". Paratype: TM 1676: ad ♂, skin and skull. Collected by: W. Powell; collection date: 26 May 1915. Roberts (1917b: 265) called this a "Metatype". - Comments: Considered a valid subspecies by Taylor (1998: 41). Monadjem *et al.* (2010d: 147) mentioned TM 1690 as type specimen, but Roberts (1917b: 265) indicated TM 1670, which is part of the eight *percivali* specimens collected by W. Powell at Mooimeisjesfontein and mentioned by the author (TM 1669 - 1676). (Name Combination).

2019. *Cloeotis percivalli:* Waghiiwimbom, Bakwo Fils, Atagana, Tsague Kenfack and Tamesse, Afr. J. Ecol., "6". Publication date: 23 October 2019. (Lapsus).

? *Cloeotis percivali australis:* (Name Combination).

? *Cloeotis percivali percivali:* (Name Combination).

? *Cloeotis percivali:* (Current Spelling).

Taxonomy:



Figure 128. *Cloeotis percivali* (TM 46644) from Miggies gat, Mpumalanga, South Africa.

Meester *et al.* (1986: 43 - 44) recognized two subspecies: *percivali* and *australis*.

Common Names:

Afrikaans: Drietand-bladneusvlermuis, Drietand-blaarneusvlermuis. Chinese: 珀氏三叉蝠. Czech: cíponos jihoafrický. English: Percival's Short-eared Trident Bat, **Percival's Trident Bat**, Short-eared Trident Bat, African Trident Bat, East African Trident Bat. French: Cléothe de Percival, Asellia d'Afrique orientale, Phyllorhine à petites oreilles, Phyllorhine de Percival. German: Percivals Kleinohr-Dreizackblattnase. Italian: Cloeòtide di Pèrcival. Kiluba (DRC): Kasusu. Portuguese: Morcego tridentado. SiSwati: Lilulwane.

Conservation Status:

Global Justification

Although poorly known and with some recorded population declines, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008do; IUCN, 2009; Monadjem *et al.*, 2017bc).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bc). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008do; IUCN, 2009). 2004: VU A2bc+A3bc, C1 ver 3.1 (2001) (Mickleburgh *et al.*, 2004db; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: E C2a(i) ver 3.1 (2001) (Balona *et al.*, 2016). 2004: CR A2a ver 3.1 (2001) (Friedmann and Daly, 2004). 1996: Indeterminate (Smithers, 1986).

Eswatini:- 2003: DD ver 3.1 (2001) (Monadjem *et al.*, 2003).

Major Threats:

There have been seemingly stochastic extinctions of colonies, though it is not known if the animals simply move to new locations. Roost disturbance seems to be an important factor, but there might be others, and there has been speculation that DDT might be a cause of population disappearances (Mickleburgh *et al.*, 2008do; IUCN, 2009; Monadjem *et al.*, 2017bc).

Conservation Actions:

Mickleburgh *et al.* (2008do) [in IUCN (2009)] and Monadjem *et al.* (2017bc) report that in South Africa, KwaZulu-Natal province they are protected from human disturbance. It might occur in some protected areas. Protection of maternity/breeding and roosting sites from disturbance is important.

GENERAL DISTRIBUTION:
Largely confined to southern Africa, with records from South Africa (KwaZulu-Natal, Limpopo, and Mpumalanga), Swaziland, south-east Botswana, southern Zambia, Zimbabwe (the core of the distribution), and extralimital records from southern Democratic Republic of Congo, Malawi, northwestern Mozambique, and coastal Kenya (Taylor, 2000). Reported from Mafia Island Tanzania, but no vouchers were collected (Kock and Stanley, 2009; O'Brien, 2011: 287).

For southern Africa (south of 8°S), Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 955,464 km^2. In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

Native: Botswana (Smithers, 1971, Tiunov, 1986: 536); Cameroon (Waghiiwimbom *et al.*, 2019b: 6), Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 536); Eswatini (Monadjem *et al.*, 2005; Monadjem *et al.*, 2010d: 536; Monadjem *et al.*, 2021: 5); Kenya; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 536); South Africa (Seamark, 2005c: 3; Monadjem *et al.*, 2010d: 536; Balona, 2016: 5); Tanzania; Zambia (Ansell, 1969; Ansell, 1986; Monadjem *et al.*, 2010d: 536); Zimbabwe (Monadjem *et al.*, 2010d: 536).

FUNCTIONAL MORPHOLOGY:
Davies *et al.* (2013b: 6) found that this species' cochlea contains a highly modified basal turn compared to the other species they studied, and these modifications are consistent with the tonotopic organisation of the cochlea in which the basal area corresponds to the highest frequencies used by this bat.

Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 6.2 Pa, aspect ratio 5.2 for a wingspan of 21 cm and a wing area of 84 cm^2 and a body mass of 5 g.

ECHOLOCATION:
For an individual from Sengwa in Zimbabwe, Jacobs (1996) and Fenton and Bell (1981) reported a maximum frequency of 212 kHz, the highest frequency pure tone documented from the natural world (Bell and Fenton, 1984 in Thiagavel *et al.*, 2017: 1). Monadjem *et al.* (2007a), using an Anabat detector reported a maximum frequency of 103.4 (± 0.74) kHz for individuals from various localities in Swaziland. While Monadjem *et al.* (2010d: 57) report a maximum frequency of 103.2 (± 0.7) using an Anabat detector. Taylor (1999b) using a Pettersson D980 detector reported a maximum frequency of 104.2 (± 0.4) kHz for *C. percivali* from Jozini in South Africa. Taylor (2000) reported a constant frequency of 104 kHz (fundamental) and 208 kHz (first harmonic). Fenton (2004b: 3) indicates that the calls are dominated by sounds higher than 200 kHz. Monadjem *et al.* (2010d: 144) report HD-CF calls with high peak frequency (207.8 ± 3 kHz, n = 6) and intermediate duration (4.6 ± 1.2 ms, n = 6), with a second harmonic, where the fundamental harmonic is at around 104 kHz.

Monadjem *et al.* (2007a) also reported sexual dimorphism in the call with males calling at a higher frequency than females (males 103.7 ± 0.71 kHz, females 102.9 ± 0.52 kHz).

In Swaziland, Monadjem *et al.* (2017c: 179) recorded the following parameters: F_{min}: 99.2 ± 1.02 (98.1 - 100.1) kHz, F_{knee}: 103.1 ± 0.65 (102.6 - 103.8) kHz, F_c: 102.6 ± 0.51 (102.2 - 103.2) kHz, duration: 2.3 ± 0.04 (2.2 - 2.3) ms.

Three bats (one unknown sex, one female and one male) from the Fikirini caves in Kenya called with F_{max} respectively: 217.1, 225.3, and 219.6 kHz and a duration of 3.9, 4.0 and 4.0 ms (Webala *et al.*, 2019b: 15).

MOLECULAR BIOLOGY:
Karyotype
2*n* = 40 (Rautenbach *et al.*, 1993).

Genetics
Eick *et al.* (2005) and Matthee *et al.* (2006).

HABITAT:
Its elevational range is from sea level to 1,000 m (Mickleburgh *et al.*, 2008do).

ROOST:
Caves and mine tunnels for day roosting (Taylor, 2000).

DIET:
It feeds exclusively on moths (Taylor, 2000).

From Zambia, Black (1979: 54) reported the occurrence of the following prey taxa in the stomachs of 55 bats: Lepidoptera (moths): 100, Coleoptera (beetles): 7.3, Diptera (flies): 5.5, Unidentified insects: 3.6, Hemiptera (bugs): 1.8, and Isoptera (termites): 1.8. Only 7 of the 55 bats had eaten prey other than moths.

For South Africa, Jacobs (2000: 201) mentioned the following prey proportions: Lepidoptera (98.7 ± 3.2), Coleoptera (0.3 ± 1.2), Diptera (0.2 ± 0.7), and unknown (0.8 ± 3.1).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
Large fluctuations in population numbers are known, and it is prone to local extinctions. It is never found in very large colonies, with the largest known colony (of about 300 individuals) being reported from KwaZulu-Natal, South Africa, on the southern section of its range. However, the current estimated population size of the KwaZulu-Natal colony is only 50 animals. There are no population estimates from elsewhere in its range, although the largest population might be in Zimbabwe (Mickleburgh *et al.*, 2008do; IUCN, 2009; Monadjem *et al.*, 2017bc).

Trend
2016: Unknown (Monadjem *et al.*, 2017bc). 2008: Unknown (Mickleburgh *et al.*, 2008do; IUCN, 2009). 2004: Unknown (Mickleburgh *et al.*, 2004db; IUCN, 2004).

REPRODUCTION AND ONTOGENY:
The single female collected in Zambia in December by Benda *et al.* (2022: 307) was lactating.

PARASITES:
DIPTERA
Streblidae
Raymondia alulata Speiser, 1908 recorded at Kanye, Botswana (Haeselbarth *et al.*, 1966: 102; Shapiro *et al.*, 2016: 253). *Raymondia hardyi* Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254). *Raymondia huberi huberi* Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254). *Raymondia seminuda* Jobling,1954 from southern Botswana (Haeselbarth *et al.*, 1966: 103; Shapiro *et al.*, 2016: 255). *Raymondia waterstoni* Jobling, 1931 (Haeselbarth *et al.*, 1966: 104).

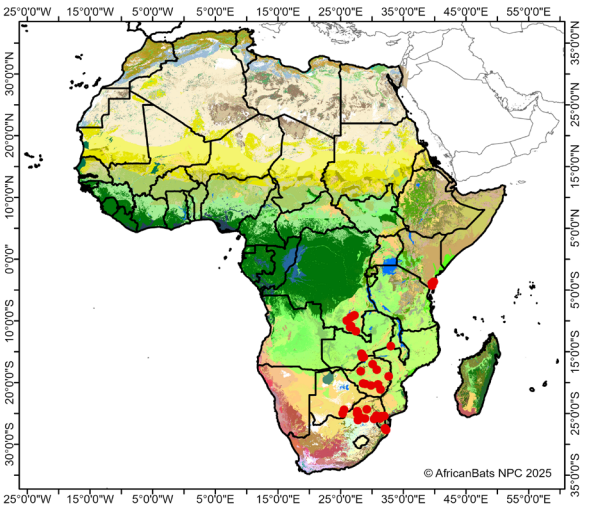

Figure 129. Distribution of *Cloeotis percivali*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Congo (Democratic Republic of the), Eswatini, Kenya, South Africa, Zambia, Zimbabwe.

Genus ***Paratriaenops*** Benda and Vallo, 2009

*2009. *Paratriaenops* Benda and Vallo, Folia Zool., 58 (1): 1, 31. - Comments: Type species: *Triaenops furcula* Trouessart, 1906. - Etymology: The name refers to close similarity of *Paratriaenops* with the genus *Triaenops*; Greek prefix *para* - means besides, next to. Masculinum.

TAXONOMY:
Differs primarily from *Triaenops* Dobson, 1871 and *Cloeotis* Thomas, 1901 in the shape and morphology of the noseleaf, and lacking of lateral supplementary leaflets (Benda and Vallo, 2009). Based on a considerable genetic distance (21.6 - 26.2 % in 731 bp sequence of cyt *b*) and substantial morphological differences from the continental forms of *Triaenops* as well as from Malagasy *T. menamena*, Benda and Vallo (2009: 1) propose generic status for the group of Malagasy species, *T. furculus*, *T. auritus*, and *T. pauliani*. They also separate *Paratriaenops* and *Triaenops* from the other hipposiderid bats in the tribus *Triaenopini*.

Ramasindrazana *et al.* (2013: 436) support the recognition of *Paratriaenops* as a separate genus based on an additional character: the inversed sexual dimorphism, where females are larger than males.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Paratriaenops*: ***auritus*** (G. Grandidier, 1912); ***furcula*** (Trouessart, 1907); ***pauliani*** (Goodman and Ranivo, 2008).

COMMON NAMES:
Czech: malí cíponosi. German: Madagaskar-Dreizack-Blattnasen.

Paratriaenops auritus (G. Grandidier, 1912)

*1912. *Triænops aurita* G. Grandidier, Bull. Mus. natn. Hist. nat., Paris, sér 1, 18 (1): 8, fext-fig. Publication date: 25 January 1912. Type locality: Madagascar: extreme N Madagascar: near Diégo-Suarez [=Antsiranana] [ca. 12 16 S 49 17 E]. [Goto Description]. Holotype: MCZ 45080: ♂, skin and skull. Collected by: Dr. Mazières. Body mummified; see Peterson (1987: 81). on label: "envoi du Dr. Mazières, Diégo Suarez - Madag. 1910": see Ranivo and Goodman (2006: 974), Helgen and McFadden (2001: 143).
2009. *Paratriaenops auritus:* Benda and Vallo, Folia Zool., 58: 33. (Name Combination, Current Combination).
? *Triaenops auritus:* (Current Spelling).

TAXONOMY:
Until recently, only known from the holotype (see Peterson *et al.*, 1995: 81), but additional specimens were reported by Ranivo and Goodman (2006: 977). Included in *furculus* (Hayman and Hill, 1971; Koopman, 1993a: 175, 1994), but Peterson *et al.*, 1995: 81), Russ *et al.* (2001), Hutson *et al.* (2001: 18), Ranivo and Goodman (2006: 974) consider it a valid species. Benda and Vallo (2009) placed it in the genus *Paratriaenops*.

COMMON NAMES:
Czech: cíponos zlatý. English: **Grandidier's trident bat**. French: Triaenops à grandes oreilles, Triénope doré. German: Grandidiers Dreizahn-Blattnase.

SIMILAR SPECIES:
Goodman *et al.* (2025: 213) reported a sexual size dimorphism with females having larger external measurements. Furthermore, pregnant females were on average 30 % heavier than non-pregnant ones.

CONSERVATION STATUS:
Global Justification
This species is listed as Vulnerable (VU B1ab(iii) ver 3.1 (2001)) as it has what appears to be restricted geographic range of less than 20,000 km^2 in northwestern Madagascar. The habitat is severely fragmented, and there is a continuing decline in the area and quality of habitat mainly due to agricultural activities. Further survey work is needed to help better ascertain the limits of the range of this species (Andriafidison *et al.*, 2008n; IUCN, 2009; Monadjem *et al.*, 2017a).

Assessment History
Global
2016: VU B1ab(iii) ver 3.1 (2001) (Monadjem *et al.*, 2017a). 2008: VU B1ab(iii) ver 3.1 (2001) [assessed as *Triaenops auritus*] (Andriafidison *et al.*, 2008n; IUCN, 2009). 2000: DD ver 2.3 (1994) [assessed as *Triaenops auritus*] (IUCN, 2000).

Regional
None known.

MAJOR THREATS:
As a forest dependent species any decline in extent or quality of the remaining forest poses a threat to this species. In northern Madagascar, forest is lost because of expanding agriculture. There is also the threat of disturbance to cave roosting sites (Andriafidison *et al.*, 2008n; IUCN, 2009; Monadjem *et al.*, 2017a).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008n) [in IUCN (2009)] and Monadjem *et al.* (2017a) report that this species is known to occur in three protected areas: Réserve Spéciale d'Ankarana, Réserve Spéciale d'Analamerana and Daraina forest (Ranivo and Goodman, 2006; Russell *et al.*, 2007). Conservation should be focused at the known cave roosts to secure the existing populations and closely monitor seasonal and annual population changes.

GENERAL DISTRIBUTION:
Paratriaenops auritus is endemic to the island of Madagascar where it has a restricted range in the dry forest of the north-western tip of the island, ranging between 50 m and 160 m above sea-level (Ranivo and Goodman, 2006; Robinson *et al.*, 2006; Russell *et al.*, 2007, Garbutt, 2022: 84). The Andrafiamena Mountains likely form the southern limit of this species (S. M. Goodman *pers. comm.*).

Native: Madagascar (Ranivo and Goodman, 2006: 963; Robinson *et al.*, 2006; Russell *et al.*, 2007).

BIOGEOGRAPHY:
See Russell *et al.* (2007).

DETAILED MORPHOLOGY:
Baculum
The only specimen examined by Rakotondramanana and Goodman (2017: 56) had an elongated baculum with a pointed tip and expanded rounded basal lobe; length: 1.78 mm, width: 0.49 mm.

SEXUAL DIMORPHISM:
Goodman *et al.* (2022: 1902) mentioned that males are smaller than females.

ECHOLOCATION:
Kofoky *et al.* (2009: 380) reported the calls from 10 individuals, which consisted of a distinctive narrowband CF component that ended with short FM sweeps with a maximum energy of 100.3 kHz.

Ramasindrazana *et al.* (2013: 434) mention the following values for 5 ♂♂ specimens: Resting frequency: 107.8 ± 1.51 (106.9 - 109.6) kHz, F_{max}: 108.8 ± 1.48 (106.5 - 110.2) kHz, F_{min}: 106.5 ± 1.59 (104.8 - 108.2) kHz, duration: 11.7 ± 3.65 (7.6 - 17.5) ms, interpulse interval: 28.9 ± 8.02 (19.5 - 38.6) ms, and for 2 ♀♀: Resting frequency: 95.6 (95.1, 96.1) kHz, F_{max}: 96.4 (95.6, 97.2) kHz, F_{min}: 93.9 (93.8, 94.1) kHz, duration: 13.7 (13.5, 14.0) ms, interpulse interval: 25.5 (25.4, 25.7) ms.

MOLECULAR BIOLOGY:
Genetics
Russell *et al.* (2007).

HABITAT:
Dammhahn and Goodman (2013: 108) mention that the bat's foraging habitat is the lower portion of forest.

DIET:
Based on fecal analyses, Razafindranosy *et al.* (2025: 219, 221) reported that *Paratriaenops auritus* feeds on Coleoptera, Hymenoptera, Lepidoptera, Hemiptera and Diptera. Adult males and non-reproductive females have a preference for Coleoptera (♂♂: 46.1 ± 4.46 % volume; ♀♀: 43.1 ± 4.02 %) and Lepidoptera (♂♂: 32.1 ± 2.46 %; ♀♀: 29.5 ± 2.43 %), whereas pregnant females consumed mainly Lepidoptera (59.1 ± 1.42 %).

POPULATION:
Structure and Density
This species is thought to be relatively abundant within a localized area in the northern part of Madagascar. The largest roost recorded was 2,000 individuals in Réserve Spéciale d'Ankarana (S. G. Cardiff *pers. obs.* in Andriafidison *et al.* (2008n) and Monadjem *et al.* (2017a)) and up to 1,000 individuals were recorded from a mine tunnel approximately 5 km from Andavokoera (J. Ranivo *pers. comm.* in in Andriafidison *et al.* (2008n) and Monadjem *et al.* (2017a).

Trend
2016: Unknown (Monadjem *et al.*, 2017a). 2008: Unknown (Andriafidison *et al.*, 2008n; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
16 females collected between 27 and 30 November at the Antsahabe cave were pregnant with a single embryo (crown-rump length 17 - 21 mm). Five females collected between 19 and 22 November at Binara were also pregnant (crown-rump length of embroys 17 - 18 mm) (Crowley and Goodman, 2025: 213). All of these females had auxiliary pubic nipples. At the same time, none of the males showed any sign of reproduction.

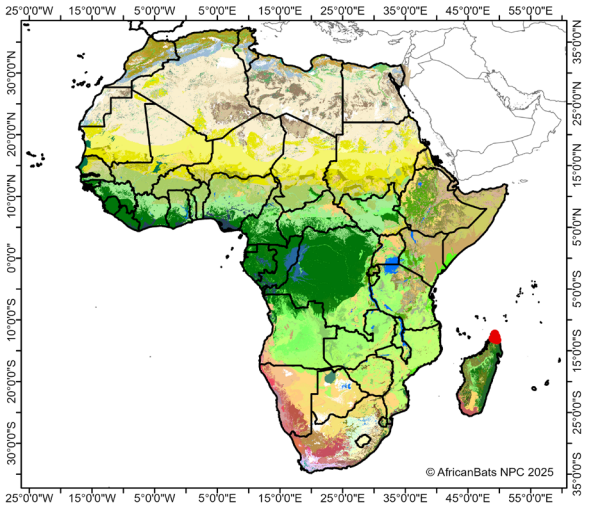

Figure 130. Distribution of *Paratriaenops auritus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Paratriaenops furcula (Trouessart, 1907)

*1907. *Triaenops furcula* Trouessart, Bull. Mus. natn. Hist. nat., Paris, sér 1, 12 (7): 446 (for 1906). Publication date: 26 February 1907. Type locality: Madagascar: Tuléar province: 20 km S Tuléar, St. Augustine Bay: Sarodrana cave [23 33 S 43 45 E]. Holotype: MNHN ZM-MO-1912-40: ♂, alcoholic (skull missing). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Rode (1941: 239) mentions numbers "186" and "1912-40". Paratype: MNHN ZM-MO-1912-40B: ♂, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Rode (1941: 239) mentions numbers "186" and "1912-40". Paratype: MNHN ZM-MO-1912-40C: ♂, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Rode (1941: 239) mentions numbers "186" and "1912-40". Paratype: MNHN ZM-MO-1997-1858: ♀, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1859: ♂, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1860: ♂, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1861: ♂, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1862: ♂, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype:

MNHN ZM-MO-1997-1863: ♂, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1864: ♀, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1865: ♀, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1866: ♀, skull and alcoholic. Collected by: Guillaume Grandidier; collection date: 19 May 1898. Paratype: MNHN ZM-MO-1997-1867: ♀, alcoholic (skull not removed). Collected by: Guillaume Grandidier; collection date: 19 May 1898. - Comments: Issue 12 (7) was for a meeting on 27 November 1906 but was only distributed around 26 February 1907 (see Bull. Vol 13 (2). Trouessart (1907: 446) mentions "*Triaenops*" in the name for the new taxon but refers to the other taxa as "*Triænops*").

2009. *Paratriaenops furculus:* Benda and Vallo, Folia Zool., 58: 33. (Name Combination).

2019. *Paratriaenops furcula:* Wilson and Mittermeier, Handbook of the mammals of the world. Vol. 9. Bats, 209. - Comments: Wilson and Mittermeier (2019: 209) mentioned that the original epithet (*furcula*) needs to be retained (over *furculus*) as it is a name in apposition and as such - doesn't need to be replaced. (Current Combination).

? *Triaenops furculus:* (Current Spelling).

Taxonomy:

Hayman and Hill (1971: 30) and Koopman (1993a: 175) included *aurita*, but see Peterson *et al.* (1995), Russ *et al.* (2001), Hutson *et al.* (2001: 18), Simmons (2005: 378), Ranivo and Goodman (2006: 963) who consider it a valid species. Benda and Vallo (2009) placed it into the genus *Paratriaenops*.

Common Names:

Czech: cíponos malý. English: **Trouessart's Trident Bat**, Trouessart's Triden Bat, Madagascar Leaf-nosed Bat. French: Triaenops malgache, Triaenops de Madagascar, Triaenops de Trouessart, Triénope de Trouessart. German: Trouessarts Dreizahn-Blattnase.

Palaeontological or archaeological records:

Sabatier and Legendre (1985: 23) and Gunnell *et al.* (2014: 3) refer to fossils from the Anjohibe, Tsimanampetsotsa, and Andrahomana caves on Madagascar.

Conservation status:

Global Justification

This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution. There is no evidence that this species is declining fast enough to place it in a category of higher threat although its roosting colonies should be monitored especially in areas undergoing habitat change (Andriafidison *et al.*, 2008o; IUCN, 2009; Monadjem *et al.*, 2017by).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017by). 2008: LC ver 3.1 (2001) [assessed as *Triaenops furculus*] (Andriafidison *et al.*, 2008o; IUCN, 2009). 1996: VU A2c ver 2.3 (1994) (Baillie and Groombridge, 1996).

Regional

None known.

Major threats:

There may be possible threats from disturbance at the cave sites. This species is tolerant to some degree of forest degradation, but appears to require forested areas to survive (Goodman *et al.*, 2005a) and may therefore be one of the few Malagasy bat species really susceptible to deforestation and forest fragmentation (Andriafidison *et al.*, 2008o; IUCN, 2009; Monadjem *et al.*, 2017by).

Conservation actions:

Andriafidison *et al.* (2008o) [in IUCN (2009)] and Monadjem *et al.* (2017by) report that this species is present in Parc National du Tsingy de Bemaraha, Parc National de Namoroka, Parc National Kirindy-Mite and Parc National Tsimanampetsotsa (Goodman *et al.*, 2005a). Roosting colonies need to be the focus of further conservation and research.

General distribution:

Paratriaenops furcula is found on Madagascar where it is restricted to lowland (an elevation span of 30 m to 200 m above sea level) areas in the west and south-west (Goodman *et al.*, 2005a; Ranivo and Goodman, 2006: 963). It is also found on Cosmoledo and Aldabra Atolls in the outer Seychelles (von Brandis, 2004: 135; Hutson, 2004a).

Native: Madagascar (Goodman *et al.*, 2005a; Ranivo and Goodman, 2006: 963); Seychelles (Hutson, 2004a).

Biogeography:

See Russell *et al.* (2007).

Detailed morphology:

Baculum

The penis bone is elongated with a slightly pointed tip and triangular basal lobe; length: 1.66 ± 0.154 (1.48 - 1.93) mm, width: 0.37 ± 0.105 (0.22 - 0.53) mm.

SEXUAL DIMORPHISM:
Goodman *et al.* (2022: 1902) mentioned that males are smaller than females.

ECHOLOCATION:
Kofoky *et al.* (2009: 380) reported the calls from 18 individuals, the pulses were of longer duration than *Triaenops menamena* and consisted of a narrowband CF component that *T. menamena*, began and ended with short FM sweeps with a high duty cycle (52.5%) and with up to two harmonics, with the second harmonic containing the most energy at about 103.4 kHz. The frequency of maximum amplitude (FMA) was reported as 100.2 ± 0.2 kHz (n = 18) by Bambini *et al.* (2011: 84).

Ramasindrazana *et al.* (2013: 434) mention for 6 ♂♂ specimens the following values: Resting frequency: 113.1 ± 1.80 (110.6 - 115.1) kHz, F_{max}: 114.8 ± 1.90 (111.9 - 116.8) kHz, F_{min}: 110.5 ± 2.16 (106.8 - 113.0) kHz, duration: 12.4 ± 2.71 (8.9 - 16.9) ms, interpulse interval: 23.4 ± 8.50 (14.4 - 36.9) ms, and for 10 ♀♀: Resting frequency: 98.2 ± 1.41 (96.8 - 101.2) kHz, F_{max}: 99.5 ± 1.21 (98.1 -102.3) kHz, F_{min}: 95.7 ± 2.20 (91.4 - 99.4) kHz, duration: 16.0 ± 4.55 (8.1 - 22.5) ms, interpulse interval: 37.7 ± 18.00 (13.9 - 68.5) ms.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003) and Russell *et al.* (2007).

HABITAT:
Hutson (2004a: 129) reports, that on Madagascar, this bat is essentially a cave inhabitant (often sea caves), but on Aldabra (Seychelles) - where there are no true caves - it might inhabit some vertical solution holes, which are at most about 5m deep, and other small hollows which might provide a limited cave-like environment.

Goodman *et al.* (2022: 1902) [referring to Manjaoazy, 2018] mention a home range of 47.9 ha (24.5 - 107.9 ha).

HABITS:
These bats can enter torpor bouts of up to seven days (Garbutt, 2022: 85; referring to Reher *et al.*, 2018).

ROOST:
Recorded in a variety of roosts including caves, shallow sea caves, rock overhangs, under bridges, and large road drainage pipes (Goodman and Ranivo, 2008). The colonies can count to up to 10,000 individuals (Garbutt, 2022: 85).

DIET:
On Madagascar, Rakotoarivelo *et al.* (2007) found that *Paratriaenops furcula* mainly consumed Lepidoptera. This was confirmed by Bambini *et al.* (2011: 81), who also indicated that Coleoptera were also part of the diet. These two order also made up the major volume percentage of preys found in feacal pellets collected by Ramasindrazana *et al.* (2012: 120-121) in the Tsimanampetsotsa NP: Lepidoptera (65.7 ± 4.8), Coleoptera (27.6 ± 4.6), Psocoptera (1.9 ± 0.5), Diptera (1.9 ± 0.7), Hymenoptera (1.5 ± 0.7), Homoptera/Hemiptera (1.0 ± 0.7), and Neuroptera (0.4 ± 0.3). The percentages of Lepidoptera and Coleoptera were about equal during the dry season (46.0 ± 8.5 versus 47.7 ± 8.3) but differed considerably during the wet season (74.7 ± 3.9 versus 18.3 ± 3.4).

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of one individual in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

POPULATION:
Structure and Density
There are few data available on *Paratriaenops furcula*, but it appears to be a relatively rare member of the chiropteran assemblage in western Madagascar as determined by mist netting and acoustic sampling (Kofoky *et al.*, 2007; Rakotoarivelo and Randrianandrianina, 2007). However, it can occur in large colonies and a roost of over 10,000 individuals was reported from the Sept Lacs in southern Madagascar (Olsson *et al.*, 2006). There is no information on population size of *P. furcula* from Aldabra, but it appears to be rather rare with only a few specimen records (Hutson, 2004a).

Trend
2016: Unknown (Monadjem *et al.*, 2017by).
2008: Unknown (Andriafidison *et al.*, 2008o; IUCN, 2009).

PARASITES:
Lagadec *et al.* (2012: 1696) and Gomard *et al.* (2016: 5) report the presence of *Leptospira* sp bacteria in this species.

Perkins and Schaer (2016: Suppl.) report the presence of an unidentified haemosporidan. Ramasindrazana *et al.* (2018: Suppl.) identified the haemosporidian *Polychromophilus melanipherus* Dionisi, 1899 from this bat species (see also Bajić *et al.*, 2023: Suppl.; Ceballos-

Pérez *et al.*, 2024: 3). Rasoanoro *et al.* (2021: 2) indicate that this bat species is rarely infected by this haemosporidian.

Ramasindrazana *et al.* (2016: 7) report one male specimen (out of five examined) to be infected by an unnamed filarial Nematode.

VIRUSES:
Astroviridae
Lebarbenchon *et al.* (2017: Suppl.) found 11 out of 31 examined bats to test positive for Astroviridae.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 1 individuals from the Madagascar using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

Mélade *et al.* (2016b: 4) tested 14 Madagascan specimens, of which one was positive for paramyxoviruses.

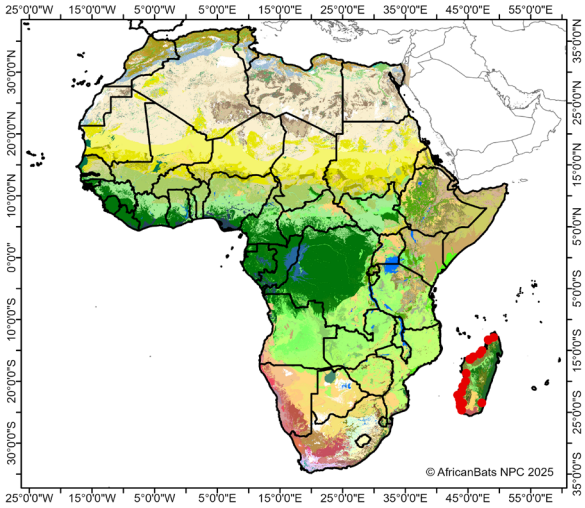

Figure 131. Distribution of *Paratriaenops furcula*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Paratriaenops pauliani (Goodman and Ranivo, 2008)

1941. *[Triaenops] furinea* Tate, Am. Mus. Novit., 1140: 3. Type locality: Seychelles: Aldabra. - Comments: Goodman and Ranivo (2008: 685) mention that Tate (1941: 3) used the name "*Triaenops furinea* Trouessart" for the species on Aldabra. To their knowledge Trouessart never named the form occurring on Aldabra; the use of "*furinea*" is presumably a misreading of the name furcula and is considered a *nomen nudum* (Hayman and Hill, 1971: 30; Hill, 1982b).

*2008. *Triaenops pauliani* Goodman and Ranivo, Zoosystema, 30 (3): 681, 685, figs 2, 3. Type locality: Seychelles: Aldabra Atoll: Picard Island [c 09 24 S 46 12 E]. Holotype: NHMUK 1913.2.18.1: ad ♂, skull and alcoholic. Collected by: J.C.F. Fryer. Based on the itinerary of the Percy Sladen Trust Expedition to the Seychelles, Fryer was in the western Seychelles (Astove, Cosmoledo, Assumption, and Aldabra) from 13 September1908 to 24 January 1909 (Gardiner *et al.*,1910), see Goodman and Ranivo (2008). Paratype: CUMZ E5609.A: ad ♀. Collected by: J.C.F. Fryer. Picard Island, between 13 September 1908 and 24 January 1909. Paratype: CUMZ E5609.B: ad ♂. Collected by: J.C.F. Fryer. Picard Island, between 13 September 1908 and 24 January 1909. Paratype: FMNH 185795: sad ♂, skull and alcoholic. Collected by: Uzice Samedi; collection date: 09 April 2004. Picard Island, Aldabra Station [09 24 04.4 S 46 12 21.4 E, 5 m]. Paratype: NHMUK 1913.2.18.2: ad ♀, skull and alcoholic. Collected by: J.C.F. Fryer. Paratype: NHMUK 1978.185: ad ♀, alcoholic (skull not removed). Collected by: J.J. Whitelaw; collection date: 04 May 1977. Picard Island, Aldabra Station [09 24 04.4 S 46 12 21.4 E, 5 m]. - Etymology: The name *pauliani* is a patronym after the late Prof. Renaud Paulian, who conducted extensive research in the western Indian Ocean islands and was responsible for a major synthesis of the bio-geography of Madagascar and neighbouring islands (Paulian 1961, see Goodman and Ranivo (2008: 685).

2009. *Paratriaenops pauliani:* Benda and Vallo, Folia Zool., 58: 33. (Name Combination, Current Combination).

TAXONOMY:
Benda and Vallo (2009) placed it into the genus *Paratriaenops*.

COMMON NAMES:
Czech: cíponos aldabránský. English: **Paulian's Trident Bat**. French: Triaenops de Paulian. German: Aldabra- Dreizahnblattnase.

CONSERVATION STATUS:
Global Justification
This species is known from two different islands in the extreme western Seychelles, which include the Aldabra and Cosmoledo Atolls. These two atolls are separate by over 100 km of seas and the occurrence of this species on the latter atoll has been questioned (Goodman and Ranivo, 2008). As nothing is known about this species' ecology and most records (observations and specimens) are of animals in human structures on Aldabra Atoll, further field data is needed to properly assess this taxon (Goodman, 2017b).

Assessment History
Global
2016: DD ver. 3.1 (2001) (Goodman, 2017b).

Regional
None known.

MAJOR THREATS:
The main threats to this species are not known (Goodman, 2017b).

CONSERVATION ACTIONS:
Goodman (2017b) report that the Aldabra Atoll has the status of a UNESCO World Heritage site since late 1982 and as such, its terrestrial habitats are well protected.

GENERAL DISTRIBUTION:
Is endemic to the Aldabra Atoll, specifically Picard Island (Goodman and Ranivo, 2008).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
The noseleafs of *P. pauliani* are shorter than those in individuals of *P. auritus* or *P. furculus*, and the external lancets are shorter than the internal lancet, and outer margins of the external lancets are distinctly arc-shaped, while in members of the *P. auritus*/*furculus* group the external lancets are distinctly spear-shaped and the difference in length of the external and internal lancets is less marked (Goodman and Ranivo, 2008).

In overall external measurements, *P. pauliani* is smaller than *P. auritus*/*furculus* group.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
The cranial measurements are similar to those of *P. auritus* and *P. furculus* and fall within the range of size variation of these latter two taxa. There is an elongation of the anterior portion of the upper toothrow, with the I^1-M^3 measurements falling outside the range for *P. furculus* and *P. auritus* (see Goodman and Ranivo, 2008).

POPULATION:
Structure and Density
Population size and trends are not known, but based on very irregular records on Aldabra Atoll (von Brandis, 2004; Hutson, 2004a), presumably it is not very common (Goodman, 2017b).

Trend
2016: Unknown (Goodman, 2017b).

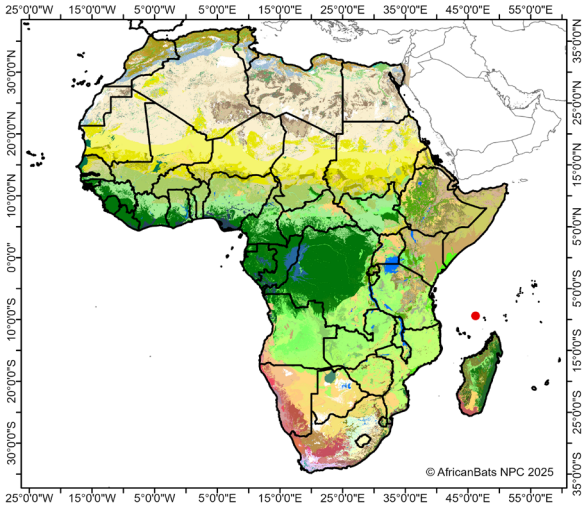

Figure 132. Distribution of *Paratriaenops pauliani*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Seychelles.

Genus ***Triaenops*** Dobson, 1871

*1871. *Triaenops* Dobson, J. Asiatic Soc. Bengal, 40 (2): 455, pl 28. Publication date: 28 December 1871. - Comments: Type species: *Triænops persicus* Dobson, 1871. - Etymology: From the Greek "*τρίαινα*" (trìaina), meaning trident and "*ώφ*", meaning face (or "*ὄφις*" (ópsis), meaning "aspect, appearance"), referring to the posterior part of the nose-leaf, which terminates in three pointed projections (see Palmer, 1904: 687); Lanza *et al.*, 2015: 155). (Current Combination).
1995. *Triaenopus:* Yoshiyuki, Bull. Nat. Sci. Mus., Tokyo, Ser A (Zool), 21 (2): 119. Publication date: 22 June 1995. (Lapsus).
2002. *Trienops:* Paniutina, Plecotus et al., pars spec: 36. (Lapsus).
? *Triaenops sp.:*

TAXONOMY:
Hill (1982b) and Garbutt (1999) suggested that *T. rufus* and *T. persicus* be synonymized. This is not supported by Russell *et al.* (2007). The Madagascan species are reviewed by Ranivo and Goodman (2006).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Triaenops*: ***afer*** Peters, 1877; ***menamena*** Goodman and Ranivo, 2009, *parvus* Benda and Vallo, 2009 - Yemen, *persicus* Dobson, 1871 - Yemen, Oman, United Arab Emirates, Iran, Pakistan.

Additionally, there is the extinct †***goodmani*** Samonds, 2007.

COMMON NAMES:
Czech: velcí cíponosi. English: Greater Trident Bats, Trident Bats, Trident Leaf-nosed Bats, Triple nose-leaf bats. French: Triaenops. German: Dreizahn-Blattnasen. Italian: Triènopi.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 55 - 57) found *Triaenops* sp. Within the deposits (NCC-1 locality) dating estimated as 69,600 to 86,800 years old within the Anjohibe cave, Madagascar.

GENERAL DISTRIBUTION:
Is broadly distributed in Africa, portions of the Middle East, and islands in the western Indian Ocean.

BIOGEOGRAPHY:
Russell *et al.* (2007)'s data reject a single-dispersal hypothesis (single origin hypothesis), which predicts that linages endemic to Madagascar form an exclusive clade. Russell *et al.* (2007) found that Malagasy *Triaenops* are paraphyletic with respect to the mainland African species *T. persicus*, indicating that the distribution of Malagasy and African *Triaenops* involved at least two independent dispersal events.
Russell *et al.* (2008a) estimate that at 2.25 Mya *Triaenops* still formed a single ancestral population between *T. rufus*/*P. auritus*, while the timing of the later *T. rufus* dispersal to Madagascar is less clear (about 148 kya and 660 kya).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Kenya, Madagascar, Somalia, Tanzania.

Triaenops afer Peters, 1877

*1877. *Triaenops afer* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 913 (for 1876). Publication date: 1877. Type locality: Kenya: Mombassa [04 03 S 39 40 E]. [Goto Description]. (Current Combination).
1878. *Triænops afer:* Dobson, Catalog of the Chiroptera of the collection of the British Museum, 125. Publication date: 15 June 1878. Holotype: ZMB 5074: ♂, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt. See Turni and Kock (2008: 40). (Alternate Spelling).
1968. *Triaenops persicus majusculus* Aellen and Brosset, Rev. suisse Zool., 75 (14): 450. Type locality: Congo: Loudima: Grotte de Doumboula [04 15 S 13 00 E]. [Goto Description]. Holotype: MNHN ZM-MO-1968-412: ad ♂, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 19 June 1964. 18 paratypes. Paratype: MHNG 1074.041: ♂. Paratype: MHNG 1074.042: ♂, alcoholic (skull not removed). Paratype: MHNG 1074.043: ♂. Paratype: MHNG 1074.044: ♂. Paratype: MHNG 1074.045: ♀. Paratype: MHNG 1074.046: ♀, alcoholic (skull not removed). Paratype: MNHN ZM-MO-1985-1349: ♀, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 19 June 1964. Paratype: MNHN ZM-MO-1985-1350: ♀, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 29 November 1966. Paratype: MNHN ZM-MO-1985-1351: ♀, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 29 November 1966. Paratype: MNHN ZM-MO-1985-1497: ♂, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: 19 June 1964.
2017. *Tr[iaenops] affer:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 4. Publication date: 6 April 2017. (Lapsus).
2017. *Triaenops affer:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 5. Publication date: 6 April 2017. (Lapsus).
2020. *Triaenops afer majusculus:* Rossoni, Demos, Goodman, Yego, Mohlman, Webala and Patterson, Zool. J. Linn. Soc., 192 (1): 12 (for 2021). Publication date: 17 September 2020. (Name Combination).
2021. *Triaenops caffer:* Smith, DeLeon, Eiting, Corbin,Bhatnagar and Santana, Anat. Rec., xxx: 16. Publication date: 21 September 2021. (Lapsus).
? *Triaenops persicus afer:* (Name Combination).
? *Triaenops persicus:*

TAXONOMY:
Benda and Vallo (2009: 26) found differences in the structure of the skull, baculum and Cyt. *b* of *Triaenops persicus* occurring in the Middle East and those in East Africa.

Benda and Vallo (2009: 118) considered *afer* to be a valid species, representing the genus on the African continent.

However, mitochondrial analyses by Rossoni *et al.* (2020: 236) suggest that some specimens from Kenya might actually represent *T. persicus*, which is confirmed by morphometric analyses of the skull, external morphology and echolocation calls. These indicate that animals from Nakuru, Baringo and Pokot counties (the Kenyan Rift Valley) are distinct from typical *T. afer* occurring in the coastal counties or in interior counties such as Laikipia and Makueni. See also Benda *et al.* (2025: 55 - 56).

COMMON NAMES:
Chinese: 非洲三叉蝠. Czech: cíponos africký, vrápenec cíponosý. English: **African Trident Bat**, Peter's Trident Bat. German: Afrikanische Dreizahn-Blattnase. Italian: Triènope àfro. Malawian: Liputiputi, Ndemiya, Namzeze. Ukrainian: Трилистоніс африканський [= Trylystonis afrykans'kyy]

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Monadjem and Shapiro, 2017a).

Assessment History
Global
2016: LC ver. 3.1 (2001) (Monadjem and Shapiro, 2017a).

Regional
None known.

MAJOR THREATS:
Monadjem and Shapiro (2017a) reports that there appear to be no major threats to this widespread species as a whole. The species is locally threatened in parts of its range by disturbance of roost sites and mining activities. Populations have been recorded roosting in caves and mines (Taylor, 2005).

CONSERVATION ACTIONS:
Monadjem and Shapiro (2017a) reports that there appear to be no direct conservation measures in place. It occurs in several protected areas in Mozambique (Monadjem *et al.*, 2010c) and Tanzania. Monadjem and Shapiro (2017a recommends further taxonomic studies are needed for specimens of *Triaenops* from the Albertine Rift.

GENERAL DISTRIBUTION:
Benda *et al.* (2025: 55) indicate that this species occurs in two disjunct areas in sub-Saharan Africa.there is a large area covering the savanna belt of eastern Africa from Djibouti, northern Ethiopia, and the western Central African Republic in the north, extending southwards to eastern Zimbabwe and central Mozambique; and a smaller area includint a few localities in the south-western Congo (B.) and north-western Angola.

Native: Angola, Djibouti, Central African Republic, Ethiopia (Kruskop *et al.*, 2016: 58); Kenya, Mozambique (Monadjem *et al.*, 2010c: 381), Tanzania, Uganda, Zimbabwe.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Lucati and López-Baucells (2016: Suppl.) refers to Howell (1980a), who mentioned two piebald (all-white fur/skin patches, eyes always normally coloured) "*T. persicus*" specimens from a mine in Tanzania.

DETAILED MORPHOLOGY:
Brain
Adult hippocampal neurogenesis was studied by Chawana R. *et al.* (2016: 1551) [as *Triaenops persicus*].

Vomeronasal complex
This complex articulates in an indentation on the superior surface of the premaxilla (Smith *et al.*, 2024: 8).

FUNCTIONAL MORPHOLOGY:
Using diceCT, Smith *et al.* (2021) studied the structure of the nasal and nasopharyngeal passageways. In this species, the nasopharyngeal airway occupies the greatest proportion of total airway length (40 % versus 16 to 24 % in other species they examined).

ECHOLOCATION:
From Mozambique, Monadjem *et al.* (2010c: 381) reported that the echolocation calls are sexually dimorphic, peak frequencies of males ranged between 71 - 75 kHz (ANABAT) and those of females, between 82 - 85 kHz (ANABAT).

The calls of nine Kenyan bats were reported by Webala *et al.* (2019b: 15) with F_{max}: 88.2 - 91.2 kHz (5 ??), 82.5 - 83.9 kHz (2 FF) and 75.2 - 75.7 kHz (2 MM). Three calls of a third male had a F_{max} of 30.1 kHz and a duration of 8.4 - 12.2 ms.

For the Boundou cave in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data: 9 FF: F_{pmin}: 79.12 ± 1.9 kHz, F_{pmax}: 87.7 ± 5.3 kHz, F_{pmean}: 80.4 ± 3.2 kHz, F_{ppeak}: 82.2 ± 1.6 kHz, F_{flat}: 81.7 ± 1.4 kHz, F_{knee}: 82.1 ± 1.9 kHz, F_{mean}: 81.1 ± 1.5 kHz, Duration: 6.2 ± 2 ms; 10 MM: F_{pmin}: 69.3 ± 7.1 kHz, F_{pmax}: 82 ± 2.9 kHz, F_{pmean}: 75.1 ± 2.9 kHz, F_{ppeak}: 75.7 ± 2.6 kHz, F_{flat}: 75.6 ± 2.5 kHz, F_{knee}: 75.5 ± 2.9 kHz, F_{mean}: 75.2 ± 2.5 kHz, Duration: 7.5 ± 1.7 ms.

MOLECULAR BIOLOGY:
Karyotype
For some Ethiopian "*Triaenops persicus*", Tolera *et al.* (2021: 125) report 2n = 36 and FN = 60/62. They were unable to determine the exact fundamental number as no male specimens were karyotyped. The autosomal chromosomes included 14 pairs of meta-submetacentrics and four pairs of acrocentrics.

HABITS:
Although Rainho *et al.* (2023: 7) mentioned that *Triaenops* was a low-flying bat (flying at < 3.5 m), they (p. 8) recorded echolocation calls of this species, with a microphone installed at an altitude of 35 m.

ROOST:
In East Africa, *T. afer* roosts in large colonies containing hundreds to thousands of individuals (Happold and Happold, 2023: 100). Howell (1980b: 27) reported a minimum of 172 000 bats

in an abandoned kaolin mine in the Pugu Forest (Tanzania).

POPULATION:
Structure and Density
Monadjem and Shapiro (2017a) report that some colonies of this bat can be quite large, with up to half a million animals recorded in the Koalin Mines of Tanzania. In peripheral parts of the range, such as Zimbabwe, colonies are often much smaller.

Trend
2016: Unknown (Monadjem and Shapiro, 2017a).

REPRODUCTION AND ONTOGENY:
Martin and Bernard (2000: 32) indicate that the corpus luteum is only present for the first part of the pregnancy after which complete regression occurs.

PARASITES:
BACTERIA
Bartonellae
Bartonella - Kosoy *et al.* (2010: 1877) and Bai and Kosoy (2012: 58) reported a prevalence of *Bartonella* spp. cultured from blood samples of 7/8 (87.5 %) *T. persicus* specimens from Kenya. Seven *Bartonella* spp. *gltA* sequences were identified, and formed a monophyletic geogroup (Kosoy *et al.*, 2010: 1878). See also Kosoy (2010: 719) for further information.

HAEMOSPORIDA
Garnham (1973: 237) refers to Adam and Landau for a record of *Polychromophilus ? murinus* in a "*Triaenops persicus*" from Africa.

SIPHONAPTERA
Ischnopsyllidae: *Araeopsylla scitula* Rothschild, 1909 was reported by Beaucournu and Kock (1996) from "*Triaenops persicus*" bat from Kenya.

DIPTERA
Streblidae
Raymondia aspera Maa, 1968 from Mozambique (Shapiro *et al.*, 2016: 254). *Raymondia huberi huberi* Frauenfeld, 1855 (Shapiro *et al.*, 2016: 254). *Raymondia seminuda* Jobling, 1954 (Shapiro *et al.*, 2016: 255). *Raymondia waterstoni* Jobling, 1931 (Shapiro *et al.*, 2016: 256).

Nycteribiidae
Penicillidia fulvida (Bigot, 1885) was reported by Verrett *et al.* (2022: 8) from Kenya.

ACARI
Trombiculidae
Stekolnikov (2018a: 50, 173) found *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957 and *Microtrombicula tanzaniae* Goff, 1982 on "*Triaenops persicus afer*".

CESTODA
Hymenolepididae
Jenzen and Howell (1983: 135) described *Vampirolepis schmidti* from Tanzanian "*Triaenops persicus*".

VIRUSES:
Astroviridae
These viruses were found by Waruhiu *et al.* (2017) in their country-wide survey of Kenyan bats. Hoarau *et al.* (2018: 2) found them in 35 of the 51 Mozambican bats they tested. Joffrin *et al.* (2021: 1) estimate the percentage of these bats shedding astroviruses in Mozambique to be between 20 and 81, depending on the season (see also Hoarau *et al.*, 2021: Suppl.)..

Coronaviridae
Alphacoronavirus
Of the 30 *T. afer* specimens Tao *et al.* (2017: 3) tested in Kenya, eight (26.7 %) were positive for CoV (subgenus *Setracovirus*; see Markotter *et al.*, 2020: 6). This is probably the NL63-related bat coronavirus BtKYNL63-9b virus mentioned by Shchelkanov *et al.* (2020b: 225) and Shchelkanov *et al.* (2020a: 16).
Joffrin *et al.* (2020: 5) reported Alphacoronaviruses from bats from Mozambique and Kenya.

Of the 29 "*Triaenops persicus*" specimens collected during the dry season in the two Congos, Kumakamba *et al.* (2021: 7) found four to be positive for coronaviruses.

Herpesviridae
Borloti *et al.* (2020: 1) reported a new virus belonging to the Gammaherpesvirinae from a "*Triaenops persicus*" captured in the Republid of Congo. Given this location, it most probably doesn't belong to that species, but rather to *T. afer*.

Gonzalez and Banerjee (2022: 24) reported the virus species as Dzifa herpesvirus.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that 12 out of 16 examined *T. afer* specimens from Kenya tested positive for *Paramyxovirus* sequences.
Positive bats were also reported from Mozambique by Hoarau *et al.* (2021: Suppl.).

Gonzalez and Banerjee (2022: 16) reported Morbillivirus-related virus.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 12 Kenyan "*T. persicus*" specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Cameron *et al.* (2021: 2) reported an unknown rhabdovirus from a *T. afer* bat collected in the Republic of Congo.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Central African Republic, Congo, Ethiopia, Kenya, Malawi, Mozambique, Somalia, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

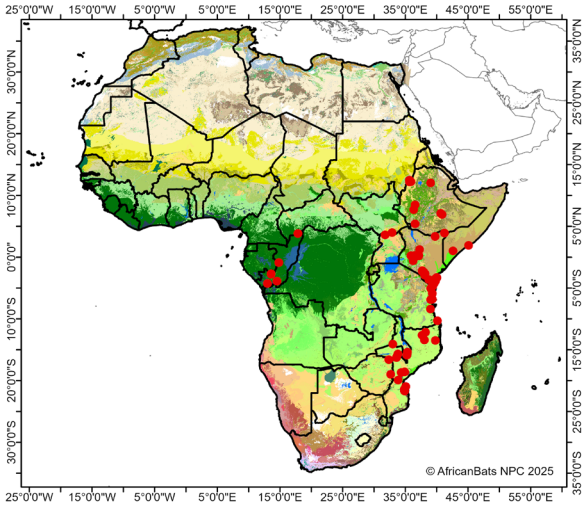

Figure 133. Distribution of *Triaenops afer*.

†*Triaenops goodmani* Samonds, 2007

*2007. *Triaenops goodmani* Samonds, Acta Chiropt., 9 (1): 46, fig 3 A-B. Type locality: Madagascar: Anjohibe cave. Holotype: UADBA 9010. Partial left dentary: see Samonds (2007: 46). - Etymology: Specific name for Dr. Steven M. Goodman, in recognition of his significant contributions to the field of modern Malagasy bat research (see Samonds, 2007). (Current Combination).

COMMON NAMES:
English: **Goodman's Trident Bat** (Armstrong *et al.*, 2016: 116).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 46 - 49) found samples in deposits (OLD SE) dated at 10,000 yrs old or younger within the Anjohibe cave, Madagascar. Michielsen *et al.* (2023: 2) mention that the fossil record is insufficient to determine whether this species' extinction occurred prior or after human arrival.

Time frame:
Pleistocene (Brown *et al.*, 2019: Suppl.).

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Triaenops menamena Goodman and Ranivo, 2009

1881. *Triænops Humbloti* A. Milne-Edwards. Type locality: : "Africa": Aden (Yemen) or Somalia. Holotype: MNHN ZM-MO-1985-836: ♂, alcoholic (skull missing). Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). The type series (184 and 184A) contains 3 MM + 3 FF) (Peterson *et al.*, 1995). Rode (1941: 239) refers to the holotype (184) and six paratypes (184a). Paratype: MNHN ZM-MO-1985-838: ♂. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-839: ♂. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-840: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-841: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-842: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). - Comments: See Goodman and Ranivo (2009) for futher discussion on the type locality. According to Ranivo and Goodman (2006: 974) the skull of the holotype has been mixed up with the skulls of the paratypes (MNHN 1985-838 and 1985-839). *T. humbloti* is retained as a synonym for both *T. persicus* and *T. menamena* due to the fact that purely taxonomically it is a synonym of *T. persicus*, but most of the specimens from Madagascar were erroneously assigned this name. In general, the authorship for the Madagascan use would be assigned to a subsequent author or to the same author in a later publication, but in this case, the author already made the error in the original publication.

1881. *Triænops rufus* A. Milne-Edwards, C. R. séances Acad. Sci., Paris, 91: 1035. Publication date: 1881. Type locality: "Africa": Aden (Yemen) or Somalia. [Goto Description]. Holotype: MNHN ZM-MO-1997-1854: ♀, skull and alcoholic. Collected by: Léon Humblot; collection date: 1880. See Peterson *et al.* (1995: 82). Ranivo and Goodman (2006: 974) indicate that the skull is still present, but in very bad shape. Specimen labled "Holotype no. 185" (see Goodman and Ranivo, 2009). Rode (1941: 239) mentions number "185". Paratype: MNHN ZM-MO-1997-1855: ♀, alcoholic (skull not removed). Collected by: Léon Humblot; collection date: 1880. See Peterson *et al.* (1995). Rode (1941: 239) mentions three specimens with number "185a". Paratype: MNHN ZM-MO-1997-1856: ♀, alcoholic (skull missing). Collected by: Léon Humblot; collection date: 1880. See Peterson *et al.* (1995). Rode (1941: 239) mentions three specimens with number "185a". Paratype: MNHN ZM-MO-1997-1857: ♀, alcoholic (skull missing). Collected by: Léon Humblot; collection date: 1880. See Peterson *et al.* (1995). Rode (1941: 239) mentions three specimens with number "185a". - Comments: (see Goodman and Ranivo, 2009).

*2009. *Triaenops menamena* Goodman and Ranivo, Mammalia, 73 (1): 48, 54, fig 1. Publication date: 31 March 2009. Type locality: Madagascar: Mahajanga province: Réserve Naturelle Intégrale de Namoroka, 4 km SSW Namoroka village: Grotte d'Ampidiranamhaja [16 25.957 S 45 17.180 E, 120 m]. Holotype: FMNH 178563: ♂, skull and alcoholic. Collected by: Julie Ranivo and Fania H. Ratrimomanarivo; collection date: 25 September 2003; original number: S.M. Goodman 13825. - Etymology: From the Malagasy word "mena" meaning "red", which, in common usage, when repeated twice, means "reddish" (see Goodman and Ranivo, 2009: 54). (Current Combination).

? *Triaenops humbloti:*

? *Triaenops rufus:*

Taxonomy:

These Madagascan specimens were previously included in *persicus* by Hayman and Hill (1971: 30), Hill (1982b), Koopman (1993a: 175), probably based on the type specimens, which are now believed to be collected either in Yemen or Somalia (see Goodman and Ranivo, 2009: 52). Based on actual Madagascan material, Peterson *et al.* (1995: 82), Russ *et al.* (2001), Hutson *et al.* (2001: 18), Goodman *et al.* (2005a: 158), and Simmons (2005: 379) recognized the specimens as representing a separate species.

See also the phylogenetic analysis by Russell *et al.* (2007: 847).

Goodman and Ranivo (2009) extensively discuss the origin of the type specimens of *Triænops Humbloti* Milne-Edwards, 1881 and *Triænops rufus* Milne-Edwards, 1881. Their conclusion is that both forms were not from Madagascar but from Yemen or Somalia. Therefore, from a strict taxonomical view, these two names are synonyms of *Triaenops persicus* Dobson, 1871. However, we are also retaining these names in the synonymy of *Triaenops menamena* Goodman and Ranivo, 2009 since these names were always used to identify Madagascan forms, which are currently assigned to *T. menamena*.

Common Names:

Czech: cíponos madagaskarský. English: **Rufous Trident Bat**, Red Madagascan Trident Bat, Red Trident Bat. French: Triaenops roux, Triénope roussâtre. German: Rötliche Dreizahn-Blattnase.

Conservation status:

Global Justification

This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution across Madagascar. It can tolerate some degree of habitat transformation, is relatively common, and is not thought to be declining fast enough to place it in a category of higher threat (Andriafidison *et al.*, 2008p; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) [assessed as *Triaenops rufus*] (Andriafidison *et al.*, 2008p; IUCN, 2009).
2000: DD ver 2.3 (1994) [assessed as *Triaenops rufus*] (IUCN, 2000).

Regional

None known.

Major threats:

There are no significant threats to this species even though it is occasionally hunted for food (Goodman, 2006) and is often associated with forests that are subject to ongoing degradation (Russell *et al.*, 2007).

Conservation actions:

Andriafidison *et al.* (2008p) [in IUCN (2009)] report that this species is known to occur in many protected areas: Réserve Spéciale d'Ankarana, Réserve Spéciale d'Analamerana, Parc National du Tsingy de Bemaraha, Parc National de Namoroka, Parc National de Tsimanampetsotsa, Parc National d'Ankarafantsika, Parc National d'Isalo, Réserve Spéciale d'Ambohitantely, Parc National de Masoala and Réserve Naturelle Intégrale de Tsaratanana (Ranivo and Goodman, 2006; Russ *et al.*, 2003; Russell *et al.*, 2007).

General distribution:

Triaenops menamena is endemic to the island of Madagascar. It is restricted to the western dry habitats and extreme northeastern and southeastern Madagascar in humid habitats (Goodman and Ranivo, 2009).

Papers prior to 2009 refer to *T. rufus*; see taxonomy section above for more details.

Native: Madagascar (Peterson *et al.*, 1995; Russ *et al.*, 2003; Goodman *et al.*, 2005a; Simmons, 2005; Ranivo and Goodman, 2006; Russell *et al.*, 2007; Rakotoarivelo *et al.*, 2007; Goodman and Ranivo, 2009).

BIOGEOGRAPHY:
See Russell *et al.* (2007).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 57) indicate that the baculum is 'stick-like' with a bifid distal tip and straight mid-shaft. Its basal part is triangular with two distinct lateral projections; length: 1.67 ± 0.12 (1.50 - 1.80) mm, width: 0.71 ± 0.07 (0.61 - 0.79) mm.

SEXUAL DIMORPHISM:
Goodman *et al.* (2022: 1902) mentioned that females are smaller than males.

ECHOLOCATION:
Kofoky *et al.* (2009: 379) reported the calls from 15 individuals, which produced relatively short CF component followed by brief FM components, the duty cycle was high (25.5 %), with the second harmonic generally contained most energy at about 93.2 kHz, a maximum of three harmonics were also observed. Bambini *et al.* (2011: 84) reported the frequency of maximum amplitude (FMA) to be 95.8 ± 0.1 kHz (n = 21).

Ramasindrazana *et al.* (2013: 434) reported the following data for 11 ♂♂: Resting frequency: 82.3 ± 1.43 (79.6 - 84.0) kHz, F_{max}: 83.6 ± 1.26 (81.4 - 85.2) kHz, F_{min}: 79.5 ± 3.21 (72.2 - 82.3) kHz, duration: 7.5 ± 0.97 (5.5 - 9.4) ms, interpulse interval: 38.3 ± 30.15 (9.8 - 107.4) ms, and for 20 ♀♀: Resting frequency: 93.5 ± 1.47 (90.0 - 96.8) kHz, F_{max}: 94.7 ± 1.49 (91.8 - 98.3) kHz, F_{min}: 91.3 ± 2.00 (87.6 - 95.4) kHz; duration: 7.8 ± 1.54 (5.1 - 10.6) ms, interpulse interval: 35.6 ± 24.75 (14.9 - 127.4) ms.

For 91 calls from the Sahamalaza-Iles Radama National Park, Hending *et al.* (2021a: 158) reported: F_{peak}: 89.0 ± 0.95 (97.0 - 91.0) kHz, F_{min}: 83.6 ± 1.08 (80.0 - 85.0) kHz, F_{max}: 99.2 ± 1.24 (93.0 - 101.0) kHz, duration: 7.0 ± 1.75 (2.5 - 10.2) ms and interpulse interval: 51.3 ± 32.72 (22.7 - 236.5) ms.

Hending *et al.* (2023: 372) mention a F_{peak}: 89.7 ± 0.9 kHz, duration: 7 ± 2 ms, and interpulse interval: 59 ± 37 ms.

MOLECULAR BIOLOGY:
Genetics
Russell *et al.* (2007).

HABITAT:
There are no significant threats to this species even though it is occasionally hunted for food (Goodman, 2006) and is often associated with forests that are subject to ongoing degradation (Russell *et al.*, 2007).

Dammhahn and Goodman (2013: 108) mention that this species' foraging habitat is the lower portion of forest. Ravelomanantsoa *et al.* (2019: 111) captured this bat near a marshy area near Ambereny.

HABITS:
Remmers *et al.* (2025: 258) found that Triaenops menamena varies its torpor seasonally and that it has the potential to use prolonged torpor when conditions are unfavourable (e.g. low food availability or heavy rain).

ROOST:
Wilkinson *et al.* (2012: 160) indicate that caves are the typical roosts for this species on Madagascar.

DIET:
On Madagascar Rakotoarivelo *et al.* (2007) found *T. menamena* (reported as *T. rufus*) mainly consumed Lepidoptera. Bambini *et al.* (2011: 87) reported that *T. menamena* showed a high preference for Hemiptera, and less for Lepidoptera.

The numbers reported by Ramasindrazana *et al.* (2012: 120-121) from the Tsimanampetsotsa NP confirmed that Lepidoptera formed the major food source of this bat with 67.2 ± 4.5 volume percentage. The Coleoptera formed the second food source with 26.9 ± 4.1. The other insect orders contributed only small amounts: Hymenoptera (3.3 ± 1.0), Psocoptera (0.9 ± 0.2), Neuroptera (0.6 ± 0.2), Diptera (0.4 ± 0.2), Homoptera/Hemiptera (0.4 ± 1.9), Blattaria (0.1 ± 0.0); and Aranea (0.1 ± 0.0). During the dry season, however, Coleoptera contributed the most to the bats diet: 69.0 ± 5.1, whereas Lepidoptera counted for 18.7 ± 4.1 volume percentage. During the wet seaon, the Lepidoptera dominated the diet with 90.5 ± 2.1 volume percent versus 6.7 ± 2.0 for the Coleoptera.

Rakotondramanana *et al.* (2015: 77) present the following volume percentages of prey types from the faeces of 16 bats: Coleoptera: 11.6 ± 19.46; Hymenoptera: 11.7 ± 24.20; Lepidoptera: 64.1 ±

32.64; Trichoptera: 0.6 ± 2.25; Isoptera: 11.5 ± 26.32; Homoptera: 0.5 ± 1.55; Arachnida: 0.06 ± 0.25. In frequency percentages, the values are: Coleoptera: 35.0 ± 43.51; Hymenoptera: 42.5 ± 40.58; Lepidoptera: 88.8 ± 30.96; Trichoptera: 3.8 ± 15.00; Isoptera: 17.5 ± 37.86; Homoptera: 3.75 ± 10.88; Arachnida: 1.2 ± 5.00.

PREDATORS:
Cardiff and Jenkins (2016: 93) mention a personal obsservation by Paul Racey, who observed a boid snake predating on a *Triaenops menamena* bat.

POPULATION:
Structure and Density
The species is thought to be locally common in many parts of western Madagascar. A single roost in deciduous forest near the Onilahy River in southern Madagascar contained over 40,000 individuals (Olsson *et al.*, 2006).

Trend
2008: Unknown (Andriafidison *et al.*, 2008p; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Three females collected at Binara and Anjakeli between 22 November and 6 December were pregnant with embryos between 11 and 23 mm in crown-rump length. All these females also had auxiilary pubic nipples (Goodman *et al.*, 2025: 214).

PARASITES:
BACTERIA
Lagadec *et al.* (2012: 1696) reported that 8 out of 10 bats they examined, tested positive for *Leptospira* sp. bacteria, and Gomard *et al.* (2016: 5) found 27 out of 42 bats (64.3 %) to be positive for this bacterium. Dietrich *et al.* (2018a: 3) identified these further as *L. interrogans, L.* sp. and a third form having sequences closely related to *L. borgpetersenii*.

VIRUSES:
Astroviridae
Eight out of 13 specimens tested by Lebarbenchon *et al.* (2017: Suppl.) were positive for Astroviridae.

Coronaviridae
Hoarau *et al.* (2021: Suppl.) reported two Madagascan bats testing positive for viruses of this family.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 10 individuals from the Madagascar using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 2 positive results for viral nucleic acids. Wilkinson *et al.* (2014) tested 30 individuals from Madagascar with a Respiro-, Morbilli- and Henipavirus specific RT-PCR assay, 19 samples tested positive for paramyxovirus RNA.

In their extensive study, Mélade *et al.* (2016b: 3) found this species to be the most infected by paramyxoviruses of all Madagascan bats (21 out of 42 specimens = 50 %).

Rhabdoviridae
Two out of 11 bats tested by Mélade *et al.* (2016a: 6) showed a seroreaction against *Lagos bat lyssavirus*.

UTILISATION:
Goodman (2006) describes the hunting method used by local inhabitants. See also Jenkins *et al.* (2007b), Goodman *et al.* (2008d) and Jenkins and Racey (2008), who refer to *T. rufus*.

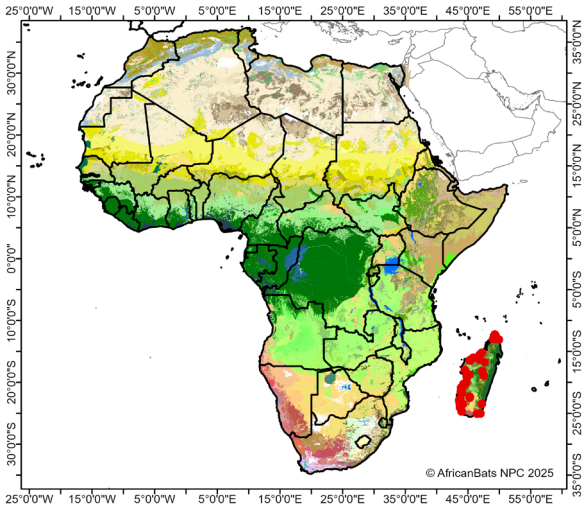

Figure 134. Distribution of *Triaenops menamena*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Triaenops persicus (Dobson, 1871)

*1871. *Triænops persicus* Dobson, J. Asiatic Soc. Bengal, 40 (2): 455, pl 28. Publication date: 28 December 1871. Type locality: Iran: Fars province: Shiraz [29 36 N 52 32 E, 4 750 ft]. Syntype: NHMUK 1876.3.10.3: Collected by: C.S.I. St. John. Formerly in Calcutta Museum; see Turni and Kock (2008). Syntype: ZMB 4370a: ♂, skull and alcoholic. Collected by: C.S.I. St. John. Formerly in Calcutta Museum; see Turni and Kock (2008). Syntype: ZMB 4370b: ♀, skull and alcoholic. Collected by: C.S.I. St. John. Formerly in Calcutta Museum; see

Turni and Kock (2008). - Etymology: Originally the species was described from a specimen from Shiraz, Iran (Persia), but has subsequently been found to occur in Arabia and Africa. (Current Combination).

1881. *Triænops Humbloti* A. Milne-Edwards, C. R. séances Acad. Sci., Paris, 91: 1035. Publication date: 1881. Type locality: "Africa": Aden (Yemen) or Somalia. [Goto Description]. Holotype: MNHN ZM-MO-1962-2659: skull only. Collected by: Léon Humblot. Holotype: MNHN ZM-MO-1985-836: ♂, alcoholic (skull missing). Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). The type series (184 and 184A) contains 3 MM + 3 FF) (Peterson *et al.*, 1995). Rode (1941: 239) refers to the holotype (184) and six paratypes (184a). Paratype: MNHN ZM-MO-1985-838: ♂. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-839: ♂. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-840: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-841: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). Paratype: MNHN ZM-MO-1985-842: ♀. Collected by: Léon Humblot; collection date: 1880; original number: 184 or 184A. See Peterson *et al.* (1995: 82). - Comments: According to Ranivo and Goodman (2006: 974) the skull of the holotype has been mixed up with the skulls of the paratypes (MNHN 1985-838 and 1985-839). See also Goodman and Ranivo (2009), and the notes with *T. menamena*.

1881. *Triænops rufus* A. Milne-Edwards, C. R. séances Acad. Sci., Paris, 91: 1035. Publication date: 1881. Type locality: "Africa": Aden (Yemen) or Somalia. [Goto Description]. - Comments: See also Goodman and Ranivo (2009) and the notes with *T. menamena*).

2020. *Triaenops afer** Rossoni, Demos, Goodman, Yego, Mohlman, Webala and Patterson, Zool. J. Linn. Soc., 192 (1): 238 (for 2021). Publication date: 17 September 2020.

? *Triaenops persicus:*

Taxonomy:

Included *rufus* (Hayman and Hill, 1971: 30; Hill, 1982b; Koopman, 1993a: 175), but recognized as a valid species by Peterson *et al.* (1995) and Simmons (2005: 378 - 379). Meester *et al.* (1986: 44) recognized three subspecies from Africa: *persicus*, *afer* and *majusculus*.

Simmons (2005) lists *T. macdonaldi* Harrison, 1955 as a synonym, with *T. p. afer* Peters, 1876 and *T. p. majusculus* Aellen and Brosset, 1968 as valid subspecies. Benda and Vallo (2009: 118) consider *afer* to be a valid species, representing the genus on the African continent.

Mitochondrial analyses performed by Rossoni *et al.* (2020: 236) suggest that some specimens from Kenya might actually represent *T. persicus*. This is also confirmed by morphometric analyses of the skull, external morphology and echolocation calls. These indicate that animals from Nakuru, Baringo and Pokot counties (the Kenyan Rift Valley) are distinct from typical *T. afer* occurring in the coastal counties or in interior counties such as Laikipia and Makueni. Rossoni *et al.* (2020: 236) also point out that the Kenyan bats are slightly different from Middle Eastern populations in terms of both cranial morphology and vocalizations.

Rossoni *et al.* (2020: 251) also indicate that *Triaenops* specimens from Djibouti have the greatest skull lengths, which fall within the range of Kenyan *T. persicus* but outside the range of *T. afer*, which might suggest that *T. persicus* extends its distribution through the Rift Valley to Djibouti or that they might have crossed the relatively narrow Red Sea separating the Arabian .Peninsula and the Horn of Africa.

Common Names:

Afrikaans: Persiese bladneusvlermuis. Czech: cíponos perský, pavrápenec cíponosý. English: Persian Greater Leaf-nosed Bat, Persian Leaf-nosed Bat, **Persian Trident Bat**, Triple leaf-nosed bat. French: Triaenops de Perse. German: Persische Dreizahn-Blattnase. Portuguese: Morcego Persa de nariz enfolhado.

Etymology of common name:

It is appropriately called the Persian trident bat because, like the short-eared trident bat (*Cloeotis percivali*), it has a three-pronged trident at the top of the nose-leaves (see Taylor, 2005).

Similar Species:

The Kenyan *T. persicus* specimens can be distinguished from the *T. afer* specimens by their size as they are significantly larger in both craniodental and external measurements (Rossoni *et al.*, 2020: 248), e.g., GLS: 19.8 (19.20 - 20.57) mm for male *afer* and 21.58 (20.93 - 22.33) mm for male *persicus*. Also the echolocation frequencies of *persicus* are lower than those found for *afer*..

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ak; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008ak; IUCN, 2009). 2004: LC ver 3.1 (2001)

(Mickleburgh *et al.*, 2004as; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this widespread species as a whole. The species is locally threatened in parts of its range by disturbance of roost sites and mining activities. The threats to this species remain unknown in Pakistan (Molur *et al.*, 2002).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ak) [in IUCN (2009)] report that there appear to be no direct conservation measures in place. In view of the species wide range, it seems likely that it is present in some protected areas. Further taxonomic studies are needed for specimens of *Triaenops* from the Albertine Rift. In South Asia there are no direct conservation measures in place for this species, and the species has not been recorded from any protected areas. Surveys to determine the status of this species are needed (Molur *et al.*, 2002).

GENERAL DISTRIBUTION:
Triaenops persicus is primarily found in the Arabian Peninsula and Iran, and South Asia. In Africa it was considered to be widely distributed through much of East Africa, but most of these records are currently considered to represent *Triaenops afer*. Rossoni *et al.* (2020: 236), however, found that specimens from the Rift Valley in Kenya (Nakuru, Baringo and Pokot counties) differ from those from the coastal area and other inland counties, and do represent *T. persicus*.

Native: Kenya; Oman; Pakistan; United Arab Emirates (Anonymus, 2008: 38); Yemen.

Uncertain: Djibouti (Rossoni *et al.*, 2020: 251).

BIOGEOGRAPHY:
See Russell *et al.* (2007), although the covers the situation prior to the recognition of *Triaenops afer* as a separate species.

DETAILED MORPHOLOGY:
Brain
Kruger *et al.* (2010a) describes based on three brains from Kenya, using immunohistochemical methods, the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems. Kruger *et al.* (2010b) describes based on three brains from Kenya, the distribution of Orexin-A immunoreactive cell bodies and terminal networks. However, as it isn't clear where these bats were exactly collected, this information might pertain to either *T. persicus* or *T. afer*.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 9.2 Pa, aspect ratio 7.4 and tip shape index of 2.06 for a wingspan of 29 cm and a wing area of 116 cm^2 and a body mass of 11 g.

ECHOLOCATION:
See Pye (1972) and Taylor *et al.* (2005).

ROOST:
Davis (2007: 6) indicates that it might roost in large colonies in caves and tunnels in the United Arab Emirates, where it occurs with other species.

REPRODUCTION AND ONTOGENY:
Davis (2007: 6) reports that females are thought to be pregnant in December-January in the United Arab Emirates.

VIRUSES:
Coronaviridae
Montecino-Latorre *et al.* (2022: 5) mention that Eidolon bat coronavirus/Kenya/KY24/2006 has been reported from this species.

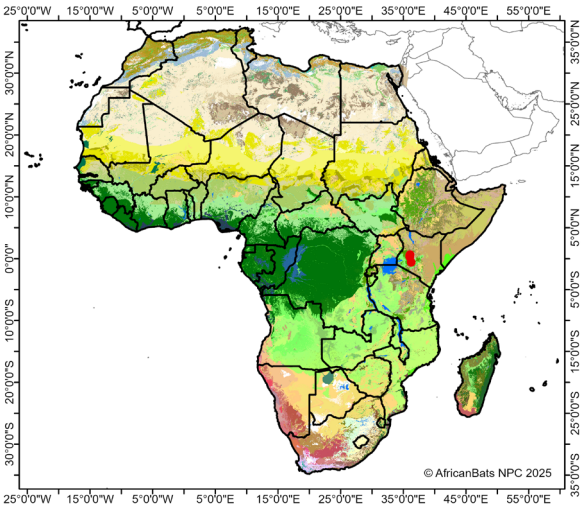

Figure 135. Distribution of *Triaenops persicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Superfamily RHINOPOMATOIDEA Dobson, 1872

*1872. *Rhinopomatoidea* Dobson. - Comments: The name of the Superfamily is based on Rhinopomatidae Dobson, 1872. (Current Combination).

TAXONOMY:
Based on morphological data, the family Rhinopomatidae was placed in the superfamily Rhinopomatoidea by Simmons (1998) and Simmons and Geisler (1998), but more recent molecular studies have contradicted many groupings based on morphological data and, pending resolution of the controversies, for this reason Simmons (2005) did not recognize any chiropteran superfamilies.

Family RHINOPOMATIDAE Dobson, 1872

1838. *Rhinopomina* Bonaparte, Syn. Vert. Syst., in Nuovi Ann. Sci. Nat., Bologna, 2: 111 (sep p 7). - Comments: .
*1872. *Rhinopomatidae* Dobson, J. Asiatic Soc. Bengal, 41 (3): 221. (Current Combination).
1907. *Rhinopomidae* Miller, Bull. U.S. natl. Mus., 57: 80. Publication date: 29 June 1907. - Comments: Type genus *Rhinopoma* Geoffroy St.-Hilaire, 1818.

TAXONOMY:
This is a monotypic family, with all extant species belonging to the genus *Rhinopoma*.

Koopman (1993a) and Simmons (2005) assigned the name Rhinopomatidae to Bonaparte, 1838 - Syn. Vert. Syst. In Nuovi Ann. Sci. Nat., Bologna, 2: 111; but see Corbet and Hill (1992: 81) and Van Cakenberghe and De Vree (1994). Miller (1907) proposed the name Rhinopomidae and this was adopted by several authors: however, the original name is most commonly used (Aulagnier, 2013d:409). The family was reviewed by Hill (1977a) and more recently by Van Cakenberghe and De Vree (1994) and Hulva *et al.* (2007b).

Currently (Simmons and Cirranello, 2024a) recognized genera of the family Rhinopomatidae: ***Rhinopoma*** E. Geoffroy, 1818.

Additionally, there are two extinct genera: †*Corbarhina* Sigé, Mein, Jousse and Aguilar, 2014 (from southern France) and †*Qarunycteris* Gunnell, Simmons and Seiffet, 2008.

COMMON NAMES:
Czech: víkonosovití. Dutch: Langstaartvleermuizen, Muisstaartvleermuizen. English: Mouse-tailed bats. French: Rhinopomes, Chauves-souris à queue de souris, Rhinopomatidés. German: Mausschwanzfledermäuse, Mausschwanz-Fledermäuse. Italian: Rinopormàtidi, Pipistrèlli a códa di tòpo. Norwegian: Langhalete flaggermus, klaffneser.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The oldest remains of extant rhinopomatids were collected from Egyptian tombs, which have been inhabited by these bats for ca. 3000 years (Aulagnier, 2013d: 410).

The family-level stem and crown ages were calculated by Shi and Rabosky (2015: 1537) to be respectively 51.9 and 26.9 mya. Based on genetic markers, Uvizl *et al.* (2025: 811) estimate that the family separated from its sister taxa some 45 mya, and radiation within the family started in the Oligocene (ca. 29 mya). The diversitication within the Rhinopomatidae probably occurred in the Oriental region or in the southern Palaearctic region, within the genus *Rhinopoma*, it probably occurred in the area of the Arabian Pensinsula and Iran (Uvizl *et al.*, 2025: 808);

Uvizl *et al.* (2025: 802) mentioned that fossil material from this family is extremely scarce with only two records dated back to the Late Pleistocene in Israel, and remains from Greece dating back some 8 - 10 mya.

GENERAL DISTRIBUTION:
The family is distributed from Africa (north of the Equator) to southern Asia through Arabia, the Middle East and India, mainly in semi-arid and arid habitats (Aulagnier, 2013d: 409).

The three species of rhinopomatids occurring in Africa occur in the tropics; two also extend northwards into temperate habitats. In Africa, one species is found in semi-desert vegetation zones, and the remaining two are found in both desert and semi-desert vegetation zones. Two species have also been found in montane habitats (but not above ca. 1200 m) (Aulagnier, 2013d:409-410).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
These bats of primitive structure are characterized by a tail that is exceptionally long and has at least half of its length projecting beyond the narrow interfemoral membrane, slit-like valvular nostrils that can be closed, and a small triangular nose leaf surmounting a hog-shaped muzzle (that gave the name to the genus) (Aulagnier, 2013d:409).

Rhinopomatids are small to medium-sized with moderately long pelage that is generally more or less sepia grey (but varying in colour and tone across the geographic range), and usually paler ventrally. The face, rump and posterior portion of the abdomen are naked and medium brown. A thickened narial pad is present on the end of the muzzle, surmounted by a distinct ridge-like dermal outgrowth (a rudimentary noseleaf). The ears are more or less triangular and joined across the forehead by a connecting band of skin; each ear has a simple but moderately long and erect tragus. Eyes are relatively large (Aulagnier, 2013d:409).

Wings rather narrow; second finger with two bony phalanges (like all other African families); all of the fingers are shorter, relative to the length of the forearm, than in any other bats. The tip of the wing can be shortened by folding to facilitate cursorial locomotion, but not to the same extent as in the Emballonuridae and Molossidae. This is achieved by the terminal phalanx of the third finger bending round, but not fully, upon the ventral surface of the wing (Rosevear, 1965). The hindlimbs are moderately long; the toes (except the hallux) have three phalanges. The tail has sensitive hairs at its distal end (Aulagnier, 2013d: 409).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^1/_2$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 28.

The upper incisor (I^2) is very small, barely emerging from the gum. The canines are conical and simple. The first and second upper molars are lacking distinct hypocones.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
The skull is relatively short and broad; there are no postorbital processes. Separate nasal swellings are present on each side of the rostrum. The sagittal crest is low and sharp. The auditory bullae are rather large. The premaxillae are separate from each other and from the adjacent part of the skull.

DETAILED MORPHOLOGY:
Rhinopomatids can accumulate fat in the lower abdominal region; this is metabolized when food is scarce (Aulagnier, 2013d: 410). Their water metabolism reflects extreme adaptations to desert habitats; the concentration of urea in the blood is high, and the skin is poorly vascularized so that loss of water through evaporation is minimal, even at high temperatures (Aulagnier, 2013d: 410).

FUNCTIONAL MORPHOLOGY:
Their wings are adapted for fast flight in open areas, gliding or rapid wing-flapping, but are poor fliers and tire quickly (Aulagnier, 2013d: 410).

SEXUAL DIMORPHISM:
Sexes similar in colour, and males are often slightly larger than females (Aulagnier, 2013d: 409).

ECHOLOCATION:
When echolocating, ultrasound pulses are emitted through the mouth; the echolocation calls are loud with little modulation of frequency when the bats are foraging, and become more frequency-modulated when the bats are approaching prey or when they are emerging from their day-roosts in groups (Schmidt and Joermann, 1986, Aulagnier, 2013d:410).

MOLECULAR BIOLOGY:
Karyotype
Within the family, Sotero-Caio *et al.* (2017: 5) indicated that the 2*n* value varies from 36 to 42.

ROOST:
Rhinopomatids roost in dry caves, crevices, various underground structures and buildings including tombs and pyramids; their day- roosts are impregnated with a characteristic smell (Aulagnier, 2013d: 409).
They sometimes share day-roosts with other species of bats, including other species of rhinopomatids, but the different species do not roost in exactly the same places (Aulagnier, 2013d: 409). Rhinopomatids sometimes roost in clusters numbering up to many thousands of individuals, but most of the groups are smaller (10 - 100 bats) (Aulagnier, 2013d: 410).

MIGRATION:
Some populations are suspected to migrate (Aulagnier, 2013d: 410).

ACTIVITY AND BEHAVIOUR:
The sexes segregate for at least part of the year (Aulagnier, 2013d: 410).

These bats do not hibernate, but they can remain torpid for several days (Aulagnier, 2013d: 410).

MATING:
Little is known of their breeding habits in Africa (Aulagnier, 2013d: 410).

†Genus ***Qarunycteris*** Gunnell, Simons and Seiffert, 2008

*2008. *Qarunycteris* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 6. - Comments: Type species - *Qarunycteris moerisae*. - Etymology: Combination of *Qarun* for Birket Qarun, a large lake near BQ-2 Quarry with *Nykteris*, Greek for bat (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

Currently recognized species of the genus *Qarunycteris*: †***moerisae*** Gunnell, Simons and Seiffert, 2008.

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

†***Qarunycteris moerisae*** Gunnell, Simons and Seiffert, 2008

*2008. *Qarunycteris moerisae* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 6, fig 4F. Type locality: Egypt: Fayum Depression: Quarry BQ-2: Umm Rigl Member of the Birket Qarun Formation. Holotype: CGM 83671. M2. - Etymology: For Lake Moeris, the ancient name of Birket Qarun (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Earliest late Eocene (Priabonian - 37.97 - 33.23 mya - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

Genus ***Rhinopoma*** E. Geoffroy St.-Hilaire, 1818

*1818. *Rhinopoma* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 113. Publication date: 1818. - Comments: Type: *Vespertilio microphyllus* Brünnich, 1782. - Etymology: From the Greek "*ρις*" (rhís) or "*ρινός*" (rhinós), meaning "nose or snout", and "*πώμα*" (pomatòs), meaning "lid, cover", referring to the valvular nostrils, which open through a narrow, transverse slit (see Palmer, 1904: 607; Lanza *et al.*, 2015: 180). (Current Combination).
1821. *Rhynopoma* Bowdich, Anal. Nat. Class. Mamm, 30. - Comments: Type: Vespertilio microphyllus Brünnich, 1782.
1854. *Rhinopomus:* Gervais, Histoire Naturelle des Mammifères, 202. - Comments: Lapsus (Allen, 1939a: 64). (Lapsus).
2017. *Rhinopona:* Loumassine, Allegrini, Bounaceur, Peyre and Aulagnier, Mammalia, 82 (1): 85. Publication date: 23 February 2017. (Lapsus).

TAXONOMY:
Revised by Hill (1977a) and Van Cakenberghe and De Vree (1994).
Allen (1939a: 64) assigned *Rhinopoma* to Oken, 1816, Lehrbuch d. Naturgesch., pt. 3, zool., Sect. 2, p. 926, but this name was rendered "Not Available" by Opinion 417 (International Commission on Zoological Nomenclature, 1956).

A key of the genus is given in Van Cakenberghe and De Vree (1994: 21).

Ethiopian records of *Rhinopoma muscatellum* Thomas, 1903, mentioned by Koopman (1993a) represent *Rhinopoma macinnesi* Hayman, 1937 (see Van Cakenberghe and De Vree, 1994: 20), therefore *R. muscatellum* is no longer included in the list of African species.

A genetic analysis by Uvizl *et al.* (2025: 811) showed that *Rhinopoma macinnesi* is imbedded within *Rhinopoma cystops*, and should be considered a synonym of the latter.

Currently recognized species of the genus *Rhinopoma*: ***cystops*** Thomas, 1903; *hadramauticum* Benda, 2009 – Yemen; *hardwickii* Gray, 1831; ***microphyllum*** (Bünnich, 1782); *muscatellum* Thomas, 1903 – United Arab Emirates, Oman, Yemen, southwestern Iran, southern Afghanistan, western Pakistan, southwestern India (Simmons, 2005: 381).

COMMON NAMES:
Czech: víkonosi, nosalecové, klaponosové. English: Mouse-tailed bats. French: Rhinopomes. German: Mausschwanz-Fledermäuse. Italian: Rhinopòma.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Uvizl *et al.* (2025: 811-812) indicated that the diversification within the genus *Rhinopoma* started around 10 mya, with the split between Rhinopoma hardwickii and Rhinopoma microphyllum occurring some 8 to 9 mya.

PARASITES:
DIPTERA
Streblidae
Brachytarsina alluaudi (Falcoz, 1923) (Haeselbarth *et al.*, 1966: 101).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Egypt.

Rhinopoma cystops Thomas, 1903

1816. *Rhinopoma brevicaudatum* Oken, Lehrbuch Naturgeschichte, Jena, 3 (2): 926. Type locality: Egypt: "Egypt". - Comments: Not available, ICZN Opinion 417, 1956 (Van Cakenberghe and De Vree, 1994: 14).

1866. *Rhinopoma longicaudatum* Fitzinger, in: Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 547. Type locality: Sudan: Sennaar [15 35 N 33 38 E, 425 m]. - Comments: Nomen nudum: Kock (1969a: 35), Van Cakenberghe and De Vree (1994: 14).

1866. *Rhinopoma sennaariense* Fitzinger, in: Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 547. Type locality: Sudan: Anglo-Egyptian Sudan, near Roseires: Sennaar and Fazoglo [=Fazughli] [ca. 11 20 N 34 45 E]. - Comments: Type locality restricted to Fazughli by Kock (1969a: 35). Nomen nudum: see Harrison and Bates (1991: 29), Van Cakenberghe and De Vree (1994: 14). Validated by Kock (1969a) according to Qumsiyeh and Jones (1986: 1).

1868. *Rhinopoma sennarense* Hartmann, Z. Gesel. f. Erdk., 3 (28/29): 44. - Comments: Nomen nudum: Van Cakenberghe and De Vree (1994: 14).

1877. *Rhinopoma senaarense, potius senarense:* Heuglin, Reise in Nordost Afrika, 2: 24. Publication date: 1877. - Comments: Emendation of *sennariense* Fitzinger 1866 (see Kock, 1969a: 35); Lapsus: Van Cakenberghe and De Vree (1994: 14). (Lapsus, Emendation).

*1903. *Rhinopoma cystops* Thomas, Ann. Mag. nat. Hist., ser 7, 11 (65): 496. Publication date: 1 May 1903. Type locality: Egypt: Qena province: Luxor [25 41 N 32 39 E]. [Goto Description]. Holotype: NHMUK 1902.1.17.2: ad ♀, skull and alcoholic. Collected by: Nathanial Charles Rothschild. Presented/Donated by: Nathanial Charles Rothschild. See Thomas (1903b: 497); Kock (1969a: 35); Qumsiyeh (1985: 20). Paratype: NHMUK 1902.1.17.1: ad ♂. Collected by: Nathanial Charles Rothschild. - Etymology: From the Greek substantive "*κύστις*" (kystis) meaning "bladder" and "*ὄφις*" (óphis) meaning "eye-ball", referring to the large eyes (see Lanza *et al.*, 2015: 182, Lanza *et al.*, 2015: 182). (Current Combination).

1917. *Rhinopoma longicaudum:* Geyr von Scheppenburg, J. Ornithol., 65 (3): 283. Publication date: July 1917. (Lapsus).

*1937. *R[hinopoma] cystops macinnesi* Hayman, in: St. Leger, Ann. Mag. nat. Hist., ser 10, 19 (113): 530. Publication date: 1 May 1937. Type locality: Kenya: Lake Rudolf, near Central Island: Bat Island [03 27 N 36 04 E, 700 m]. [Goto Description]. Holotype: NHMUK 1936.11.4.45: ad ♂, skull and alcoholic. Collected by: D.G. MacInnes; collection date: 24 April 1934. - Etymology: In honour of Mr. Donald Gordon MacInnes, eminent English palaeontologist, who worked in eastern Africa and collected of the type specimen (see Lanza *et al.*, 2015: 189).

1954. *Vespertilio brevicauda* Stresemann, Abh. d. Akad. Wiss., Berlin, 1: 172. Type locality: Egypt: Giza province: Saqqara [29 51 N 31 13 E]. Holotype: ZMB 46211: ♂, skull and alcoholic. Collected by: Friedrich Wilhelm Hemprich and Christian Gottfried Ehrenberg; collection date: April 1821; original number: A.1.6.69. Formerly ZMB 564.3 "Sendung Nr 69-71"; see Kock (1969a: 35); Turni and Kock (2008). - Comments: Label name from Hemprich, without nomenclatural status, see Kock (1969a: 35), Van Cakenberghe and De Vree (1994: 14).

1954. *Vespertilio ferox* Stresemann, Abh. d. Akad. Wiss., Berlin, 1: 172. Type locality: Egypt: Giza province: Saqqara [29 51 N 31 13 E]. Holotype: ZMB 46210: ♂, skull and alcoholic. Collected by: Friedrich Wilhelm Hemprich and Christian Gottfried Ehrenberg; collection date: April 1821; original number: A.1.6.68. Formerly ZMB 564.2 "Sendung nr 67-68"; see Kock (1969a: 35), Turni and Kock (2008). - Comments: Label name from Hemprich, without nomenclatural status, see Kock (1969a: 35), Van Cakenberghe and De Vree (1994: 14).

1956. *Rhinopoma hardwichei cystops:* Möhres and Kulzer, Verh. D. zool. Ges., 19: 60. - Comments: Lapsus (see Van Cakenberghe and De Vree, 1994: 15). (Lapsus).

1961. *Rhinopoma lardwickei cystops:* Madkour, Bull. Zool. Soc. Egypt, 16: 50. - Comments: Lapsus (see Kock, 1969a: 35; Van Cakenberghe and De Vree, 1994: 15). (Lapsus).

1969. *Rhinopoma hardwickei sennaariense* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 40, 51. Type locality: Sudan: Blue Nile province: Fazogli [=Fazughli] [11 20 N 34 45 E]. [Goto Description]. - Comments: Validation

of *sennaariense* Fitzinger, 1866, *nomen nudum*. Hill (1977a) pointed out that *sennaariense* Kock, 1969 is a synonym of *arabium* (see Harrison and Bates, 1991: 30).
1971. *Rhinopoma hardwickei sennaarinese:* Hill and Morris, Bull. Br. Mus. (nat. Hist.) Zool., 21 (2): 30. - Comments: Lapsus (see Van Cakenberghe and De Vree, 1994: 15). (Lapsus).
1975. *Rhinopoma senaariense:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 367. - Comments: Lapsus (see Van Cakenberghe and De Vree, 1994: 15). (Lapsus).
1985. *R[hinopoma] h[ardwickei] sinaariense:* Qumsiyeh, Spec. Publ. Mus. Texas Tech. Univ., 23: 22. - Comments: Lapsus: attributed to Kock (1969a) by Qumsiyeh (1985: 22). (Lapsus).
2015. *Rhinopoma cytops:* Kangoyé, Ouéda, Granjon, Thiombiano, Guenda and Fahr, Biod. J., 6 (2): 613. Publication date: 30 June 2015. (Lapsus).
2015. *Rhinopoma hardweickei:* Mohammed, Endocrinol. Metab. Synd., 4: 1. Publication date: 5 January 2015. - Comments: *Rhinopoma hardweickei* for *R. harwickei* [= *R. cystops*]. (Lapsus).
? *Rhinopoma hardwickei arabium:* (Alternate Spelling).
? *Rhinopoma hardwickei cystops:* (Name Combination).
? *Rhinopoma hardwickei hardwickei:* - Comments: Only for the African specimens.
? *Rhinopoma hardwickei:* - Comments: Emendation of *hardwickii*, since the species was named after Maj. Gen. Hardwicke, but according to Hill (pers. comm.) this was unjustified since Gray latinized the name. Only for the African specimens. (Emendation).
? *Rhinopoma hardwickii arabium:* (Lapsus).
? *Rhinopoma hardwickii cystops:* (Name Combination).
? *Rhinopoma Hardwickii:* - Comments: Not of Gray (1831), which is restricted to Asia (see Hulva *et al.*, 2007b), but when used for the African specimens.
? *Rhinopoma macinnesi:* (Name Combination).

TAXONOMY:

See Schlitter and Qumsiyeh (1996, Mammalian Species, 263), Van Cakenberghe and De Vree (1994: 20) as *Rhinopoma hardwickii*.

Hulva *et al.* (2007b) restrict *R. hardwickii* to Asia (Iran to Indonesia) and reinstate *cystops* as the species name for the African and Western Asian representatives.

Ahmim and Tahri (2017: 71) indicate that in Algeria, Niger, and Egypt, two forms of "*R. Hardwickii*" differing in size are known, which casts doubt on the recent taxonomic discrimination of the genus *Rhinopoma*, implying that besides *R. cystops* another small sized species might need to be recognized in northern Africa.

Benda *et al.* (2020: 2586) found that Ethiopian bats are very similar in size to the animals from the southern part of the Arabian peninsula, and smaller than those from Somalia, and they suggest that possibly all specimens from the Horn of Africa should be assigned to *Rhinopoma cystops arabium* rather than to *R. c. cystops*, although they can not exclude that there might be a mosaic-like border between the two lineages.

Genetic analyses by Uvizl *et al.* (2025: 811) showed that the two specimens they examined scored nested within the *cystops* clade and led them to conclude that this name should be considered a junior subjective synonym of *Rhinopoma cystops*.

COMMON NAMES:

Arabian: Khafash abu danab saghir, Khaffash. Czech: víkonos africký. Dutch: Kleine klapneusvleermuis. English: Hardwicke's Mouse-tailed Bat, Lesser Mouse-tailed Bat, Small mouse-tailed bat, Lesser Rat-tailed Bat, Egyptian Mouse-tailed bat, Arabian Mouse-tailed bat. French: Petit Rhinopome, Rhinopoma moyen, Rhinopome de Hardwicke, Chauve-souris à queue de souris. German: Hardwickes Mausschwanz-Fledermaus, Kleine Mausschwanzfledermaus. Hebrew: Yaznuv Katan. Italian: Rhinopòma àfro-ovestasiàtico.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Uvizl *et al.* (2025: 806) found that the divergence of *Rhinopoma cystops* started some 1.44 mya in western Africa, and expanded eastwards with a further split between Moroccan and Kenyan haplotypes occurring some 0.9 mya ago.

CONSERVATION STATUS:

Global Justification

Assessed as Least Concern (LC ver 3.1 (2001)) as it is a widespread and common species with no major threats (Benda, 2017a).

Assessment History

Global

2016: LC ver 3.1 (2001) (Benda, 2017a). 2008: LC ver 3.1 (2001) [assessed as part of *Rhinopoma hardwickii*] (Benda *et al.*, 2008e; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as part of *Rhinopoma hardwickii*] (Benda, 2004b; IUCN, 2004). 1996: VU [assessed as *R. hadithaensis*] (Baillie and Groombridge, 1996); LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

Benda (2017a) reports that no specific measures are known or are in place but occurs in protected

areas across the range. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

Aerial hawking and water stress are considered to be the major risk factors related to climatic change (Sherwin *et al.*, 2012: 174 as *Rhinopoma hardwickei*).

Mansour *et al.* (2016: 66) examined the occurrence of heavy metals in bats from two caves in the Saqqara region of Egypt and found that cobalt was not detected in any sample analysed. Cd, Mo, Ni and Pb were found in low concentrations (generally less than 1.0 µg/g tissue). In the livers, moderate concentrations of Ba, Cr, Cu and Mn and very high concentrations of Ca, Fe and Mg were recorded. Liver tissue from males contained much higher levels of Al and Ba than those from females.

CONSERVATION ACTIONS:
Benda *et al.* (2008e) [in IUCN (2009)] and Benda (2017a) reported that no specific measures are known or are in place, but presumably occurs in protected areas across the range. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
Rhinopoma cystops occurs across central and northern Africa; from Morocco to Israel, Palestine, Jordan Iraq and Afghanistan and south to Kenya. Occurs up 1,100 m asl in Morocco and Algeria.

The Kenyan material mentioned by Koopman (1993a) belongs to *R. macinnesi*, see Van Cakenberghe and De Vree (1994: 17 - 18).

Native: Afghanistan; Algeria (Horáček *et al.*, 2000: 97); Burkina Faso (Kangoyé *et al.*, 2015a: 613); Cameroon; Chad; Djibouti (Pearch *et al.*, 2001: 392); Egypt (Sinai; first record; see Benda *et al.*, 2008e: 1; Carpenter *et al.*, 2014: 180); Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147, Benda *et al.*, 2020: 2585); India; Iran, Islamic Republic of; Iraq; Israel; Jordan; Kenya (but see note above); Kuwait; Libyan Arab Jamahiriya; Mali; Mauritania (Brito *et al.*, 2010: 452, as *R. hardwickei*, Allegrini *et al.*, 2011: 3); Morocco (Benda *et al.*, 2004d; Benda *et al.*, 2010a: 154; El Ibrahimi and Rguibi Idrissi, 2015: 358, as *R. hardwickei;* Dbiba *et al.*, 2025: 6); Niger; Nigeria; Oman; Saudi Arabia; Somalia; Sudan; Syrian Arab Republic; Tunisia (Horáček *et al.*, 2000: 97; Dalhoumi *et al.*, 2016b: 866); Western Sahara; Yemen (Socotra).

DETAILED MORPHOLOGY:
Mohammed (2015) extensively discuss the pituitary gland of Egyptian "*R. hardwickei*", whereas El-Nahass *et al.* (2025) do the same for the brain of these bats.

Tongue
Abumandour *et al.* (2022) studied the ultrastructure of the tongue of Egyptian "*R. hardwickii*" specimens and found three types of lingual papillae: one filiform mechanical and two gustatory (fungiform
and circumvallate). The filiform papillae are subdivided in five subtypes.

FUNCTIONAL MORPHOLOGY:
King *et al.* (2025) investigated the olfactory system of this species.

SEXUAL DIMORPHISM:
Kangoyé *et al.* (2015a: 613) indicate that most of the average body measurements are larger in females than in males, but that the average cranial measurements are larger in males.

ECHOLOCATION:
Frequency of CF-component (second harmonic) during pursuit of insect (Egypt): 36 - 40 kHz; call-duration 6 - 10 ms; call-repetition rate ca. 10 call/s. Darting flight is accompanied by shortening the signals to 1 ms or less and increasing the call-repetition rate to ca. 100 calls/s; laboratory tests indicated that Doppler shift compensation is probably not used by this species (Simmons *et al.*, 1984). When three individuals flew together in the laboratory, each used a different CF-frequency suggesting that they regulate the CF-frequency to avoid jamming each other (Habersetzer, 1981). After landing, CF calls of mean duration 74 ms are emitted and these have maximum energy in fundamental harmonic; the purpose of these calls (echolocation and/or communication) is not known (ibid.). The first harmonic frequencies (18 - 20 kHz; Simmons *et al.*, 1984) of calls made in a roost in Morocco were audible to humans (Aulagnier and Destre, 1985).

In Jordan, Benda *et al.* (2010b: 204) reported the following parameters for 59 calls: F_{start}: 36.4 ± 1.5 (33.2 - 39.6) kHz, F_{end}: 32.5 ± 1.4 (29.5 - 35.8) kHz, F_{peak}: 34.3 ± 1.2 (32.0 - 37.1) kHz, Call duration: 8.0 ± 1.6 (4.5 - 12.0) ms, Inter-pulse interval: 116.0 - 29.9 (60.0 - 210.0) ms.

From Tunisia, Dalhoumi *et al.* (2016b: 866) reported an almost constant frequency with three or four harmonics and maximum energy in the second harmonic (at 32 kHz).

Moores and Brown (2017: 612) recorded the following parameters in southern Morocco: F_{start}: 34.6 ± 0.5 (33.6 - 35.6) kHz, F_{max}: 33.6 ± 0.4 (32.8 - 34.4) kHz, F_{end}: 33.0 ± 0.5 (32.5 - 34.1) kHz, duration: 9.4 ± 0.8 (8.6 - 11.1) ms, interpulse interval: 260 ± 122 (69 - 520) ms.

MOLECULAR BIOLOGY:

Karyotype

Ray-Chaudhuri *et al.* (1968) and Rushton (1970: 463) reported 2*n* = 36, FN = 68, BA = 34, a submetacentric X chromosome and an acrocentric Y chromosome for specimens from India, this data now relates to *Rhinopoma hardwickii*. Qumsiyeh and Baker (1985) reported an identical karyotype for specimens from Palestine, which are now referred to *Rhinopoma cystops* see Hulva *et al.* (2007a). Sayed (2011: 659) also reported 2*n* = 36 and FN = 68 for *R. hardwickei* specimens from Egypt, with a medium-sized submetacentric X chromosome and an acrocentric Y chromosome. Pairs 13 and 15 show a broad G-negative region around their centromere, and complete heterochromatin in the short and long arm. Pair 5 also shows a broad G-negative region around its centromere, and the Y chromosome has complete heterochromatin.

Genetics

Giannini and Simmons (2005); Ali (2011).

ROOST:

In Israel, Levin *et al.* (2015: 1, 3) found that *R. cystops* hibernates during five months in winter in caves that were geothermally heated to a stable temperature of 20 °C, with almost 100 % relative humidity. They also found that the bat's skin temperature was 1 - 3 °C above the average cave temperature, and that during the same period, the outside temperatures fluctuated between 4 and 22 °C. During the hibernation, no period arousal or periods of normothermy were observed.

Benda *et al.* (2014c: 10) observed a colony of about 40 specimens in two ground floor rooms of a ruin of an Italian fortress in the Al Jaghbub oasis (Libya).

Węgiel *et al.* (2024: 3) reported this species (44 bats) from undamaged domed tombs at the Old Dongola archaeological site (Sudan), and also indicated that none of the damaged tombs housed bats. A colony of about 12 bats was also found in the ruins of St. Anthony's Monastery.

DIET:

Benda *et al.* (2014c: 14) examined 40 faecal pellets of *R. cystops* from the Al Jaghbub oasis (Libya). The diet consisted primarily of ants (Hymenoptera: Formicoidea; 81 % of volume) and furthermore of beetles (Coleoptera, mostly of the family Tenebrionidae).

PREDATORS:

In Sudan, Tryjanowski *et al.* (2024: 2) found remains of this bat in scats of the striped polecat (*Ictonyx striatus* (Perry, 1810)).

POPULATION:

Structure and Density

Appears to be particularly abundant near oases. However, both distribution and abundance are undoubtedly insufficiently investigated because the roosts and suitable habitats are often unreachable. Colonies range in size from a few individuals up to several hundred; maximum is about 1000 individuals (Egypt) (Benda, 2017a). This species is assumed stable throughout its distribution range. Population information remains unknown for most of its African distribution. Loumassine *et al.* (2017c:28) reported on a colony of about 100 animals in an old mine in Algeria.

Trend

2016: Stable (Benda, 2017a).

REPRODUCTION AND ONTOGENY:

Gharaibeh (1997: 47) reported two pregnant females captured in Tunisia on 26 May 1996.

MATING:

Khajuria (1972: 307) report on the mating behaviour of the closely related Indian *R. h. hardwickei*, but whether this is also applicable for *R. cystops* is uncertain.

PARASITES:

TREMATODA

Morsy *et al.* (2018: 319) reported the presence of *Urotrema scabridum* (Braun, 1900) and *Renschetrema indicum* Kifune, 1984 in "*R. hardwickii*" specimens collected in Cairo.

ARACHNIDA

Argasidae

Argas vespertilionis Latreille, 1802 was reported from Libyan bats by Benda *et al.* (2014c: 15), and two larvae of *Argas confusus* Hoogstraal, 1955 on *R. cystops* specimens in Jordan (Benda *et al.*, 2010b: 212). Sándor *et al.* (2021a: 4) reported the same tick species, but as members of the genus *Chiropterargas*.

Trombiculidae

Grandjeana mauritanica Kalúz and Ševčík, 2014 on *R. cystops* specimens from Mauritania (Kalúz and Ševčík, 2014: 31; Stekolnikov, 2018a: 136; Zajkowska *et al.*, 2018: 107).

Bendjeddou *et al.* (2017: 15) reported the following ectoparasites from Algeria: *Nycteribia (Listropoda) schmidlii schmidlii* Schiner, 1853 (Nycteribiidae) and *Argas vespertilionis* (Latreille, 1802) (Arachnida).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Carios vespertilionis* Latreille, 1802; Nycteribiidae: *Nycteribia schmidlii schmidlii* Schiner, 1853; Pulicidae: *Synosternus cleopatrae pyramidis* (Rothschild, 1903), *Xenopsylla ramesis* (Rothschild, 1904); and Trombiculidae: *Grandjeana mauritanica* Kalúz and Ševčík, 2014.

VIRUSES:
Coronaviridae
Lane *et al.* (2022: 221) found Eidolon bat coronavirus and PREDICT_CoV-114 in Ethiopian "*Rhinopoma hardwickii*" specimens.

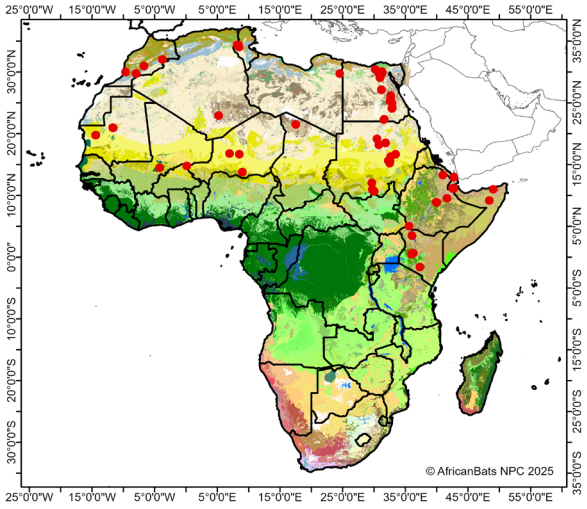

Figure 136. Distribution of *Rhinopoma cystops*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Burkina Faso, Chad, Djibouti, Egypt, Eritrea, Ethiopia, Kenya, Libya, Mali, Mauritania, Morocco, Niger, Senegal, Somalia, South Sudan, Sudan, Tunisia.

Rhinopoma microphyllum (Brünnich, 1782)

*1782. *Vespertilio Microphyllus* Brünnich, Dyrenes Historie, 1: 50, pl 6; figs 1 - 4. Type locality: Egypt: Giza province: Giza [30 01 N 31 13 E]. Holotype: MNHN A.121/T196: ♀, alcoholic (skull not removed). Number 196 in Rode (1941: 242), who calls this the holotype. Holotype: ZMUC |TS101|: Collected by: Hasselquist. See Kock (1969a). Paratype: MNHN A.123/196B: ad, alcoholic (skull not removed). Number 196b in Rode (1941: 242). Paratype: MNHN A.124/196C: ad ♀, alcoholic (skull not removed). Number 196c in Rode (1941: 242). Paratype: MNHN A.125/196D: ad ♂, alcoholic (skull not removed). Number 196d in Rode (1941: 242). Paratype: MNHN ZM-MO-1986-1040: ♀, alcoholic (skull not removed). Collected by: Etienne Geoffroy-Saint-Hilaire. Allotype: MNHN A.122/196A: ♂, alcoholic (skull not removed). Number 196a in Rode (1941: 242). - Comments: Corbet and Hill (1992: 82) and Horáček *et al.* (2000: 96) mention "Arabia and Egypt" as type locality. Type locality fixed by Koopman (1975: 366) but also Aellen (1957), Anderson and de Winton (1902), Kock (1969a) - See Schlitter and Qumsiyeh (1996: 1). - Etymology: From the Greek "*μικρός*" (mikrós), meaning "small" and "*φύλλον*" (phýllon), meaning "leaf" (see Schlitter and Qumsiyeh, 1996: 4; Lanza *et al.*, 2015: 193).

1820. *Rhinopoma microphylla:* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 129. Publication date: 1820. (Current Combination, Alternate Spelling).

1859. *Rhinopoma Lepsianum* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 222. Publication date: 1859. Type locality: Sudan: Khartoum [15 40 N 32 35 E]. [Goto Description]. Lectotype: ZMB 2578: ad ♂, skull and alcoholic. Collected by: Lepsius; collection date: 1844?. Lectotype designated by Kock (1969a: 54, 57); skull extracted in the 1960's by D. Kock (see Turni and Kock (2008: 22). Paralectotype: ZMB A.3243: ad, skull only. Paralectotype designated by Turni and Kock (2008: 22). - Comments: Type locality mentioned as Blue Nile by Kock (1969a: 58); as White Nile by Koopman (1975: 366), Turni and Kock (2008: 22). See Turni and Kock (2008: 22) for a discussion on the fact that Peters possibly used this skull to describe *lepsianum*).

1877. *Rhinopoma cordofanicum* Heuglin, Reise in Nordost Afrika, 2: 24. Publication date: 1877. Type locality: Sudan: Jebel Arashkool: W bank of the White Nile [ca. 14 15 N 32 10 E]. - Comments: Allen (1939a: 64) mentions Heuglin and Fitzinger, 1866. Sitzb. K. Akad. Wiss. Wien, 54, sec 1, 547 as author. Nomen Nudum. Included in *hardwickei* by Kock (1969a: 35).

1969. *Rhinopoma microphyllum tropicalis* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 58. Type locality: Sudan: Kordofan province: 2 km NE Kadugli: Jebel Talao [11 02 N 29 43 E, 550 m]. [Goto Description]. Holotype: SMF 33216: sad ♂, skin and skull. Collection date: 12 February 1963; original number: SUD.06.3. See Kock (1969a: 58) mention SMF 33265 as number for the holotype, but the online catalog confirms the number should be 33216. Paratype: SMF 33198: ♂, skull and alcoholic. Collected by: Dr. Dieter Kock; collection date: 6 January 1965. Locality: Jebel Talao. Paratype: SMF 33199: ♂, skull and alcoholic. Collected by: Dr. Dieter Kock; collection date: 6 January 1965. Locality: Jebel Talao. Paratype: SMF 33200: ♂, skull and alcoholic. Collected by: Dr. Dieter Kock; collection date: 6 January 1965. Locality: Jebel Talao. Paratype: SMF 33214: ♂, skull and alcoholic. Collection date: 22 October 1962. Locality: Jebel Talao. Paratype: SMF 33215: ♀, skull and alcoholic. Collection date: 16 February 1963. Locality: Jebel Talao. - Comments: Most likely a synonym of *R. m. microphyllum*. If a valid subspecies, *lepsianum* or *cordofanicum* may have priority (see Schlitter and Qumsiyeh, 1996: 1).

1985. *Rhinopoma mircophylum kineari:* Bhatnagar and Parveen, Nat. Acad. Sci. Letters, 8 (2): 64. - Comments: Lapsus for *microphyllum*. (Lapsus).

2025. *R[hinopoma] mycrophyllus:* Conenna, Muñoz-Garcia and Korine, Mammal Rev., xxx (e70005): 2. Publication date: 7 May 2025. (Lapsus).

? *Rhinopoma microphyllum microphyllum:* (Name Combination).

? *Rhinopoma microphyllum:* (Name Combination).

TAXONOMY:
See Schlitter and Qumsiyeh (1996, Mammalian Species, 542).

Bagherfard *et al.* (2020: 43) assigned the African representatives to *R. m. microphyllum*, together with the specimens from Jordan and the Levant.

COMMON NAMES:
Arabian: Khafash abu danab kabir, Khaffash. Bengali: Indur-lenji Chamchika. Czech: víkonos velký, nosalec malolupenný, klaponos egyptský, víkonos, víkonos egyptský, víkonos asijský. Dutch: Grote klapneusvleermuis. English: Larger Mouse-tailed Bat, Long-tailed Bat, Greater Mouse-tailed Bat, Rat-tailed Bat, Brunnich's Mouse-tailed Bat, Larger Rat-tailed Bat, Greater Rat-tailed Bat. French: Grand Rhinopome, Rhinopome microphylle. German: Ägyptische Mausschwanz-Fledermaus. Hebrew: Atalef Yaznuv Gadol. Indonesian: Kelelawar ekor lembing, Kelelawar Ekor-tikus. Italian: Rinopòma microfillo.

CONSERVATION STATUS:
Global Justification
Rhinopoma microphyllum is listed as Least Concern (LC ver 3.1 (2001)) as it is widespread and common in at least parts of its range, with no known major threats (Aulagnier and Palmeirim, 2008b; IUCN, 2009; Monadjem *et al.*, 2017bp).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bp). 2008: LC ver 3.1 (2001) (Aulagnier and Palmeirim, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Aulagnier, 2004b; IUCN, 2004). 1996: LR: lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Human disturbance in roost sites and use of pesticides for locusts affect the species but are not considered major threats at present (Aulagnier and Palmeirim, 2008b; IUCN, 2009; Monadjem *et al.*, 2017bp).

CONSERVATION ACTIONS:
Aulagnier and Palmeirim (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017bp) reported that no specific measures are known for this species, but presumably it occurs in some protected areas. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
The distribution range of *Rhinopoma microphyllum* extends from northern Africa through southwest Asia to Afghanistan, Pakistan and India. In southeast Asia, there are single old records from Thailand and Sumatra. Recorded from sea level in Egypt up to 1,200 m in Morocco (Aulagnier and Palmeirim, 2008b; IUCN, 2009).

Native: Afghanistan; Algeria (Loumassine *et al.*, 2017b: 85); Bangladesh; Benin; Burkina Faso (Kangoyé *et al.*, 2015a: 613); Central African Republic; Chad; Côte d'Ivoire; Djibouti (Pearch *et al.*, 2001: 393); Egypt; Eritrea; Ethiopia (Benda *et al.*, 2020; 2584); Ghana; Guinea; India; Indonesia; Iran (Bagherfard *et al.*, 2020), Islamic Republic of; Iraq; Israel; Jordan; Lebanon; Liberia; Mali; Mauritania (Benda *et al.*, 2004a: 105); Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 358; Dbiba *et al.*, 2025: 6); Myanmar (see Corbet and Hill, 1992); Niger; Nigeria; Oman; Pakistan; Saudi Arabia; Senegal; Sierra Leone; Sudan; Sumatra; Syrian Arab Republic; Togo; Western Sahara; Yemen.

Presence uncertain: Libyan Arab Jamahiriya; Thailand; Tunisia.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 20.5 Pa, aspect ratio 8.0 and tip shape index of 1.24 for a wingspan of 35 cm and a wing area of 153 cm^2 and a body mass of 32 g.

Hajyahia *et al.* (2025: 1, 4) showed that *Rhinopoma microphyllum* wags its long free tail in a pendulum like pattern (with a frequency of 5 - 6 Hz))when moving backwards up walls and between obstacles. They also found that the tail is used to navigate around obstacles and is used to discriminate between textures.

ECHOLOCATION:
Search-phase call-shape (locality not given): CF (multiharmonic) (Schmidt and Joermann, 1983). Frequency of CF-component (second harmonic): 27 - 31 kHz (but each individual emits only one frequency); call-duration "long". When flying in a flight-tunnel, this species emits shorter and slightly frequency-modulated calls (as does *R. hardwickii*). However, if 3 individuals fly together in the flight-tunnel, instead of avoiding jamming by changing to three different frequencies (see *R. hardwickii*), the main response of these bats is to greatly increase the intensity of their calls (ibid.). Cvikel *et al.* (2014: 2) showed that *R.*

microphyllum doesn't show the classical jamming avoidance response: they altered their signals as if they were responding to a nearby (silent) object. They also found that individuals exhibit sufficient frequency spread to allow individual recognition without any jamming avoidance response.

In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for 9 calls: F_{start}: 29.6 ± 0.3 (28.9 - 30.0) kHz, F_{end}: 25.7 ± 0.6 (25.2 - 26.7) kHz, F_{peak}: 28.0 ± 0.7 (27.0 - 29.0) kHz, Pulse duration: 11.7 ± 0.8 (10.5 - 13.0) ms, and Inter-pulse Interval: 202.3 ± 46.8 (110.0 - 267.0) ms.

Benda *et al.* (2012a: 182) reported the following values from Iran (hand released): F_{start}: 29.8 ± 0.6 (29.0 - 30.4) kHz, F_{end}: 25.3 ± 0.2 (25.0 - 25.5) kHz, F_{peak}: 27.1 ± 0.4 (26.8 - 27.7) kHz, Pulse duration: 7.9 ± 0.3 (7.6 - 8.3) ms, and inter-pulse interval: 114.6 ± 7.9 (106.5 - 127.2) ms.

From Israel the following parameters were reported by Hackett *et al.* (2016: 223): 116 calls: Pulse duration: 8.37 ± 2.51 ms, F_{start}: 30.21 ± 1.95 (28.0 - 31.2) kHz, F_{end}: 28.99 ± 1.72 (27.0 - 30.2) kHz, F_{peak}: 29.42 ± 1.72 (28.0 - 30.2) kHz.

From Algeria, Loumassine *et al.* (2017b: 87) reported on four harmonics, of which the second one had the most energy: F_{start}: 31.9 - 37.9 Khz, F_{max}: 28.2 - 31.2 kHz, F_{end}: 23.1 - 25.2 kHz, and pulse duration: 3.2 - 6.1 ms.

Davies *et al.* (2013b: Table S8) report a peak-frequency of 28 kHz and a range between 27 and 30 kHz.

Boonman *et al.* (2013b: 6) determined the detection range to be between 2 and 6.5 m at 20 dB and 5.5 and 14 m at 0 dB.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 29.42 kHz, F_{start}: 30.21 kHz, F_{end}: 28.99 kHz, Band width: 1.22 kHz, and duration: 8.37 ms.

Molecular Biology:

Karyotype

Handa and Kaur (1979), and Qumsiyeh and Baker (1985) reported $2n$ = 42, FN = 66, BA = 26, a metacentric X and an acrocentric Y chromosome.

Genetics

Hulva *et al.* (2007a).

Roost:

From northern Israel, Levin *et al.* (2013: 1) report that *R. microphyllum* forms sexually-segregated colonies composed of 3,000 to 5,000 individuals during the summer (June to September). At the end of August non-reproductive males left their roost and were occasionally observed in the southern female roosts between September and October.

Also in Israel, Levin *et al.* (2015: 1, 3) found that *R. microphyllum* hibernates during five months in winter in caves that were geothermally heated to a stable temperature of 20 °C, with almost 100 % relative humidity. The bat's skin temperature was 1 - 3 °C above the average cave temperature. During the same period, the outside temperatures fluctuated between 4 and 22 °C.

Diet:

Egert-Berg *et al.* (2017: 3668, 3670) indicate that this species relies on ephemeral resources (i.e. insect swarms), whose distribution in time or space is hard to predict. They also determined a maximum distance travelled to the foraging size of 9.8 (8.3 - 13.5) km and found that the bat's activity time (being away from their day roost) was 5.5 (2.8 - 6.8) hours.

In July from Israel, more than 50 % of the bats diet comprised queen carpenter ants (*Camponotus felah* Dalla Torre, 1893), while other insect groups in the faces comprised mainly Coleoptera and Heteroptera (Levin *et al.*, 2012; Prat and Yovel, 2020: 170). This suggests that the gradual increase in the proportion of queen carpenter ants in the diet during summer results from an increase in this insect's availability, combined with a high preference for this prey item. To search for these queen swarms, the bats travel dozens of kilometres.

Benda *et al.* (2012a: 196) analyses faeces from two localities in Iran, and found in the pellets from one of the localities only remains from ants (Hymenoptera, Formicoidea), whereas the other sample contained Coleoptera (60 % of volume), Heteroptera (30 %) and small nematoceran Diptera (10 %).

Population:

Structure and Density

According to Aulagnier and Palmeirim, 2008b) [in IUCN (2009)] and Monadjem *et al.* (2017bp) , *Rhinopoma microphyllum* is uncommon in the western part of the Mediterranean range, but populations probably occur in areas not yet surveyed. Colonies of several thousands have been reported in Egypt. Very rare in Jordan, found in the same caves as *R. hardwickei* but in much lower numbers (Amr, 2000). In Iran the species is common, the most populated cave is in the Mesopotamian plain and has around 20,000

individuals; the total population of Iran is approximately 30,000 and is considered stable (M. Sharifi *pers. comm.,* 2005). In Africa there are large colonies of up to 5,000 individuals in several areas (GMA Africa Workshop, 2004).

Trend
2016: Stable (Monadjem *et al.*, 2017bp). 2008: Stable (Aulagnier and Palmeirim, 2008b; IUCN, 2009).
R. microphyllum populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

ACTIVITY AND BEHAVIOUR:
A sharp increase in body mass was observed from mid-July (Levin *et al.*, 2012). Levin *et al.* (2012) also found that the fatty acids composition of *R. microphyllum* body fat reflects the composition of their main prey item-queen carpenter ants. They accumulate significant fat reserves towards the end of summer (Levin *et al.*, 2012). Levin *et al.* (2012) found white adipose tissue accumulates in pre-hibernating *R. microphyllum*.

Cvikel *et al.* (2015: 206) used miniature GPS devices that allowed simultaneous ultrasonic recording and found that one of their tracked bats flew continuously for over 5 hours and that another on flew more than 90 km. All of the bats spent a substantial proportion of their time in high conspecific density. They estimated that bats spent at least 41 ± 14 % of their foraging at less than 150 m from a conspecific and even 8 ± 2 % at less than 12 m from a conspecific

PARASITES:
Hirst (1923: 979) indicates that Kolenati stated that either *R. microphyllum* or *Pteropus ægyptiacus* [=*Rousettus aegyptiacus*] is the host for *Ancystropus zelebori* Kolenati, 1856 (Acari).

In Iran, Benda *et al.* (2012a: 196) found the following parasites to be present: bat flies *Brachytarsina flavipennis* Macquart, 1851 and *B. alluaudi* (Falcoz, 1923) [= *diversa* (Frauenfeld, 1857)]. They also refer to Maa (1965), who reported the presence of streblid bat flies *Ascodipteron namrui* Maa, 1964 and *A. rhinopomatos* Jobling, 1952 from Israel and Egypt, and to Dusbábek (1970), who reported the Macronyssid mites *Macronyssus leucipe* (Domrow, 1959) and *Steatonyssus afer* Radovsky and Yunker, 1963 from Afghanistan (but these came from a mixed collection of *R. microphyllum* and *R. hardwickii*). Furthermore, the presence of the chigger mites *Sasatrombicula rhinopoma* (Vercammen-Grandjean, 1963) and *S. multisternalae* (Vercammen-Grandjean, 1963) was reported from Afghanistan too.

Sándor *et al.* (2021a: 4) reported the presence of the argasid mite *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933).

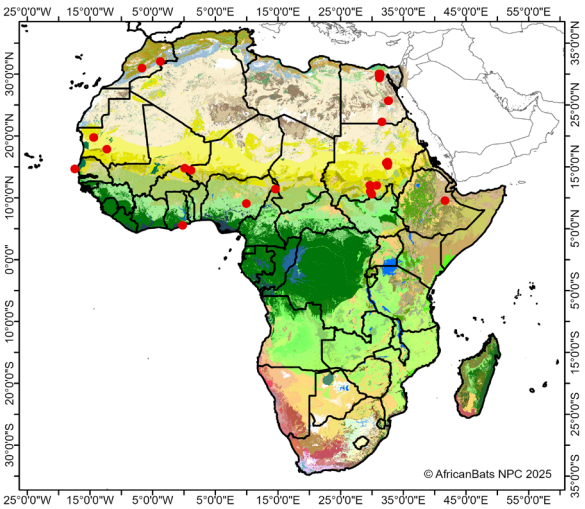

Figure 137. Distribution of *Rhinopoma microphyllum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Burkina Faso, Cameroon, Egypt, Ethiopia, Ghana, Mauritania, Morocco, Niger, Nigeria, Senegal, Sudan.

†Family TANZANYCTERIDIDAE Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003

*2003. *Tanzanycteridae* Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, Pal. Electr., 5(3): 3. (Current Combination).
2013. *Tanzanycteridae:* Habersetzer, Engels, Gunnell and Simmons, 16th International Bat Research Conference & 43rd North American Symposium on Bat Research. San José, Costa Rica, 11-15 August 2013, 64. (Lapsus).

TAXONOMY:
Known genera of the family Tanzanycteridae: †***Tanzanycteris*** Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003.

†Genus ***Tanzanycteris*** Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003

*2003. *Tanzanycteris* Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, Pal. Electr., 5(3): 3. (Current Combination).

TAXONOMY:
Using micro-CT scans, Habersetzer *et al.* (2013: 64) examined the inner ear morphology of *T. mannardi* and found that this was very similar to the highly sophisticated echolocation system found in current days *Hipposideros*. They suggest that *Tanzanycteris* might actually be a Hipposiderid rather than a member of a family by its own.

Currently recognized species of the genus *Tanzanycteris*: †***mannardi*** Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Simmons and Jones (2024: 27) indicate that Tanzanycteris had extremely enlarged cochlea, which are very similar to those of current day bats using high duty-cycle Doppler shift echolocation.

†***Tanzanycteris mannardi*** Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, 2003

*2003. *Tanzanycteris mannardi* Gunnell, Jacobs, Herendeen, Head, Kowalski, Msuya, Mizambwa, Harrison, Habersetzer and Storch, Pal. Electr., 5(3): 5. Type locality: Tanzania: Mahenge: approximately 50 km west of Singida [044750.2S 341554.5E]. Holotype: TNM MP-207. Partial skeleton including skull, axial skeleton anterior to sacrum, partial left and right humeri, and partial left radius. - Etymology: For George W. Mannard who explored the Singida Kimberlite Field and made the first excavation at the type locality in 1957. (Current Combination).

TAXONOMY:
Ravel *et al.* (2011: 403) indicate that the phylogenetic position of *T. mannardi* is still uncertain due to its poor state of preservation, but that it shows many similarities with the Hassianycteridae.

Phillips (2015: 9) refers to Gunnell *et al.* (2003), who identified characters that put *T. mannardi* within the Yinpterochiroptera, more specifically the Rhinolophoidea. These characters include extremely enlarged cochlea, broadened first rib, and a dorsally flared iliac blade. However, it remains unclear whether *Tanzanycteris* is directly linked to the Rhinolophoidea or to the Yinpterochiroptera (which also include the Pteropodidae). Phillips (2015) estimates the Hard Minimum Age for this taxon to be 45.0 million years ago and the Soft Maximum Age at 58.9 mya. Ravel *et al.* (2016: 356) place it in the Middle Eocene.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Middle Eocene (Lutetian - 47.8 - 41.3 mya - Brown *et al.*, 2019: Suppl.)

SUBORDER VESPERTILIONIFORMI Van Cakenberghe, Kearney and Seamark, 2007

1821. *INSECTIVORAE* J. E. Gray, 299. - Comments: Proposed as an order of bats, for the same content as that of MICROCHIROPTERA Dobson 1875. Originally included the families Noctilionidae J. Gray, 1821 and Vespertilionidae J. Gray, 1821. Not Insectivora Bowdich, 1821 (Mammalia, Lipotyphla) (see Jackson and Groves, 2015: 252).

1855. *Gymnorhina* Giebel, Die Säugethiere in Zoologischer, anatomischer und palaeontologischer Beziehung umfassend dargestellt, xii, 926. - Comments: Originally included the genera *Furia* F. Cuvier, 1828 [= *Furipterus* Bonaparte, 1837 [1832–1841]]; *Nycticejus* [sic = *Nycticeius*] Rafinesque, 1819; *Vespertilio* Linnaeus, 1758; *Thyroptera* de Spix, 1823; *Dysopes* Illiger, 1811 [= *Molossus* É. Geoffroy, 1805]; *Emballonura* Kuhl [= Temminck, 1838]; *Diclidurus* Wied-Neuwied, 1820; *Noctilio* (Geoff) [= Linnaeus, 1766]; *Taphozous* É. Geoffroy, 1818; and *Mormops* [sic = *Mormoops*] Leach, 1821] (see Jackson and Groves, 2015: 252).

1866. *Entomophaga* A. Murray, The Geographical Distribution of Mammals, xiv. - Comments: Originally included the Istiophora Giebel, 1855 [= Phyllostomidae Gray, 1825] and Gymnorhini Giebel, 1855 [= Yangochiroptera Koopman, 1985; part]. Not Entomophaga Owen, 1839 (Mammalia, Dasyuromorphia [= Marsupialia Illiger, 1811], nor Entomophaga Owen, 1859 (Mammalia, Didelphimorphia) (see Jackson and Groves, 2015: 252).

1866. *ENTOMOPHAGA:* Murray, xiv. - Comments: Not ENTOMOPHAGA Owen 1859, used for didelphoid marsupials.

1979. *PHYLLOSTOMATIA* Van Valen, Evol. Theory, 4 (3): 103, 109. Publication date: July 1979. - Comments: Proposed as infraorder and originally included the superfamilies Rhinopomatoidea Bonaparte, 1838 (containing of the families Rhinopomatidae Bonaparte, 1838, Emballonuridae Gervais, 1855 and Craseonycteridae Hill, 1974); Rhinolophoidea J. Gray, 1825 (containing the families Rhinolophidae J. Gray, 1825, Nycteridae Van der Hoeven, 1855 and Megadermatidae H. Allen, 1864); and Noctilionoidea J. Gray, 1821 (containing the families Noctilionidae J. Gray, 1821, Mormoopidae de Saussure, 1860, Phyllostomatidae Coues and Yarrow, 1875 [= Phyllostomidae J. Gray, 1825] and Desmodontidae Bonaparte, 1845: 5). Jackson and Groves (2015: 252) considered the name as a synonym of the Yangochiroptera Koopman, 1985, but the listing suggests it might rather be a synonym of the Chiroptera.

1979. *VESPERTILIONIA* Van Valen, Evol. Theory, 4 (3): 103, 109. Publication date: July 1979. - Comments: Proposed as infraorder and originally included the superfamily Vespertilionoidea J. Gray, 1821, containing the families Natalidae J. Gray, 1866, Vespertilionidae J. Gray, 1821, Mystacinidae Dobson, 1875 and Molossidae Gervais, 1855 (see Jackson and Groves, 2015: 252).

1985. *YANGOCHIROPTERA* Koopman, Bat Res. News, 25 (3/4): 26. - Comments: Proposed as Infraorder in the suborder Microchiroptera and originally included the superfamilies Phyllostomoidea J. Gray, 1825 and Vespertilionoidea J. Gray, 1821 (see Jackson and Groves (2015: 252).

1995. *VESPERTILIIFORMES* Zagorodniuk, Godovanets, Pokynchereda and Kyseliuk, Rakhiv (Proceed. Intern. Conf. "ACANAP-1995" 18 - 21 October 1995). - Comments: also Zagorodniuk *et al.* (1995); Zagorodniuk and Pokynchereda (1997).

1997. *VESPERTILIFORMES* Zagorodniuk.

1998. *Microchiropteraformes* Simmons and Geisler, Bull. Am. Mus. Nat. Hist., 235: 136. - Comments: Originally included the fossil genus *Eppsinycteris* Hooker, 1996; the fossil families Palaeochiropterygidae Revilliod, 1917 and Hassianycteridae Habersetzer and Storch, 1987; and the suborder Microchiroptera Dobson, 1875 [= Chiroptera Blumenbach, 1779; part] (see Jackson and Groves, 2015: 253).

1998. *Microchiropteramorpha* Simmons and Geisler, Bull. Am. Mus. Nat. Hist., 235: 135, 136. - Comments: Originally included the fossil genus *Australonycteris* Hand et al., 1994; the fossil families Icaronycteridae Habersetzer and Storch, 1987 and Archaeonycteridae Revilliod, 1917; and the unranked Microchiropteraformes (see Jackson and Groves, 2015: 253).

1998. *VESPERTILIONIFORMES* Zagorodnyuk. - Comments: Zagorodnyuk (1998a, b and c); Zagorodniuk (1999, 2001a and b, 2002, 2003a and b, 2004). Jackson and Groves (2015: 228) assigned this name to Hutcheon and Kirsch (2004b: 44), who included the families Phyllostomidae J. Gray, 1825: 242, Mormoopidae de Saussure, 1860, Noctilionidae J. Gray, 1821, Mystacinidae Dobson, 1875, Emballonuridae Gervais, 1855, Vespertilionidae J. Gray, 1821, Miniopteridae Dobson, 1875, Molossidae Gervais, 1855, Natalidae J. Gray, 1866 and Nycteridae Van der Hoeven, 1855.

2001. *YINPTEROCHIROPTERA* Springer, Teeling, Madsen, Stanhope and De Jong, Proc. Natl. Acad. Sci. USA, 98 (11): 6423. - Comments: In part.

2004. *VESPERTILIONIFORMES* Hutcheon and Kirsch, J. mamm. Evolut., 11 (1): ???. - Comments: .

*2007. *VESPERTILIONIFORMI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Infraorder is based on *Vespertilio* Linnaeus, 1758 (type of VESPERTILIONIDAE Gray, 1821). (Current Combination).

2008. *Microcheroptera:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Lapsus).

2014. *Vespertilionimorpha* Zagorodniuk, Proc. Theriol. School, 12: 8.

2018. *Yinpterachiroptera:* Skirmuntt and Katzourakis, Virus Research, 270 (197645): 2. Publication date: 1 July 2018. (Lapsus).

TAXONOMY:

The suborder name follows the typified name used by Zagorodniuk *et al.* (1995) - Vespertiliiformes, Zagorodniuk (1997) - Vespertiliformes, Zagorodniuk and Pokynchereda (1997) - Vespertiliiformes, Zagorodniuk (1998a, 1998b and 1998c) - Vespertilioniformes, Zagorodniuk (1999, 2001a and 2001b, 2002, 2003a and b, 2004) - Vespertilioniformes and Hutcheon and Kirsch (2004b,2006) -

Vespertilioniformes, but with the ending changed to follow the format proposed for standardization of nomenclature of higher taxa by Alonso-Zarazaga (2005). '-formes' indicates ordinal level, while ending '-formi' indicates subordinal level.

Currently three Infraorders are recognized within the suborder VESPERTILIONIFORMI from Africa: **NOCTILIONIFORMACEI** Van Cakenberghe, Kearney and Seamark, 2007; **NYCTERIFORMACEI** Van Cakenberghe, Kearney and Seamark, 2007; **VESPERTILIONIFORMACEI** Van Cakenberghe, Kearney and Seamark, 2007.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Guan *et al.* (2025: 7) estimate that the split between the Vespertionoidae and Noctilionoidea occurred 54.20 mya;

FUNCTIONAL MORPHOLOGY:
Rydell *et al.* (2019: 1, 2) suggested that whitish wings (as found in 17 species of African emballonurid, vespertilionid and molossid bats) reduce the contrast against the sky and may prevent overheating in bats flying during the day. This would also enable the bats the leave their roosts earlier in the evening and returning later in the morning, allowing them to capture crepuscular and diurnal insects.

MOLECULAR BIOLOGY:
Genetics
Volleth (2010: 308) found no cytogenetic synapomorphy for Vespertilioniformes [= Vespertilioniformi], which indicates that this group has a monophyletic origin.

INFRAORDER NOCTILIONIFORMACEI Van Cakenberghe, Kearney and Seamark, 2007

*2007. *NOCTILIONIFORMACEI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Superfamily is based on *Noctilio* Linnaeus, 1766. (Current Combination).

TAXONOMY:
Currently a single superfamily is known from within the Infraorder NOCTILIONIFORMACEI for Africa: **NOCTILIONOIDEA** Gray 1821.

Superfamily NOCTILIONOIDEA J. E. Gray, 1821

*? *Noctilionoidea* - Comments: The name of the Superfamily is based on *Noctilio* Linnaeus, 1766. (Current Combination).

TAXONOMY:
The placement of the Family Myzopodidae, with in the superfamily Noctilionoidea follows Teeling *et al.* (2005).
Simmons *et al.* (2013: 145) include seven families: Myzopodidae, Mystacinidae, Thyropteridae, Furipteridae, Noctilionidae, Mormoopidae, and Phyllostomidae, which were already distinct by the end of the Eocene.

COMMON NAMES:
Czech: vampýrovci.

INFRAORDER NYCTERIFORMACEI Van Cakenberghe, Kearney and Seamark, 2007

*2007. *NYCTERIFORMACEI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Infraorder is based on *Nycteris* G. Cuvier and E. Geoffroy, 1797 (type Family NYCTERIDAE Van der Hoeven, 1855). (Current Combination).

GENERAL COMMENTS:
We followed the format proposed for standardization of nomenclature of higher taxa by Alonso-Zarazaga (2005), then for typified names this would be standardized, using the connector -acei and the ending -iformacei. But, for those without typified names there may well be occasions where incertae-sedis is used.

TAXONOMY:
Currently a single superfamily is known from within the Infraorder NYCTERIFORMACEI for Africa: **NYCTEROIDEA** Van der Hoeven, 1855.

Superfamily NYCTEROIDEA Van der Hoeven, 1855

*1855. *Nycteroidea* Van der Hoeven. - Comments: The Superfamily name is based on *Nycteris* G. Cuvier and E. Geoffroy, 1797 (type Family NYCTERIDAE Van der Hoeven, 1855). (Current Combination).
2005. *Emballonuroidea* Teeling, Springer, Madsen, Bates, O'Brien and Murphy, Science, 307: 581.
2025. *Emballonuridea:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: 1. Publication date: 18 July 2025. (Lapsus).

GENERAL COMMENTS:

TAXONOMY:
This name is used contrary to the superfamily name EMBALLONUROIDEA (used by Teeling *et al.*, 2005, Ravel *et al.*, 2016: 377, and Amador *et al.*, 2016: 22) because the oldest typified name is *Nycteris* G. Cuvier and E. Geoffroy, 1795, rather than *Emballonura* Temminck, 1838 (or even Emballonuridae Gervais, 1855).

Family EMBALLONURIDAE Gervais, 1855

*1855. *Emballonuridae* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool, (Sec 7), Vol 1, pt 2 (Mammifères): 62 footnote. Publication date: 23 July 1855. - Comments: Type genus: *Emballonura* Temminck. . - Etymology: The name of this family is derived from the Greek "*ἐμβάλλω*", meaning to throw in and "*οὐρά*", meaning tail, referring to the tail structure of all its members, which resembles a spear thrown into the ground at an angle (see Palmer, 1904: 257; Taylor, 2005).
1866. *Brachyura* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 257. - Comments: Originally included the genera *Mystacina* J. Gray, 1843; *Noctilio* Linnaeus, 1766; *Taphozous* É. Geoffroy, 1818; *Emballonura* Temminck, 1838; *Diclidurus* Wied-Neuwied, 1820; and *Furia* F. Cuvier, 1828 [= *Furipterus* Bonaparte, 1837 [1832–1841] (see Jackson and Groves, 2015: 253). Pavlinov *et al.* (1995: 74) mentioned it "In part". Simmons (*pers. comm.*): "This name is a tough one, no type genus was noted and taxa now placed in 5 families were included. I have left it out because it is not clear just what it would be a junior synonym of. There seems no point in restricting it since it is not the oldest name for any of the family groups now recognized. Fixed".
1866. *Diclidurina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 92. Publication date: 1 February 1866.
1866. *Emballonurina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 92. Publication date: 1 February 1866. - Comments: Type genus: *Emballonura* Temminck, 1838. Proposed as tribe, and originally including the genera *Urocryptus* Temminck, 1838 [= *Saccopteryx* Illiger, 1811]; *Diclidurus* Wied-Neuwied, 1820; *Saccopteryx* Illiger, 1811; *Emballonura* Temminck, 1838; *Proboscidea* Spix, 1823 [= *Rhynchonycteris* Peters, 1867]; *Centronycteris* J. Gray, 1838; and *Furia* F. Cuvier, 1828 [= *Furipterus* Bonaparte, 1837 [1832–1841] (see Jackson and Groves, 2015: 253).
1875. *Emballonuridae* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (95): 349. Publication date: 1 November 1875. - Comments: Type genus: *Emballonura* Temminck, 1838. Originally included the subfamilies Emballonurinae Gervais, 1855 and Molossinae Gervais, 1855 (see Jackson and Groves, 2015: 253).
1893. *Emballonurini* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 24. - Comments: Proposed as tribe (?), and originally including the genera *Mosia* J. Gray, 1843; *Emballonura* Temminck, 1838; *Coleura* Peters, 1867; *Saccopteryx* Illiger, 1811; *Rhynchonycteris* Peters, 1867; *Vespertiliavus* Schlosser, 1887; *Diclidurus* Wied-Neuwied, 1820; and *Taphozous* É. Geoffroy, 1818 (see Jackson and Groves, 2015: 253).
1907. *Diclidurinae* Miller, Bull. U.S. natl. Mus., 57: 94. Publication date: 29 June 1907. - Comments: Type genus: *Diclidurus* Wied, 1819.
1928. *Emballonuroidea* Weber, Die Säugetiere, 154. - Comments: Originally included the families Rhinopomatidae Bonaparte, 1838, Emballonuridae Gervais, 1855 and Noctilionidae J. Gray, 1821. Jackson and Groves (2015: 253) considered this name a synonym of the Emballonuridae.
2013. *Emballanuridae:* Taylor, Sowler, Schoeman and Monadjem, S. Afr. J. Wildl. Res., 43 (1): 18. Publication date: April 2013. (Lapsus).

TAXONOMY:
Koopman (1993a: 156) mentions Gervais, 1856 as author, whereas Corbet and Hill (1992: 83) mention Dobson, 1875e: 349. Simmons (2005) and Uvizl *et al.* (2019: 23) recognise two subfamilies: Emballonurinae (including the African genera *Coleura* and *Emballonura*), and Taphozoinae (including the African genera *Saccolaimus* and *Taphozous*). Goodwin (1942: 120) considers Diclidurinae to be a valid subfamily. Uvizl *et al.* (2019: 23), however, recognize the New World representatives of the Emballonurinae as differing on tribe level from the Old World forms: Diclidurini versus Emballonurini.

Cytogenetic investigations by Volleth *et al.* (2020b: 268) led them to support the suggestion made by Ruedi *et al.* (2012: 210) that the Emballonurinae and Taphozoinae should be elevated to family rank, although neither of them do this explicitly. However, Kruskop and Artyushin (2021: 119) do mention them explicitly, referring to analogy with other taxa in the order (p. 118).

The discovery of the Late Middle Miocene *Afrillonura namibensis* by Rosina and Pickford (2021: 1), as well as the presence of other fossile taxa, led them to support the hypothesis that the Emballonuridae are African in origin. Additionally (p. 9), the similarity in dental characters between *Afrillonura* and the insular forms *Coleura seychellensis* and *Paremballonura atrata* suggests that the origin of the latter two lineages is to be found on the African continent.

Currently, Simmons and Cirranello (2024b) do not recognize extant subfamilies, tribes, subtribes, and genera, but they do mention the following species:
- Emballonurinae Gervais, 1855:
Diclidurini Gray, 1866:
Diclidurina Gray, 1866: *Balantiopteryx* Peters, 1867; *Cormura* Peters, 1867; *Cyttarops* Thomas, 1913; *Diclidurus* Wied-Neuwied, 1820; *Peropteryx* Peters, 1867.
Saccopterygina Lim, 2007: *Centronycteris* Gray, 1838; *Rhynchonycteris* Peters, 1867; *Saccopteryx* Illiger, 1811.
Emballonurini Gervais, 1855: ***Coleura*** Peters, 1867; *Emballonura* Temminck, 1838; *Mosia* Gray, 1843; ***Paremballonura*** Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, 2012.
- Taphozoinae: ***Saccolaimus*** Temminck, 1838; ***Taphozous*** E. Geoffroy, 1818.

COMMON NAMES:
Castilian (Spain): Murciélagos de cola envainada. Czech: pochvorepovití, netopýři hladkonosí, embalonurovití. Dutch: Schedestaartvleermuizen. English: Sheath-tailed Bats, Tomb Bats, Sac-winged Bats. Finnish: Hautalepakot. French: Emballonuridés, Taphiens. German: Flattnasenfreischwänze, Sackflügel-Fledermäuse, Glattnasen-Freischwänze. Italian: Emballonùridi. Norwegian: Frihalete flaggermus, gravflaggermus. Russian: Футлярохвостые. Vietnamese: Họ dơi bao.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The Emballonuridae are known from the early Miocene (Butler and Hopwood, 1957; Butler, 1969; 1978).
The stem and crown ages for this family were reported as 52.8 and 47.7 MYA by Shi and Rabosky (2015: 1537), and 51 and 45 MYA by Amador *et al.* (2016: 22).

Ravel *et al.* (2016: 416) indicate that *Chambinycteris pusilli* is the most basal taxon of this family.

PARASITES:
The Old World Emballonuridae are host for the genus *Ugandobia* (Acari: Myobiidae), containing nine species (Fain, 1994: 1280). Two additional species were described from Hipposideridae and Pteropodidae, but Fain (1994: 1280) suggests this was due to contamination of the jars in which they were found, and that the representatives of this genus are actually restricted to the Emballonuridae.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 8 % of the species belonging to this family are confirmed viral carriers.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Africa.

Subfamily Emballonurinae Gervais, 1855

*1855. *Emballonurinae* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud. Zool. (Sec. 7), Vol. 1, pt. 2 (Mammifères), 62, footnote. Publication date: 23 July 1855.

TRIBE Emballonurini Gervais, 1855

*1855. *Emballonurini* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool. (Sec. 7), Vol. 1, pt. 2 (Mammifères), 62, footnote. Publication date: 23 Juny 1855.

†Genus ***Afrillonura*** Rosina and Pickford, 2021

*2021. *Afrillonura* Rosina and Pickford, Hist. Bio., xxx: 1, 4. Publication date: 14 September 2021. - Etymology: The name is derived from "Africa" and the ast three syllables of the genus name of *Emballonura* Temminck, 1838 (Rosina and Pickford, 2021: 4).

TAXONOMY:
This genus currently includes one species: ***Afrillonura namibensis*** Rosina and Pickford, 2021.

Rosina and Pickford (2021: 9) suggest that *Afrillonura* probably represent an ancestral line of the Emballonurini, which might have led to the present day *Coleura* and *Paremballonura*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Remains of this genus were found in layers of Late Middle Miocene age (12 - 13 Mya).

ROOST:
Based on the large amount of fossil remains found in the Berg Aukas I site, Rosina and Pickford (2021: 9) suggest that this species most probably inhabited caves and/or karst fissure roosts.

†***Afrillonura namibensis*** Rosina and Pickford, 2021

*2021. *Afrillonura namibensis* Rosina and Pickford, Hist. Bio., xxx: 1, 4, figs 1, 2. Publication date: 14 September 2021. Type locality: Namibia: SE part of Otavi Mountains, ca. 20 km E Grootfontein: Berg Aukas I, [19 30 58 S 18 15 10 E]. Holotype: NESM BA I 52 94Ch3. - Etymology: Referring to Namibia, where the type material of this species was found. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Middle Miocene (Morgan and Czaplewski, 2023: 167).

GENERAL DISTRIBUTION:
Namibia (Morgan and Czaplewski, 2023:167).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Namibia.

Genus ***Coleura*** Peters, 1867

*1867. *Colëura* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 479. - Comments: Type species: *Emballonura afra* Peters. - Etymology: From the Greek "*κολεόν*" (coleon), meaning "sheath, scabbard" and "*οὐρά*" (ūrá), meaning tail, referring to the tail being enveloped in the interfemoral membrane as far as the last caudal vertebra (see Palmer, 1904: 195; Lanza *et al.*, 2015: 201).
1939. *Coleura:* Allen, Bull. Mus. comp. Zool., 83: 65. (Current Spelling).
2018. *Coelura:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Lapsus).

TAXONOMY:
Key provided in Dunlop (1997, Mammalian Species, 566).

Uvizl *et al.* (2019: 28) indicated that *C. afra* separated some 6.3 mya from the two other extant species, and the separation between the Djibouti-Arabian group and the mainland Tanzanian group occurred some 3.8 mya.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Coleura*: ***afra*** (Peters, 1852); ***gallarum*** Thomas, 1915; ***kibomalandy*** Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, 2012; ***seychellensis*** Peters, 1868. Additionally, there is also the extinct ***†muthokai*** Wesselman, 1984.

COMMON NAMES:
Czech: buldočí pochvorepi. English: Sheath-tailed bats, Peters's sheath-tailed bats. French: Chauves-souris à queue gainée. German: Schiebeschwanz-Fledermäuse.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Ethiopia, Kenya, Tanzania.

Coleura afra (Peters, 1852)

*1852. *Emballonura afra* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 51, pl 12, pl 13, fig 18, 19. Publication date: 1852. Type locality: Mozambique: Lower Zambesi River: Tete [16 10 S 33 35 E, 230 m]. [Goto Description]. Syntype: NHMUK 1907.1.1.703: ♀. See Turni and Kock (2008: 23). These latter specimens might possibly be the missing ZMB ones, but I did not find any proof of this (Van

Cakenberghe, *pers com*). Syntype: RMNH MAM.27333. Syntype: ZMB 429. See Turni and Kock (2008: 23) [missing]. Syntype: ZMB 430. See Turni and Kock (2008: 23) [missing]. Syntype: ZMB 54845: skull and alcoholic. (Skull damaged) see Turni and Kock (2008: 23). Syntype: ZMB 571a: ♂, skull and alcoholic. see Turni and Kock (2008: 23). Syntype: ZMB 571b: ♀, skull and alcoholic. see Turni and Kock (2008: 23). Syntype: ZMB 67559: skull and alcoholic. See Turni and Kock (2008: 23). Syntype: ZMB 67561: skull and alcoholic. See Turni and Kock (2008: 23). Syntype: ZMB 67562: skull and alcoholic. See Turni and Kock (2008: 23). Syntype: ZMB 85667: ♂, complete skeleton. See Turni and Kock (2008: 23). Syntype: ZMB 85668: skin only. See Turni and Kock (2008: 23). Syntype: ZMB 85669: ♀. See Turni and Kock (2008). - Etymology: From the feminine Latin adjective *àfra* meaning "African" (see Lanza *et al.*, 2015: 156).

1915. *C[oleura] g[allarum] nilosa* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 576, 577. Publication date: 1 June 1915. Type locality: Sudan: Upper Nile: Bahr-el-Zeraf, near mouth of [ca. 14 42 N 31 14 E]. [Goto Description]. Holotype: NHMUK 1915.3.6.76: ad ♂, skin only. Collected by: Willoughby P. Lowe; collection date: 3 February 1914; original number: 77. - Comments: Thorn *et al.* (2009: 41), however, mention 09 25 N 31 10 E for the coordinates. May be valid as a subspecies (Kock, 1969a; Koopman, 1975). In the key presented in the original description on p. 576, the name is given as *C. g. nilosa*, on the description itself (p. 577) it is mentioned as *Coleura gallarum nilosa*. (Name Combination).

1939. *Coleura kummeri* Monard, Arq. Mus. Bocage, 10: 55, fig 1. Publication date: March 1939. Type locality: Guinea-Bissau: Madina Boé [11 45 N 13 13 W]. [Goto Description]. Syntype: MHNG 1326.003: ad ♀. Collected by: Dr. Albert Monard; collection date: 5 March 1938. Baud (1977: 203) mentioned the registration number as MHNG 1328.03, whereas Vallo *et al.* (2018: 74) mention it as MHNG 1326.03. The latter is within a series of bats collected by Albert Monard, so this is probably correct. Syntype: MHNG 861.057: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 5 March 1938; original number: 305. Syntype: MHNG 861.058: ♀, alcoholic (skull missing). Collected by: Dr. Albert Monard; collection date: 5 March 1938; original number: 305. Syntype: MNHN ZM-MO-1940-1209: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard. Mentioned as paratype by Rode (1941: 244) with numbers "201" and "1940-1209". This is either number 879, 884, 886 or 887 from Monard (1939: 55). Syntype: NMBA 5277: ad ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 5 March 1938; original number: 881. See https://www.nmbs.ch/home/en/museum/sammlungen/biowissenschaftlich/typenkataloge/saeugetiere.html. Syntype: NMBA 5278: ad ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 5 March 1938; original number: 890. See https://www.nmbs.ch/home/en/museum/sammlungen/biowissenschaftlich/typenkataloge/saeugetiere.html. Syntype: RMCA 15313: ad ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; original number: 883. - Comments: Monard (1939: 55) used 13 specimens and three skulls for the description on this taxon. The whereabouts of specimens 879 ♂, 880 ♀, 882 ♀, 884 ♂, 886 ♂, 887 ♂, 888 ♀, 889 ♂, 891 ♀, 892 (3 skulls) has not yet been determined, although one of the male specimens is the syntype in the Paris Museum.

? *Coleura afra afra:* (Name Combination).

? *Coleura afra kummeri:* (Name Combination).

? *Coleura afra nilosa:* (Name Combination).

? *Coleura afra:* (Current Combination).

? *Coleura gallarum nilosa:* (Name Combination).

Taxonomy:

See Dunlop (1997, Mammalian Species, 566). The recently discovered population in Madagascar could prove to be a distinct species (Goodman *et al.* (2005a).

Vallo *et al.* (2018: 73) investigated the genetic and morphological variation of various African and Arabian populations and found that specimens from Kenya, Tanzania and Ghana could be assigned to the nominotypical subspecies. The (smaller) specimens from Yemen and Gabon represented two different lineages. Morphologically, these seemed to correspond with *gallarum/nilosa* (NE Africa + Arabia) and *kummeri* (W Africa), but this was not confirmed by their molecular analyses. The analyses by Uvizl *et al.* (2019: 29) suggest that *Coleura afra* might represent a complex of species rather than one highly variable species.

Common Names:

Afrikaans: Skedestertvlermuis. Chinese: 非洲鞘尾蝠. Czech: pochvorep buldočí, netopýr buldočí. English: Southern Sheath-tailed Bat, African Sheath-tailed Bat, Sheath-tailed Bat, Mozambique Sheath-tailed Bat. French: Chauve-souris à queue gainée d'Afrique, Emballonure d'Afrique, Chauve-souris à queue en fourreau d'Afrique. German: Afrikanische Schiebeschwanz-Fledermaus. Italian: Còleura africàna. Portuguese: Morcego de cauda.

Etymology of common name:

The colloquial name refers to the peculiar situation of the tail, which is enclosed by the interfemoral membrane between the back legs (Taylor, 2005).

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dq; IUCN, 2009; Monadjem *et al.*, 2017n).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017n). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008dq; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004h; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not well understood. Disturbance of roost sites could potentially be a threat, but the effect of this on the population is not well known (Mickleburgh *et al.*, 2008dq; IUCN, 2009; Monadjem *et al.*, 2017n).

Kioko *et al.* (2015: 19) report a roadkill on the Arusha Highway (Tanzania).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dq) [in IUCN (2009)] and Monadjem *et al.* (2017n) indicate that on the African continent, there are no species-specific conservation measures in place, but there are some protected areas within its range. Both of the known sites for this species in Madagascar are within protected areas (the Ankarana Special Reserve and Namoroka National Park).

GENERAL DISTRIBUTION:
Coleura afra is found in much of east and eastern-central Africa, with an isolated record from central Mozambique. It is also found in West Africa, with records from Guinea and Guinea Bissau, Sierra Leone, northern Côte d'Ivoire, Ghana, Togo, Benin, and western Nigeria. There is also a small distribution in western Angola. This species was recently discovered in Madagascar (Goodman *et al.*, 2005a) and is known only from the Ankarana Special Reserve in the north of the island and the Namoroka National Park in the west.

Harrison (1967: 166) reported a specimen collected in the Strait of Bab el Mandeb, at the southern approach of the Red Sea. However, this might represent *C. gallarum*.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 535; Taylor *et al.*, 2018b: 62); Benin; Burkina Faso (Kangoyé *et al.*, 2012: 6024; 2015a: 614); Cameroon (Lebreton *et al.*, 2014: 2); Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire; Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Ghana; Guinea; Guinea-Bissau (Monard, 1939; Rainho and Ranco, 2001: 39); Kenya; Madagascar (Goodman *et al.*, 2005a); Mozambique Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 535) ; Nigeria (Happold, 1987); Sierra Leone (Weber *et al.*, 2019: 25 - first record); Somalia; Sudan; Tanzania (including the island of Pemba [see O'Brien, 2011: 287]); Togo (Capo-Chichi *et al.*, 2004: 161); Uganda.

Presence uncertain: Burundi; Rwanda.

Possibly extinct: Congo (Mickleburgh *et al.*, 2008dq; IUCN, 2009).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Lucati and López-Baucells (2016: Suppl.) report on a piebald (all-white fur/skin patches, eyes always normally coloured) specimen from a cave in Kenya (https://www.inaturalist.org/observations/877909).

DETAILED MORPHOLOGY:
Brain
Based on three brains from Kenya, using immunohistochemical methods, Kruger *et al.* (2010a) describe the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems, and Kruger *et al.* (2010b) also describe the distribution of Orexin-A immunoreactive cell bodies and terminal networks.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wingspan of 3 cm and a body mass of 12 g.

SEXUAL DIMORPHISM:
Kangoyé *et al.* (2015a: 614) confirm the sexual dimorphism found by Goodman *et al.* (2008b): in both body and cranial measurements, the females are larger than the males.

ECHOLOCATION:
Musila *et al.* (2018c: 43) [referring to Monadjem *et al.* (2010d: 246)] mention a narrow band, low-duty pulse call, composed of constant frequency, with peak frequency of 32.9 kHz and a bandwidth of 2.4 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats, 2 calls): F_{peak}: 34.2, 31.2 kHz and duration: 10.7, 7.7 ms.

See also Pye (1980) and Taylor *et al.* (2005).

MOLECULAR BIOLOGY:
Karyotype
Robbins (1983b: 35) reported 2*n* = 38 and FN = 68.

HABITAT:
In Nigeria, the African sheath-tailed bat is found in localised rocky habitats in southern Guinea savanna (Happold, 1987). Rosevear (1965) stated that they occur in woodland but only where there are acceptable roosting places. It is likely that other colonies occur in suitable rocky habitats in the southern Guinea savanna of western Nigeria (Mickleburgh *et al.*, 2008dq).

On Madagascar this bat taxon appears to be more varied in its habits, with some roost sites typically very dark and others quite close to the cave entrance. The two known sites on Madagascar are within dry deciduous tropical forest on a karst substrate (Goodman *et al.*, 2005a).

ROOST:
On mainland Africa, the African sheath-tailed bat is found in well illuminated caves, rocky crevices and cellars of houses (Rosevear, 1965). It preferentially roosts in caves along the sea and lake shores (Kingdon, 1974).

Lebreton *et al.* (2014: 2) report on a colony of about 5,000 specimens roosting in a cave in a rocky, forest-covered hill in Cameroon, which was also occupied by *Rousettus aegyptiacus*. Kangoyé *et al.* (2015a: 614) observed thousands of individuals in a cave on a hill at Néguéni, Burkina Faso.

MIGRATION:
Some authors suggest that *Coleura afra* migrates (Happold, 1987; Skinner and Smithers, 1990).

DIET:
Altringham (2011: 125) mentioned reports of *C. afra* returning to their roost with cheek pouches filled with insects, probably to feed their young

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Dark chanting goshawk (*Melierax metabates* Heuglin, 1861) as diurnal avian predator.

POPULATION:
Structure and Density
In the African portion of *Coleura afra* distribution, it roosts in large colonies (in the 1,000s of animals) (Mickleburgh *et al.*, 2008dq; IUCN, 2009; Monadjem *et al.*, 2017n). The population and local abundance of this species in Madagascar is not known, but there is a minimum estimate of 500 individuals in one cave complex in Ankarana, Madagascar.

Trend
2016: Unknown (Monadjem *et al.*, 2017n). 2008: Unknown (Mickleburgh *et al.*, 2008dq; IUCN, 2009). 2004: Unknown (Mickleburgh *et al.*, 2004h; IUCN, 2004).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 113) indicates that *C. afra* is monoestrous in parts of their range and polyoestrous in others. McWilliam (1987b) observed that this species has two reproductive cycles per year in Kenya. He also showed that early postnatal growth rates in *C. afra* were higher during the short rainy season than during the long rainy season which followed an extended dry period. This can be attributed to the poor condition of females following a pregnancy when food resources were low.

MATING:
Webber *et al.* (2017: Suppl.) indicate that this species has a polygyny mating system.

PARASITES:
BACTERIA
Bartonellae
Bartonella
Kosoy *et al.* (2010: 1877), Bai and Kosoy (2012: 58) and Stuckey *et al.* (2017: 23) reported a prevalence of *Bartonella* spp. In *C. afra* from Kenya of 4/9 (44.4 %) cultured from blood samples. Four genotypes of *Bartonella* spp. Identified in *C. afra* differed slightly from one another but clustered tightly within a genogroup (Kosoy *et al.*, 2010: 1878). See also Kosoy (2010: 719) for further information.

ACARI
Fain (1959c: 249, 254) described *Chirnyssus africanus* (Sarcoptidae) from a *C. afra* specimen collected on Mount Wago, near Bukwa, Haut-Ituri, DRC and from a "*Coleura gallarum*" from Moba, DRC. In a subsequent paper, Fain (1959e: 150, 159) described *Notoedres (Notoedres) benoiti* (Sarcoptidae) from the same hosts and localities.

Bochkov and Fain (2003: 9) mentioned that *C. afra* is the type host for *Ugandobia ituriensis* Fain, 1972 (Myobiidae).

HEMIPTERA
Polyctenidae
Eoctenes coleurae Maa, 1964 from Sudan (Haeselbarth *et al.*, 1966: 16, host as *Coleura gallarum*).
Eoctenes intermedius (Speiser, 1904) (Szentiványi *et al.*, 2022: 4).

DIPTERA
Streblidae
Raymondia huberi Frauenfeld, 1856 from Mozambique and Ethiopia (Haeselbarth *et al.*, 1966: 102; Shapiro *et al.*, 2016: 254). *Raymondi seminuda* Jobling, 1954 from Tanzania (Jobling (1954) in Haeselbarth *et al.* (1966: 104)).

Nycteribiidae
Penicillidia fulvida (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114, host as *Coleura gallarum*; Obame-Nkoghe *et al.*, 2016: 5, Gabon; Verrett *et al.*, 2022: 8, Kenya); *Nycteribia schmidlii scotti* Falcoz, 1923 (Obame-Nkoghe *et al.*, 2016: 5, Gabon), which was infected by the blood parasite *Polychromophilus melanipherus* (Szentiványi *et al.*, 2019a; Suppl.). These two flies were also mentioned by Dick *et al.* (2023).

VIRUSES:
Conrardy *et al.* (2014) tested 2 individuals from Kenya for the presence of adenoviruses, rhabdoviruses and paramyxoviruses, none of which tested positive. Maganga *et al.* (2014b) tested 94 *C. afra* samples collected from the Belinga caves of Gabon of which 14 tested positive to an unclassified paramyxovirus named Belinga bat virus (BelPV), one individual presented with haemorrhagic legions at necropsy.

In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Coleura afra*: Adenoviruses, Astroviruses, Paramyxoviruses.

Coronaviridae - Coronaviruses
SARS-CoV
During February 2008, Pfefferle *et al.* (2009) tested 33 faecal samples from two localities in Ghana, and these were negative for coronavirus (CoV) RNA. None of the 85 Kenyan bats tested by Tao *et al.* (2017: Suppl.) were positive for CoV.

Flaviviridae
Pegivirus
Nieto-Rabiela *et al.* (2019: Suppl.) reported the presence of the non-Zoonotic Bat Pegivirus.

Nairoviridae
Orthonairovirus
Six out of 14 *C. afra* specimens from Gabon tested by Müller *et al.* (2016: 3) were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridiae
Drexler *et al.* (2012a: 4) report that morbili-related viruses found in *Myotis myotis* in Germany were also found in one *Coleura afra* specimen from Ghana (out of 96 examined).

Maganga *et al.* (2014b) described a new Paramyxovirus (Belinga bat virus, BelPV) from 14 *C. afra* specimens from the Belinga caves (Gabon). One of these bats died due to several haemorrhagic lesions. None of the other bat species inhabiting the same caves were infected by this virus (*Hipposideros* cf. *ruber, Hipposideros gigas, Miniopterus inflatus, Rousettus aegyptiacus, Rhinolophus alcyone*).

Picornaviridae
Hepatovirus
Zeghbib *et al.* (2019: Suppl.) mention this virus from a bat from Ghana.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 30 Kenyan *C. afra* specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

In their overview table, Maganga *et al.* (2014a: 8) reported that the following viruses were already found on *C. afra*: Morbillivirus unclassified. Fagre and Kading (2019: 4) also reported that serologic evidence was found for Crimean-Congo Haemorrhagic Fever Virus (CCHF).

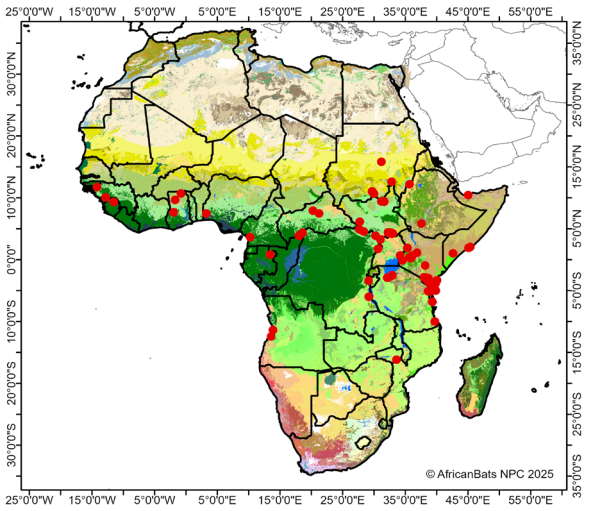

Figure 138. Distribution of *Coleura afra*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Mozambique, Nigeria, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, Uganda.

Coleura gallarum Thomas, 1915

*1915. *C[oleura] gallarum* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 576, 577. Publication date: 1 June 1915. Type locality: Somalia: Zeyla [=Zsyla]. [Goto Description]. Holotype: NHMUK 1911.8.2.4: ad ♀. Collected by: Dr. Ralph Evelyn Drake-Brockman; collection date: 29 October 1910; original number: 336. Presented/Donated by: Dr. Ralph Evelyn Drake-Brockman. - Comments: In the key presented in the original description on p. 576, the name is given as *C. gallarum*, on the description itself (p. 577) it is mentioned as *Coleura gallarum*. (Current Combination).

? *Coleura afra gallarum:* (Name Combination).

TAXONOMY:
A phylogenetical analysis by Uvizl *et al.* (2019: 30) indicated that the cyt-*b* of the Arabian-Djiboutian lineage of "*Coleura afra*" differed by 5.0 to 6.3 %, which is similar to the distance between *C. seychellensis* and *C. kibomalandy*. This led these authors to raise *gallarum* in rank from subspecies to full species.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: southern Yemen, Oman, Djibouti, north-western Somalia, and eastern Sudan (see Uvizl *et al.*, 2019: 30).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
Dick *et al.* (2023: 77) mentioned the nycteribiid fly *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) has been found on *Coleura gallarum*.

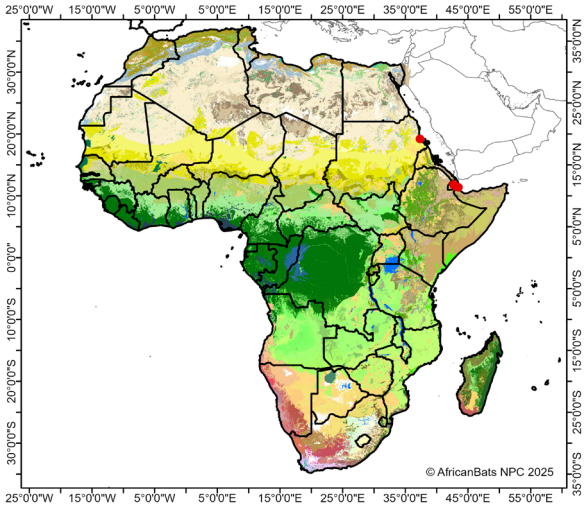

Figure 139. Distribution of *Coleura gallarum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Djibouti, Somalia, Sudan.

Coleura kibomalandy Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, 2012

*2012. *Coleura kibomalandy* Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, J. Mamm., 93 (6): 1442, 1446, figs 3, 4. Publication date: December 2012. Type locality: Madagascar: Antsiranana province: Ankarana National Park, 2.2 km ESE Amboandriky: Ambatoharanana cave (Crocodile cave) [12.98838S 49.02178E, 20 m]. Holotype: FMNH 213598: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman and Martinus Corrie Schoeman; collection date: 2 November 2010; original number: SMG 16954. Paratype: FMNH 183864: ♀, skull and alcoholic. Paratype: FMNH 183865: ♂, skull and alcoholic. Paratype: FMNH 183866: ♂, skull and alcoholic. Paratype: FMNH 183867: ♀, skull and alcoholic. Paratype: FMNH 183907: skull only. Collected by: Scott G. Cardiff. Paratype: FMNH 213591: ♀, skull and alcoholic. Paratype: FMNH 213592: ♀, skull and alcoholic. Paratype: FMNH 213593: ♀, skull and alcoholic. Paratype: FMNH 213594: ♀, skull and alcoholic. Paratype: FMNH 213595: ♀, skull and alcoholic. Paratype: FMNH 213596: ♂, skull and alcoholic. Paratype: FMNH 213597: ♂, skull and alcoholic. Paratype: FMNH 213599: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Martinus Corrie Schoeman. Paratype: FMNH 213600: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Martinus Corrie Schoeman. Paratype: FMNH 213601: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Martinus Corrie Schoeman. Paratype: FMNH 213602: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Martinus Corrie Schoeman. Paratype: FMNH 213603: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Martinus Corrie Schoeman. Paratype: UADBA 43497: ♂, alcoholic (skull not removed). Collected by: Richard K.B. Jenkins. - Etymology: The name *kibomalandy* is derived from a northern Malagasy dialect and means white (*malandy*) and belly (*kibo*) and

refers to this species' distinctive underside, which distinguishes it from other described species of *Coleura, Paremballonura*, and *Emballonura* (see Goodman *et al.*, 2012a: 1446). (Current Combination).

TAXONOMY:
Goodman *et al.* (2012a) described a new species of *Coleura* based on morphology and molecular data.

COMMON NAMES:
English: Madagascar Sheath-tailed Bat. French: Emballonure de Madagascar. German: Madagaskar-Schiebeschwanzfledermaus.

CONSERVATION STATUS:
Global Justification
Goodman *et al.* (2012a: 1449) suggest that this is a species of conservation concern due to its restricted distribution and its apparent limited number of individuals. While, Goodman (2017c) justify the Data Deficient status as this species is known from two sites in the western half of Madagascar, both within existing protected areas. Even though extensive bat surveys have been conducted in the region of one of these sites, vast areas of limestone karst remain largely unstudied in western Madagascar and we await further field data to properly assess this taxon.

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2016: DD ver. 3.1 (2001) (Goodman, 2017c).

Regional
None known.

MAJOR THREATS:
Threats to this species are currently unknown (Goodman, 2017c).

CONSERVATION ACTIONS:
Goodman (2017c) report that two sites this species is known from include the Ankarana National Park and Namoroka National Park.

GENERAL DISTRIBUTION:
This species is known from two sites on Madagascar: the Ankarana National Park and the Namoroka National Park.

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 57) described the baculum as a distinctly small structure, which, in dorsal view, has a sort of oblong shape. It is constricted along the mid-shaft and has a rounded tip that is smaller than the rounded basal portion. In lateral view, it tapers from the proximal to distal side, and it also is slightly constricted along the mid-shaft in this view. There is a slight hook to the tip. Length: 0.12 mm, width: 0.09 mm.

ECHOLOCATION:
Goodman *et al.* (2012a: 1448) mention the following parameters: low PF (< 35 kHz), narrow BW (< 7 ms), and short Dur (< 6 ms).

HABITAT:
Dammhahn and Goodman (2013: 108) indicate that the foraging habitat of this species is unknown, but probably is in open areas or in open forests.

ROOST:
This species roosts deep in limestone caves in colonies of up to 500 bats (Garbutt, 2022: 88; Goodman *et al.*, 2022: 1903).

PREDATORS:
Razakaratrimo *et al.* (2019: 114) mention the bat hawk (*Macheiramphus alcinus anderssoni* (Gurney, 1866)). This predator is also mentioned by Goodman *et al.* (2022: 1903), who also mention the barn owl (*Tyto alba* (Scopoli, 1769)).

POPULATION:
Structure and Density
Goodman *et al.* (2012a: 1449) indicate that in July 2004, there were about 500 animals in the Ambatoharanana cave, and that no information is available on the population in the other cave. Population size and trend is not known for this species (Goodman, 2017c).

Trend
2016: Unknown (Goodman, 2017c).

REPRODUCTION AND ONTOGENY:
Although the data are scarce, *C. kibomalandy* seems to reproduce twice a year (Goodman and Ramasindrazana, 2013 in Garbutt, 2022: 88).

Goodman *et al.* (2023b: 237) mention that ten bats collected in the Bemanavy Cave on 21 May 2016 and one on 3 November 2019 (5 ♂♂ and 6 ♀♀) showed no signs of breeding activity.

PARASITES:
BACTERIA
Gomard *et al.* (2016: 5) and Esteves *et al.* (2022: 8) reported the presence of *Leptospira* bacteria in one out of three tested bats.

VIRUSES:
Mélade *et al.* (2016b: 4) found Paramyxoviruses in two out of six *C. kibomalandy* specimens they tested.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

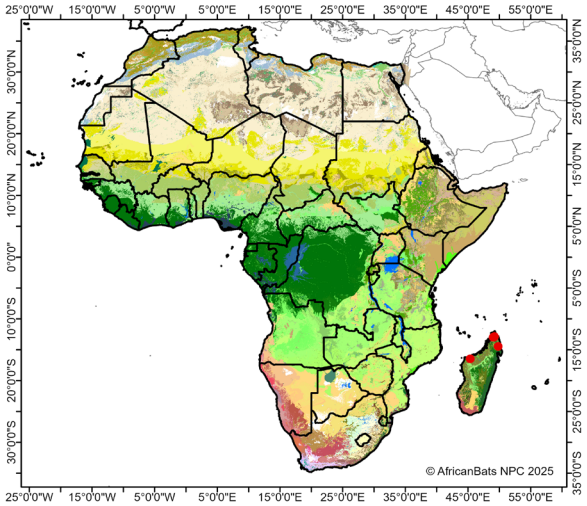

Figure 140. Distribution of *Coleura kibomalandy*.

†*Coleura muthokai* Wesselman, 1984

*1984. *Coleura muthokai* Wesselman, Contributions to vertebrate evolution, 7: 52. - Etymology: The taxon is named in honor of Muthoka, son of Kivingo, a Wakamba tribesman from Kikoko, Kenya, who worked with Henry ("Hank") Barnard Wesselman as his assistant during the field seasons of 1972 and 1973 (Wesselman, 1984: 52). (Current Combination).

TAXONOMY:
Closely resembles the extant and larger species *C. afra* (Wesselman, 1984; Lim, 2007).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late Pliocene (2.58 Mya) of southwestern Ethiopia (Lim, 2007, Brown *et al.*, 2019: Suppl.).

Coleura seychellensis Peters, 1868

*1868. *Coleura seychellensis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 367. Publication date: 1869. Type locality: Seychelles. Syntype: ZMB 3470a: ♂. Presented/Donated by: Prof. Edward Percival Wright. University of Dublin, see Turni and Kock (2008: 22). Syntype: ZMB 3470b: ad ♂. Presented/Donated by: Prof. Edward Percival Wright. University of Dublin, see Turni and Kock (2008: 22). Cotype: NHMUK 1869.2.19.2: ad ♂. See Thomas (1915b: 579); Turni and Kock (2008: 22) indicate that the NHMUK specimen can not be a (co-)type since Peters only used the ZMB specimens for his description, therefore they also reject Thomas' restriction of the type locality to Mahé Island. - Comments: Allen (1939a: 65) mentions "1869, for 1868". - Etymology: Referring to the island group where the species occurs. (Current Combination).

1915. *C[oleura] silhouettæ* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 576, 578. Publication date: 1 June 1915. Type locality: Seychelles: Silhouette Island. [Goto Description]. Holotype: NHMUK 1906.3.18.2: ad ♂, skin and skull. Collected by: Prof. J. Stanley Gardiner. Presented/Donated by: Prof. J. Stanley Gardiner. - Comments: In the key on page 576 mentioned as *C. silhouettæ*, and in the description on p. 578 as *Coleura silhouettæ*.

TAXONOMY:
Two subspecies are recognized *Coleura seychellensis seychellensis* from Mahé and Praslin, and *C. s. silhouettae* from Silhouette and La Digue (Hill, 1971a: 575; Rocamora and Joubert, 2004; Simmons, 2005).

COMMON NAMES:
Creole: Sousouri banann. Czech: pochvorep seychelský, netopýr seychelský. English: Seychelles Sheath-tailed Bat. French: Chauve-souris à queue gainée des Seychelles, Emballonure des Seychelles, Chauve-souris à queue en fourreau des Seychelles. German: Seychellen Schiebeschwanz-Fledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Critically Endangered (CR C2a(i) ver 3.1 (2001)) because its population size is estimated to number fewer than 250 mature individuals, with no subpopulation greater than 50 individuals, and it is experiencing a continuing decline (Gerlach *et al.*, 2008; IUCN, 2009; Jones *et al.*, 2009b: 506). Bambini *et al.* (2005) reported that the bats may have become extinct on the island of Praslin within the first five years of the 21th century. While Mondajem *et al.* (2017da) report that the roosting cave at La Passe contained just 32 individuals in 2003, but

more recently only 27 individuals were recorded there.

The mathematical predictor-rich model developed by Welch and Beaulieu (2018: 10) placed *Coleura seychellensis* in the seventh position of the top ten worldwide bat species at risk of extinction.

Assessment History
Global
2016: CR C2a(i) ver 3.1 (2001) (Mondajem *et al.*, 2017da). 2008: CR C2a(i) ver 3.1 (2001) (Harrison and Lewis, 1961; IUCN, 2009). 2004: CR C2a(I,ii) ver 3.1 (2001) (IUCN, 2004; Mickleburgh *et al.*, 2004g). 2002: CR B1+2cde, C2b, D (Mickleburgh *et al.*, 2002a). 1996: CR (Baillie and Groombridge, 1996). 1994: EN (Groombridge, 1994). 1993 - EN (World Conservation Monitoring Centre, 1993). 1990: EN (IUCN 1990). 1988: EN (IUCN Conservation Monitoring Centre 1988).

Collen *et al.* (2011: 2615) put this species on position 26 of their top 100 mammals that need urgent conservation attention on the basis of a combination of high Evolutionary Distinctiveness (ED) and high threat status.

Regional
None known.

MAJOR THREATS:
Gerlach (2004) reports that the most catastrophic decline of this species probably occurred in the late 1800s and early 1900s when lowland forests were cleared, converting the mosaic of woodland and open gaps to intensively managed coconut plantations with no shrub layer to support the invertebrate diet of this species. Invasive plants including the Kudzu vine (*Pueraria phaseoloides*) and coconut scrub from abandoned plantations threaten remaining suitable habitat for this species. Kudzu vine threatens to overgrow roost cave entrances or to change the temperature gradient within caves (Gerlach and Taylor, 2006). Senior *et al.* (2007: 9) also added that - upon leaving their roosts - all the bats follow the same route, which follows the line with the least vegetation cover. Any encroachment of vegetation will make entry and exit to the roosts more difficult and could be a reason for roost abandonment. The species is sensitive to disturbance of roosting caves and this remains a threat to any active roost sites. Other suggested threats have been the predation of bats by the barn owl, *Tyto alba*, introduced in 1949, and feral cats (Gerlach *et al.*, 2008; IUCN, 2009). Burgess and Lee (2004: 69) mention that pesticide contamination is probably not a significant threat.

CONSERVATION ACTIONS:
Gerlach *et al.* (2008) [in IUCN (2009)] and Mondajem *et al.* (2017da) report that Rocamora and Joubert (2004) recommend annual census of individuals along established transects; regular sensitive visits to all known roosting localities with additional surveys to locate any additional sites; re-evaluation of the species distribution every three or four years; legal protection of all known roosting sites and their immediate surroundings; control of introduced predators (barn owl *Tyto alba* and cats); habitat protection within known feeding areas; public awareness campaigns; ongoing and additional research into the distribution, ecology and threats to this species. Gerlach and Taylor (2006) also outline the importance of removing invasive vegetation from existing and abandoned roost sites, and restoring lowland forests through the control of coconut and cinnamon, and replanting native vegetation.

GENERAL DISTRIBUTION:
This species is endemic to the Seychelles, and is currently found on the islands of Silhouette, Mahé (in the northwest of the island) and Praslin. It is thought to have become extinct on La Digue island and Praslin since 1980s (Gerlach *et al.*, 2008). Senior *et al.* (2007: 3), however, indicated that these bats were only found on Silhouette and Mahé, and that they were last seen on Praslin in 2001 and on La Dique in 1976.

The Zanzibar record is extremely dubious (Simmons, 2005).

Native: Seychelles,
Presence uncertain: Zanzibar.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 8.1 Pa, aspect ratio 6.5 for a wingspan of 29 cm and a wing area of 126 cm^2 and a body mass of 10 g.

SEXUAL DIMORPHISM:
Nicoll and Suttie (1982) [in Ball (2004: 136)] indicate that females are almost 10 % heavier than males: 10.2 grams versus 11.1 grams.

ECHOLOCATION:
Burgess and Lee (2004: 72) report ultrasounds of 28 to 29 kHz, produced when flying in and out the entrances of their roosting caves. Inside the caves, sounds with a frequency between 24 and 26 kHz were produced. However, Clark (2004: 77) mentions sounds at around 30 - 40 kHz. Joubert (2004: 58) indicates that two harmonic bands are present: one at 40 kHz and one at 25 - 30 kHz. Ball (2004: 136) mentions an

echolocation range from 20 to 50 kHz, but that it is usually around 30 kHz when flying within the roost.

HABITAT:
This species has been recorded from coastal boulder field caves with stable cool temperatures and access into native palm woodland or marsh habitat (Gerlach and Taylor, 2006).

ROOST:
It appears to need boulder caves with horizontal ceilings; low, stable temperatures; and clear cave flyways not obscured by vegetation (Gerlach and Taylor, 2006). Abandoned roosts have been recorded from all four islands in the species historical distribution. A detailed study of the roosting site at La Passe is provided by Burgess and Lee (2004).

DIET:
Joubert (2004: 61) reports the following percentage of prey eaten by *C. seychellensis*: Diptera (30.5 %), Hymenoptera (25 %), Lepidoptera (19.5 %), Coleoptera (22 %), and Hemiptera (3 %).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention *C. seychellensis* to be predated upon by *Falco* sp. and an unidentified species of diurnal avian predator.

POPULATION:
Structure and Density
The species was noted by Wright (1868) to be 'very common in the neighbourhood of the town of Port Victoria'. Joubert (2004) mentions that the species was seemingly still abundant up to the 1970s, and that the use of guano deposits as an indicator suggests that the magnitude of decline may have been as high as 90 %. The global population is now clearly very small, and although the precise number is not known, it is believed to be fewer than 100 mature individuals (Rocamora and Joubert, 2004; Gerlach *et al.*, 2008). The roosting cave at La Passe was recorded to contain 32 bats in total in 2003 (Gerlach, 2004; Gerlach *et al.*, 2008). More recently only 27 animals have been recorded roosting at this locality (Gerlach *et al.*, 2008), but Gerlach (2011: 54) mentioned that the size of this colony has increased to 40 in 2009, and that it split up in two parts of approximately 20 individuals in 2010, one remaining at La Passe and the second at Anse Lascars.

Senior *et al.* (2007: 16) indicate that the population might be higher than estimated IF this species has indeed a harem structure as was suggested by Nicoll and Suttie (1982) as non-harem males would not roost with mating groups. However, this might also have a negative influence due to greater levels of inbreeding.

Trend
2016: Decreasing (Mondajem *et al.*, 2017da). 2008: Decreasing (Gerlach *et al.*, 2008; IUCN, 2009). 2004: Decreasing (Mickleburgh *et al.*, 2004g; IIUCN, 2004).

ACTIVITY AND BEHAVIOUR:
Joubert (2004) and Gerlach and Taylor (2006) provide specific details on the ecological requirements of this rare species.

Smotherman *et al.* (2016: 537) refer to Gerlach (2009b) in describing the song-like structure for *C. seychellensis* as consisting of different syllable types in series.

REPRODUCTION AND ONTOGENY:
Nicoll and Suttie (1982) [in Krutzsch (2000: 113)] indicate that *C. seychellensis* is a polyoestrous species.

MATING:
Burgess and Lee (2004: 69) indicate that a harem structure might exist, but their observations were inconclusive.

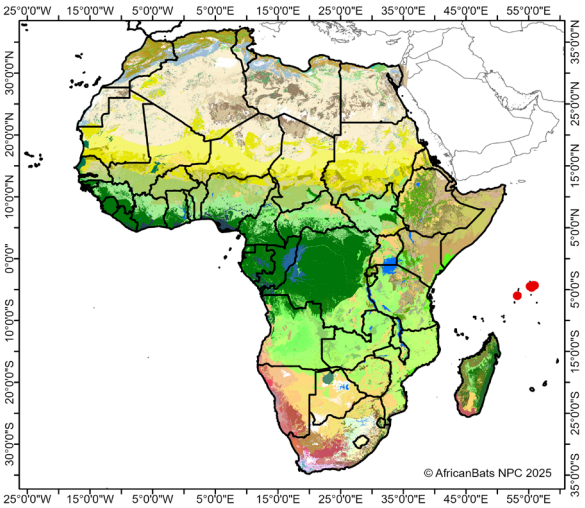

Figure 141. Distribution of *Coleura seychellensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Seychelles.

†Genus ***Dhofarella*** Sigé, Thomas, Sen, Gheerbrant, Roger and Al-Sulaimani, 1985

*1994. *Dhofarella* Sigé, Thomas, Sen, Gheerbrant, Roger and Al-Sulaimani, Munch. Geowiss. Abh, (A) 26: 35 - 48. - Comments: See Gunnell *et al.* (2008: 5).

TAXONOMY:
Morpholigally considered closer to *Taphozous* than to *Vespertiliavus* (Lim, 2007).

Based on morphological affinities, Rosina and Pickford (2021: 9) assigned this genus to the Emballonurinae, and the similarities with *Afrillonura* led them to conclude that the Oligocene *Dhofarella thaleri* has the most basal phylogenetic position within the tribe Emballonurini.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The oldest known emballonurid fossils from Africa. Early Oligocene age (33.9 Mya) (Lim, 2007).

Timeframe:
Late Eocene (Priabonian) - Early Oligocene (Rupelian) (33.9 Mya).

GENERAL DISTRIBUTION:
Oman (Sigé *et al.*, 1994; Lim, 2007).

†***Dhofarella sigei*** Gunnell, Simons and Seiffert, 2008

*2008. *Dhofarella sigei* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 5, fig 6. Type locality: Egypt: Fayum Depression: Quarry L-41: Lower Sequence, Jebel Qatrani Formation. Holotype: CGM 83670. A left dentary series m1-m3. - Etymology: Named for Bernard Sigé, in recognition of his many contributions to the study of Cenozoic bats (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Latest Eocene: Priabonian (37.97 - 33.23 mya), Lower Sequence, Jebel Qatrani formation.

Early Oligocene: Rupelian (32.46 - 29 mya) (see Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008; Morgan and Czaplewski, 2023: 167).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

†***Dhofarella thaleri*** Sigé et al., 1994

*1994. *Dhofarella thaleri* Sigé, Thomas, Sen, Gheerbrant, Roger and Al-Sulaimani, Munich. Geowiss. Abh, (A) 26: 35 - 48. Type locality: Oman. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Oligocene (see Lim, 2007).

Genus ***Paremballonura*** Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, 2012

*2012. *Paremballonura* Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, J. Mamm., 93 (6): 1445. Publication date: December 2012. - Etymology: From the Greek prefix *para-*, meaning close to or besides, and the genus *Emballonura* Temminck, 1838 (see Goodman *et al.*, 2012a: 1445).
2016. *Paraemballonura:* Amador, Moyers Arévalo, Almeida, Catalano and Giannini, J. mamm. Evolut., 25 (1): 43 (for 2018). Publication date: 24 November 2016. (Lapsus).

TAXONOMY:
Goodman *et al.* (2012a: 1440) found this genus to be paraphyletic, which resulted in the description of a new genus for the Malagasy *Emballonura* clade: *Paremballonura*. Uvizl *et al.* (2019: 29) estimate the separation between the two genera took place about 26.0 mya (Upper Oligocene).

Currently (Simmons and Cirranello, 2024b) recognized species of the genus of *Paremballonura*: ***atrata*** (Peters, 1874); ***tiavato*** (Goodman, Cardiff, Ranivo, Russell, and Yoder, 2006).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
There are fossil *Paremballonura* (referred to as *Emballonura*) of probable Pleistocene age (1.81 Mya) from Madagascar (McKenna and Bell, 1997; Lim, 2007).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Paremballonura atrata (Peters, 1874)

*1874. *Emballonura atrata* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 693. Type locality: Madagascar: "Interior of Madagascar". Holotype: ZMB 4692: ♀. Collected by: Alfred Crossley. See Dobson (1878: 363) and Peterson *et al.* (1995: 56). Goodman *et al.* (2006a: 19) mention that the assumption by Peterson *et al.* (1995) that J.M. Hildebrandt is the collector, is wrong. Instead, Alfred Crossley is the collector, and they also indicate that the type locality remains unclear.

2012. *Paremballonura atrata* Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, J. Mamm., 93(6): 1445. (Name Combination, Current Combination).

2016. *Paraemballonura atrata:* Amador, Moyers Arévalo, Almeida, Catalano and Giannini, J. mamm. Evolut., 25 (1): Suppl (for 2018). Publication date: 24 November 2016. (Lapsus).

TAXONOMY:
Following a recent taxonomic revision based on genetic and morphological comparisons, *Paremballonura atrata* is now confined to the east of Madagascar, with the smaller *P. tiavato* occurring in the west (Goodman *et al.*, 2006a). Reviewed by Peterson *et al.* (1995). *atrata* species group Simmons (2005: 388).

COMMON NAMES:
English: Madagascar sheath-tailed bat, Peter's Sheath-tailed Bat, Peters's Sheath-tailed Bat. French: Chauve-souris malgache à queue en fourreau, Emballonure de Madagascar, Emballonure de Peters. German: Madagaskar-Freischwanzfledermaus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Sabatier and Legendre (1985: 23) and Gunnell *et al.* (2014: 3) refer to fossils material from Tsimanampetsotsa, on Madagascar.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) because it is relatively widespread in eastern Madagascar and although its population is certainly decreasing as the humid forest is converted into agricultural areas there is no evidence that the decrease has been rapid enough to warrant Near Threatened or threatened status (Jenkins *et al.*, 2008d; IUCN, 2009; Monadjem *et al.*, 2017r).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017r). 2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008d; IUCN, 2009). 1996: VU A2c ver 2.3 (1994) (IUCN, 1996).

Regional
None known.

MAJOR THREATS:
Paremballonura atrata is collected by people for bushmeat in one part of eastern Madagascar (D. Andriafidison *pers comm.,* in Jenkins *et al.*, 2008d and Monadjem *et al.*, 2017r). Otherwise, forest clearance for expanding agriculture threatens the foraging and roosting sites for this species (Jenkins *et al.*, 2007b; Jenkins *et al.*, 2008d; IUCN, 2009; Monadjem *et al.*, 2017r). Jenkins *et al.* (2007b: 219) also point out that fire (started by farmers?) is a potential threat, as traces of fire were found at the entrances of their roosting caves.

CONSERVATION ACTIONS:
Jenkins *et al.* (2008d) [in IUCN (2009)] and Monadjem *et al.* (2017r) note that *P. atrata* has been recorded from Parc National de Mantadia (Randrianandrianania *et al.*, 2006) and Parc National de Midongy du Sud (Goodman *et al.*, 2006a) as well as from a network of protected sites around the Baie de Antogil (Goodman *et al.*, 2006a). It probably does not require specific conservation action as long as forest vegetation is protected, but local populations should be monitored at roosting sites (Jenkins *et al.*, 2008d; IUCN, 2009; Monadjem *et al.*, 2017r).

GENERAL DISTRIBUTION:
This species is restricted to the humid zone of eastern Madagascar and has been recorded from around Maroantsetra in the north to Tolagnaro (Fort Dauphin) in the south (Goodman *et al.*, 2006a). It is known from a wide elevational range, from as low as 30 m (Goodman *et al.*, 2006a) to at least 900 m (Randrianandrianania *et al.*, 2006).

Native: Madagascar (Goodman *et al.*, 2006a) - Ile Sainte-Marie (Rakotonandrasana and Goodman, 2007: 6).

DETAILED MORPHOLOGY:
Baculum
The baculum is small and circular in shape (Rakotondramanana and Goodman, 2017: 58); length: 0.09, 0.12 mm; width: 0.09, 0.12 mm.

ECHOLOCATION:
Kofoky *et al.* (2009: 379) reported the call from two individuals flown in a flight cage as FM/CF/FM with the most energy in the second harmonic at 52.9 kHz.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003) and Goodman *et al.* (2006a).

HABITAT:
It is considered to be dependent on relatively intact forest (Goodman *et al.*, 2005a; 2006a). However, Goodman *et al.* (2023b: 236) reported it was also found in *savoka* (regenerating secondary grassland), vanilla plantations and in rock shelters.

ROOST:
Paremballonura atrata is usually found roosting in caves and small crevices in or near to relatively intact humid forest (Goodman *et al.*, 2006a; Randrianandrianania *et al.*, 2006; Kofoky *et al.*, 2007; Jenkins *et al.*, 2007b). It has also been found below exposed tree roots (Garbutt, 2022: 87) and in drainage tunnels under roads (Goodman *et al.*, 2023b: 236).

DIET:
Based on droppings from five specimens, Rasoanoro *et al.* (2015: 64) report the following volume percentages of prey types: Coleoptera: 26.7 ± 8.09, Diptera: 40.9 ± 12.55, Hemiptera: 12.0 ± 1.16, and Hymenoptera: 31.3 ± 8.76. Goodman *et al.* (2023b: 237) [referring to Falimiarintsoa (2022)] mention: Hymenoptera (36.4 %), Diptera (21.0 %), Lepidoptera (18.2 %), Coleoptera (16.3 %), Hemiptera (8.1 %), and a few mites (Acaria) for fecal samples of 10 bats from the Sarahandrano site.

POPULATION:
Structure and Density
There is no information on population size. This species is rarely trapped in flight or detected acoustically and information on populations and distribution is mainly from bats found in caves (Jenkins *et al.*, 2008d; Monadjem *et al.*, 2017r). Colony size in caves rarely exceeds 20 individuals (Jenkins *et al.*, 2007b).

Trend
2016: Unknown (Monadjem *et al.*, 2017r). 2008: Unknown (Jenkins *et al.*, 2008d; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
A single young is born in November (Garbutt, 2022: 87).

Goodman *et al.* (2023b: 237) mention two females captured in mid to late October 2019 of which one carried an embryo of 12 mm, whereas the other did not show any signs of pregnancy. A male bat was non-reproductive. Of 13 females captured in early March - late April at Andatsakala, five were lactating and eight showed no signs of reproduction. Of the 38 males captured in the same period, six had slightly enlarged testicles and convoluted epididymes and 32 were not in reproductive condition Six females captured in Sarahandrano in late March to early April 2021 included two bats with small embryos, whereas the others did not show any signs of reproduction, neither did any of the seven males.

UTILISATION:
Paremballonura atrata is collected by people for bushmeat in one part of eastern Madagascar (D. Andriafidison *pers comm.* in Jenkins *et al.*, 2008d).

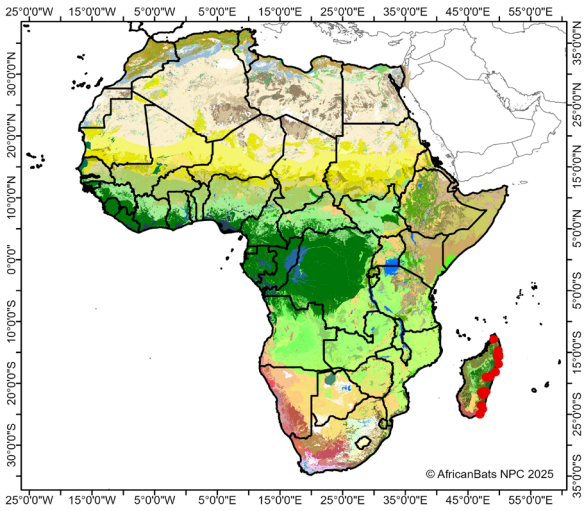

Figure 142. Distribution of *Paremballonura atrata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Paremballonura tiavato (Goodman, Cardiff, Ranivo, Russell and Yoder, 2006)

*2006. *Emballonura tiavato* Goodman, Cardiff, Ranivo, Russell and Yoder, Am. Mus. Novit., 3538: 1, 6, figs, 2, 3, 4, 5. Publication date: 19 October 2006. Type locality: Madagascar: Antsiranana province: Réserve Spéciale d'Ankarana, 2.6 km E Andrafiabe: Andrafiabe cave, in forest near [12 55.9 S 49 03.4 E, 50 m]. Holotype:

FMNH 169705: ad ♂, skin and skull. Collected by: Steven M. Goodman; collection date: 22 January 2001; original number: 11923a. - Etymology: From the Malagasy for "like rocks", referring to the tendency of this bat to occur in areas with exposed rock outcrops and caves (see Goodman *et al.*, 2006a: 6).

2012. *Paremballonura tiavato* Goodman, Puechmaille, Friedli-Weyeneth, Gerlach, Ruedi, Schoeman, Stanley and Teeling, J. Mamm., 93(6): 1445. (Name Combination, Current Combination).

2016. *Paraemballonura tiavato:* Amador, Moyers Arévalo, Almeida, Catalano and Giannini, J. mamm. Evolut., 25 (1): Suppl (for 2018). (Lapsus).

TAXONOMY:
Described as a new species in a split from "*Emballonura atrata*" (Goodman *et al.*, 2006a).

COMMON NAMES:
Czech: pochvorep madagaskarský. English: Western Sheath-tailed Bat, Rock-dwelling Sheath-tailed Bat, Rock-loving Sheath-tailed Bat. French: Emballonure des rochers, Emballonure rupestre. German: Tsingy-Freischwanzfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) because although this species is declining due to the impacts of ongoing forest loss due to shifting agriculture and logging the reduction of suitable habitat is not thought to be sufficient to warrant listing in a higher category of threat. However, this species is not abundant within its range and requires close population monitoring and a reassessment may be needed in the near future (Jenkins *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017s).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017s). 2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008e; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Paremballonura tiavato is threatened by habitat loss due to slash-and-burn agriculture (tavy) and from charcoal collecting and logging (Jenkins *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017s). Other potential threats come from the disturbance of roosting caves from tourists (Kofoky *et al.*, 2007), fire (Jenkins *et al.*, 2007b) or mining (Cardiff, 2006).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008e) [in IUCN, 2009)] and Monadjem *et al.* (2017s) report that it is known from three protected areas, Parc National Tsingy de Bemaraha, Réserve Spéciale d'Ankarana, Réserve Spéciale d'Analamerana (Goodman *et al.*, 2005a).

GENERAL DISTRIBUTION:
Endemic to Madagascar (Goodman *et al.*, 2006a). It is restricted to the karstic lowland areas in the western part of the island, extending from the drier areas in the north in Diana Region to Parc National Tsingy de Bemaraha in the west (Goodman *et al.*, 2005a). A record from Toliara in the extreme south has also been attributed to this species (Peterson *et al.*, 1995), but the specimen was not examined as part of the recent reassessment of *Emballonura* taxonomy on Madagascar (Goodman *et al.*, 2006a). The distribution of this species would be significantly reduced if the Toliara specimen was omitted. It is currently known to range between 10 and 330 m elevation (Goodman *et al.*, 2006a).

Native: Madagascar (Goodman *et al.*, 2005a; Goodman *et al.*, 2006a) - Nosy Be (Peterson *et al.*, 1995: 57; Rakotonandrasana and Goodman, 2007: 6) and Nosy Komba (Rakotonandrasana and Goodman, 2007: 6).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Goodman *et al.* (2006a).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2006a).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 58) indicate that the baculum of this species is more elongated than the rounded form of *P. atrata*; length: 0.09 mm, width: 0.08 mm.

Other
For a description of the crania, teeth, ears and tragus see Goodman *et al.* (2006a).

ECHOLOCATION:
Kofoky *et al.* (2009: 377) reported the call as a FM/CF/FM with up to five harmonics, produced short calls with a medium IPI and a low duty cycle, with a maximum energy at 55.2 kHz.

Hending *et al.* (2023: 372) mention F_{paek}: 54.4 ± 0.8 kHz, duration: 11 ± 6 ms and interpulse interval: 97 ± 30 ms.

HABITAT:
It appears to be associated with relatively intact forest and is believed to be forest dependent (Goodman *et al.*, 2005a; Goodman *et al.*, 2006a).

Dammhahn and Goodman (2013: 108) indicate that the lower portion of forest is this bat's foraging habitat.

HABITS:
At night it has been observed resting on buildings (Goodman *et al.*, 2006a). It feeds in forest understorey and over small streams with bank side vegetation (Robinson *et al.*, 2006).

ROOST:
Usually found roosting in the entrance to caves and rock overhangs that receive weak sunlight (Cardiff, 2006; Goodman *et al.*, 2006a; Kofoky *et al.*, 2007), usually in groups of less than 20 individuals (Garbutt, 2022: 87).

DIET:
In the stomach of one individual, remains of Lepidoptera were found (Razakarivony *et al.*, 2005; Goodman *et al.*, 2006a; Goodman *et al.* (2022: 1902).

POPULATION:
Structure and Density
Roosting colonies of *E. tiavato* are usually relatively small (< 20 individuals) (Jenkins *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017s).

Trend
2016: Unknown (Monadjem *et al.*, 2017s). 2008: Unknown (Jenkins *et al.*, 2008e; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
A single young is born in February (Goodman *et al.* (2006a: 15; Garbutt, 2022: 87).

Of a number of females collected in November-December, five were pregnant (embryos with crown-rump length 10 - 18 mm), two were non-pregnant and one was lactating (Goodman *et al.*, 2025: 214).

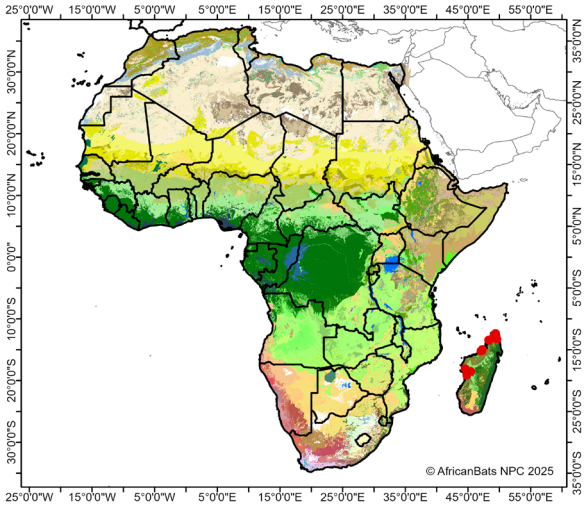

Figure 143. Distribution of *Paremballonura tiavato*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

†Genus ***Pseudovespertiliavus*** Ravel, 2016

*2016. *Pseudovespertiliavus* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 388. Publication date: 30 September 2016. - Etymology: The name refers to the multiple morphological similarities with the genus Vespertiliavus (see Ravel et al. 2016: 388).

†***Pseudovespertiliavus parva*** Ravel, 2016

*2016. *Pseudovespertiliavus parva* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 388, figs 16, 17. Publication date: 30 September 2016. Type locality: Algeria: Béchar province: Gour Labiz region (Sahara, Hammada du Dra).: Glib Zegdou [29 42 49 N 04 45 58 W]. - Etymology: From the Latin *parva* meaning small, referring to the small size of this bat (see Ravel *et al.*, 2016: 388).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene (Lutetian).
Morgan and Czaplewski (2023: 167) mentions Middle Eocene - Early Oligocene.

GENERAL DISTRIBUTION:
Fossils of this species were found in Algeria (Morgan and Czaplewski, 2023: 167).

Subfamily Taphozoinae Jerdon, 1867

1867. *Taphozoinae* Jerdon, Mammals of India, 30. - Comments: Jackson and Groves (2015: 253) mention 1867 as year of publication. Other authors (e.g. Palmer, 1904: 773) mention 1874 or 1877. These latter dates represent reprints of the "Mammals of India", but the name was already published in the 1867 version. Considered a valid subfamily by McKenna and Bell (1997: 302), Simmons (2005: 381), Jackson and Groves (2015: 253).

1988. *Taphozoini* Robbins and Sarich, J. Mamm., 69 (1): 10. Publication date: 25 February 1988. - Comments: Proposed as tribe and originally included the genera *Taphozous* É. Geoffroy, 1818 and *Saccolaimus* Temminck, 1838 (see Jackson and Groves, 2015: 253).

Genus ***Saccolaimus*** Temminck, 1838

*1838. *Saccolaimus* Temminck, in: Van der Hoeven, Tijdschr. Nat. Gesch. Physiol., 5: 14. - Comments: Corbet and Hill (1992: 85), Grubb *et al.* (1998: 72) mention "1838: 6 (and 1841a: 277, 279) [C&H]". Type species: *Taphozous saccolaimus* Temminck, 1838. - Etymology: From the Greek "*σάκκος*", meaning sac and "*λαιμός*", meaning throat, gullet, referring to the well-developed gular sacs of the type species (see Palmer, 1904: 615; Flannery, 1995a: 328; 1995b: 401). - Phonetics: sak'-oh-lay'-mus, sak-oh-lie'-mus. (Current Combination).

1876. *Taphonycteris* Dobson, Proc. zool. Soc. Lond., 1875, IV: 548. Publication date: April 1876. - Comments: Type species: *Taphozous saccolaimus* Temminck, 1838, by subsequent designation by Palmer (1904: 661) (see Jackson and Groves, 2015: 254). - Etymology: From the Greek "*τάφος*", meaning grave and "*νυκτερίς*", meaning bat (see Palmer, 1904: 661).

TAXONOMY:
Considered a subgenus of *Taphozous* by Ellerman and Morrison-Scott (1951: 104), Corbet and Hill (1980: 45), Corbet and Hill (1992: 85), and Kock and Dobat (2000: 87), but see Barghoorn (1977: 5), Robbins and Sarich (1988) and Chimimba and Kitchener (1991).

Key to the species provided by Chimimba and Kitchener (1991).

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Saccolaimus*: *flaviventris* (Peters, 1867) – Australia (except Tasmania), southeastern New Guinea (Simmons, 2005: 382); *mixtus* Troughton, 1925 – southeastern New Guinea, northeastern Queensland (Australia) (Simmons, 2005: 382); ***peli*** (Temminck, 1853); *saccolaimus* (Temminck, 1838) – Bangladesh, India and Sri Lanka through south east Asia (including Burma, Cambodia, Thailand and the Nicobar Islands) to the Philippines, Sulawesi and Borneo, Sumatra, Java, Bali and Timor (Indonesia); New Guinea; New Britain and Bougainville Islands (Papau New Guinea); northeastern Queensland (Australia); Guadalcanal Island (Solomon Islands) (Simmons, 2005: 382).

Additionally, there is the extinct African ***†abitus*** Wesselman, 1984.

COMMON NAMES:
Czech: vakoví hrobkovci. English: Pouched Bats. French: Saccolaime. German: Taschenfledermäuse.

†*Saccolaimus abitus* (Wesselman, 1984)

*1984. *Taphozous abitus* Wesselman, Contributions to vertebrate evolution, 7: 44. Type locality: Ethiopia: upper member B, Shungura Formation. - Etymology: From the Latin verb *abeo* meaning to go away, the past participle of which is *abitus* meaning vanished or departed (Wesselman, 1984).

2004. *Saccolaimus abitus:* Lim. (Name Combination, Current Combination).

2011. *Saccolaimus abditus:* Gunnell, Eiting and Geraads, N. Jb. Geol. Paläont. Abh., 260 (1): 70. Publication date: January 2011. (Lapsus).

TAXONOMY:
Closest affinity to the extant *Saccolaimus peli* (Wesselman, 1984; Lim, 2007).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Late Pliocene (2.58 Mya) of southwestern Ethiopia (Wesselman, 1984; Lim, 2007, Brown *et al.* (2019: Suppl.)

†*Saccolaimus kenyensis* Gunnell and Manthi, 2018

*2018. *Saccolaimus kenyensis* Gunnell and Manthi, J. Hum. Evol., p "4", fig 5D. Publication date: 6 April 2018. Type locality: Kenya: Nzube's Mandible Site [02 24 00 N 36 06 00 E]. Holotype: NMK KP-44927. The holotype consists of a M^1. - Etymology: Referring to country where the type was found (Gunnell and Manthi, 2018: "5").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe: Pliocene (Brown *et al.*, 2019: Suppl.).

Saccolaimus peli (Temminck, 1853)

*1853. *Taphozous peli* Temminck, Esquisses zoologiques sur la Côte de Guiné. 1e partie, les Mammifères, 82. Type locality: Ghana: Boutry River [=Butre river] [ca. 04 49 N 01 55 W]. [Goto Description]. Lectotype: RMNH MAM.35897: ad ♂, mounted skin and skull. Collected by: Hendrik Severinus Pel; collection date: 1843 - 1844.
? *Saccolaimus peli:* (Name Combination, Current Combination).
? *Taphozous (Saccolaimus) peli:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Chinese: 贝尔墓蝠. Czech: hrobkovec guinejský. English: Pel's Pouched Bat. French: Saccolaime de Pel, Chauve-souris à queue gainée de Pel. German: Pels Taschenfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bl; IUCN, 2009; Monadjem *et al.*, 2017ap).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ap). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bl; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bn; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Selective logging of large trees with cavities results in substantial roost destruction. Parts of *S. peli* range are fragmented by agricultural activities, but as it lives in clearings, it is not known whether or not this is having a significant negative impact on the species (Mickleburgh *et al.*, 2008bl; IUCN, 2009; Monadjem *et al.*, 2017ap).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bl) [in IUCN (2009)] and Monadjem *et al.* (2017ap) report that it is found in several protected areas. Research is needed to determine the effects of habitat fragmentation on the species.

GENERAL DISTRIBUTION:
Saccolaimus peli ranges widely through the equatorial forest belt of west and central Africa. In the Upper Guinea region, it occurs in Liberia, Guinea, Côte d'Ivoire and Ghana. Its main range extends from southwestern Nigeria to western Uganda, with isolated records from western Kenya and eastern Angola.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 535); Cameroon; Congo (Tolovou and Lenga, 2025: 52); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 535); Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Guinea; Kenya; Liberia; Nigeria (Capo-Chichi *et al.*, 2004: 161); Uganda.
Presence uncertain: Central African Republic; Sierra Leone.

Bates *et al.* (2013: 338) reject the presence of *S. peli* in the Republic of Congo because Malbrant and Maclatchy (1949) only mention it 'likely' to occur in that country.

FUNCTIONAL MORPHOLOGY:
Bahlman *et al.* (2016: 122) indicate that *S. peli* has long, cartilaginous distal phalanges with tendons running to the distal-most portion of the tip of digits IV and V. They speculate that the flexor muscles and tendons not only flex the terminal IP joint, but also may provide some additional curvature along the length of the cartilaginous phalanges.

MOLECULAR BIOLOGY:
Karyotype
Robbins (1983b: 35) reported 2*n* = 48 and FN = 68, with a metacentric X and an acrocentric Y chromosome.

HABITAT:
R.B. Woosnam [in Thomas and Wroughton, 1910: 489] reported that vast numbers were seen in the Congo Forest, but not anywhere else. He also indicated that they were seen hanging in trees, but never in houses.

POPULATION:
Structure and Density
S. peli occurs in low densities across its wide range (Mickleburgh *et al.*, 2008bl; IUCN, 2009; Monadjem *et al.*, 2017ap).

Trend
2016: Unknown (Monadjem *et al.*, 2017ap).
2008: Unknown (Mickleburgh *et al.*, 2008bl; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 113) assigned *S. peli* to the group of polyoestous species.

PARASITES:
ACARI
Myobiidae
Bochkov and Fain (2003: 42) mentioned the presence of *Ugandobia taphozous* Fain, 1972 on bats from the DRC.

DIPTERA
Nycteribiidae
Tripselia aequisetosa Theodor, 1956 from Liberia and Congo (Haeselbarth *et al.*, 1966: 112). Dick *et al.* (2023: 74) mentioned *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817).

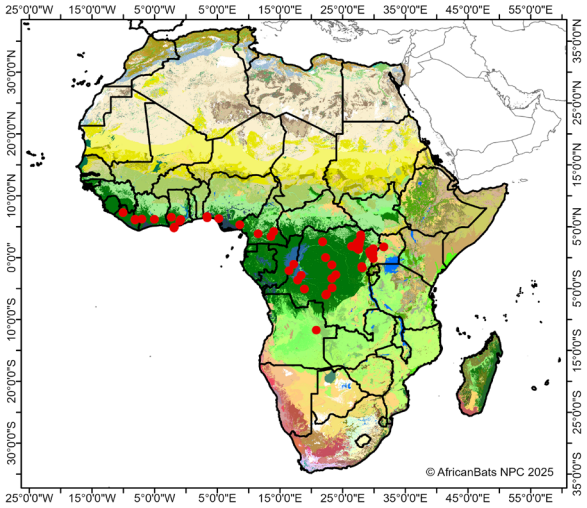

Figure 144. Distribution of *Saccolaimus peli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Liberia, Nigeria, Uganda.

Genus ***Taphozous*** E. Geoffroy St.-Hilaire, 1818

*1818. *Taphozous* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 113. Publication date: 1818. - Comments: Type species: *Taphozous perforatus* E. Geoffroy, 1818, by monotypy (according to Colket and Wilson, 1998: 1) or subsequent designation by Miller (1907: 93) (according to Jackson and Groves, 2015: 255). Mahoney and Walton (1988a: 116) in Grubb *et al.* (1998: 72) considered the date of Geoffroy's publication to be 1813. Gardner and Hayssen (2004: 12) mention that the correct date should be 1818, not 1813 as mentioned on the publication itself. - Etymology: From the Greek "*τάφος*" (táfos), meaning "grave" or "tomb" and "*ξωός*" (zóos), meaning "living" (see Palmer, 1904: 662). - Phonetics: taf'-oh-zoh'-us. (Current Combination).
1821. *Thaphosores:* J. E. Gray, London Med. Repos., 15 (1): 300. - Comments: Jackson and Groves (2015: 256) indicate that this is possibly an incorrect subsequent spelling as Gray refered to "Geoff." as author. Generally, the name is given as "*Taphosores*", but Gray (1821: 300) actually mentioned *Thaphosores.* (Lapsus).
1821. *Thaphozous:* Bowdich, An analysis of the natural classification of mammalia, for the use of students and travellers, 30. (Lapsus).
1822. *Thaphozus:* Fleming, The Phylosophy of Zoology, 179. (Lapsus).
1914. *Taphrozous:* Alluaud and Jeannel, in: Jeannel and Racovitza, Arch. Zool. exp. gen., 53: 373. Publication date: 7 March 1914. (Lapsus).
1922. *Liponycteris* Thomas, Ann. Mag. nat. Hist., ser 9, 9 (51): 267. Publication date: 1 March 1922 [Goto Description]. - Comments: Type species: *Taphozous nudiventris* Cretzschmar, 1830, by original designation (see Colket and Wilson, 1998: 1; Jackson and Groves, 2015: 256). Valid as a subgenus.
1998. *Tapozous:* Yom-Tov and Kadmon, Diversity Distrib., 4: 67. (Lapsus).
2018. *Thapozous:* Leopardi, Holmes, Gastaldelli, Tassoni, Priori, Scaravelli, Zamperin and De Benedictis, Infec. Gen. Evol., 58: 286. Publication date: 30 January 2018. (Lapsus).
2021. *Taphazous:* Thiombiano, Boungou, Kangoyé, Kaleme, Sinare, Soubeiga, Sawadogo, Ouéda and Kabre, J. Entomol. Zool. Stud., 9 (3): 30. (Lapsus).
2024. *Taphazois:* Gippoliti, J. Vertebr. Biol., 73 (23110): 2. Publication date: 5 April 2024. (Lapsus).
? *Taphozous sp.:*

TAXONOMY:
Some authors (e.g., Allen, 1939a: 66) consider Oken (1816), Lehrbuch d. Naturg., pt. 3., zool., sect 2, p. 926 to be the author of this genus.

Meester *et al.* (1986): Barghoorn (1977), followed by Koopman (1982, and in litt.) regard *Saccolaimus* as generically distinct from *Taphozous*, but L.W. Robbins (Abstracts, 4th International Colloquium on Taxonomy and

Ecology of African Small Mammals: 33, 1984) states that on the basis of protein electrophoresis and immunology *Taphozous* and *Saccolaimus* are closely related. Simmons (2005:382) recognized two subgenera *Taphozous* and *Liponycteris*, but this was rejected by Uvizl *et al.* (2019: 31). Only members of the former subgenus *Taphozous* occur in Africa and its associated islands.

Includes *Liponycteris* but not *Saccolaimus*; see Hayman and Hill (1971: 15) and Barghoorn (1977: 5), Robbins and Sarich (1988) and Chimimba and Kitchener (1991), though also see Corbet and Hill (1992). Corbet and Hill (1992: 85) include *Saccolaimus* as a subgenus. A key is provided by Colket and Wilson (1998: 1, Mammalian Species, 597).

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Taphozous*: *achates* Thomas, 1915 – Kei, Savu, Roti, Semau and Nusa Penida Isls (Indonesia) (Simmons, 2005: 382); *australis* Gould, 1854 – northern Queensland (Australia), Torres Strait Isls, southeastern New Guinea (Simmons, 2005: 383); *georgianus* Thomas, 1915 – northern and western Australia (Simmons, 2005: 383); ***hamiltoni*** Thomas, 1920; ***hildegardeae*** Thomas, 1909; *hilli* Kitchener, 1980 – Western Australia, South Australia and Northern Territory (Simmons, 2005: 383); *kapalgensis* McKean and Friend, 1979 – Northern Territory (Australia) (Simmons, 2005: 383); *longimanus* Hardwicke, 1825 – Sri Lanka; India and Bangladesh to Burma, Cambodia and Thailand; Peninsular Malaysia; Sumatra, Borneo, Java, Bali, Sumbawa and Flores (Indonesia) (Simmons, 2005: 383); ***mauritianus*** E. Geoffroy Saint-Hilaire, 1818. *melanopogon* Temminck, 1841 – Sri Lanka; India; Burma; Thailand; Laos; Cambodia; Vietnam; southern China; Malay Peninsula and adjacent islands; Borneo; Sumatra, Java, Lombok, Sumbawa, Moyo, Alor, Timor and Sulawesi (Indonesia), Philippines (Simmons, 2005: 384); ***nudiventris*** Cretzschmar, 1830; ***perforatus*** E. Geoffroy Saint-Hilaire, 1818; *theobaldi* Dobson, 1872 – central India to Vietnam; Java, Borneo and Sulawesi (Simmons, 2005: 385); *troughtoni* Tate, 1952 – northwestern Queensland (Australia) (Simmons, 2005: 385).

Common Names:

Czech: praví hrobkovci, večerníkové, netopýři bradožlází. English: Tomb Bats, Pouched Bats. French: Chauve-souris des Tombes, Taphiens. German: Grabfledermäuse, Grabflatterer. Italian: Tafozòi, Pipistrèlli délle tómbe.

Etymology of common name:

The type species of the genus, *T. perforatus*, was taken from a royal tomb in Egypt (see Taylor, 2005).

Parasites:

HEMIPTERA

Polyctenidae

Eoctenes intermedius (Speiser, 1904) originally described from a *Taphozous* species from Egypt (Haeselbarth *et al.*, 1966: 16; Szentiványi *et al.*, 2022: 4).

DIPTERA

Streblidae

Brachytarsina alluaudi (Falcoz, 1923) (Haeselbarth *et al.*, 1966: 101).

Viruses:

Flaviviridae

Pegivirus (BPgV)

2 out of 2 unidentified *Taphozous* specimens from Cameroon were infected by clade G type *Pegivirus*, and one of them also with clade K type *Pegivirus* (Quan *et al.*, 2013: Table S5).

Paramyxoviridae

Mortlock *et al.* (2015: 1841) reported that three out of 12 examined *Taphozous* sp. specimens from Cameroon tested positive for *Paramyxovirus* sequences.

Rhabdoviridae

Lyssavirus - Rabies related viruses

Horton *et al.* (2014: Table S1) tested 1 Kenyan *Taphozous* sp. specimen but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Distribution based on voucher specimens:

"Africa", Cameroon, Chad, Egypt, Ethiopia, Kenya, Senegal, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia.

Taphozous hamiltoni Thomas, 1920

*1920. *Taphozous hamiltoni* Thomas, Ann. Mag. nat. Hist., ser 9, 5 (25): 142. Publication date: 1 January 1920. Type locality: Sudan: Equatoria province: Mongalla [05 10 N 31 50 E, 500 m]. [Goto Description]. Holotype: NHMUK 1919.12.18.1: ad ♀. Collection date: 13 June 1918. Presented/Donated by: The Wellcome Research Laboratories. Formerly Stevenson Hamilton collection, nr 118 (see Thomas, 1920: 143). - Etymology: In honour of Major James Stevenson-Hamilton (1867 - 1957), eminent British regular soldier and conservationist, born in Ireland, considered father of the Kruger National Park. The species is named in his honour as the type specimen came from his collection (see Lanza *et al.*, 2015: 210). (Current Combination).

? *Taphozous (Liponycteris) hamiltoni:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Chinese: 苏丹墓蝠. Czech: hrobkovec východoafrický. English: Hamilton's Tomb Bat, Hamilton's Naked-rumped Tomb Bat, Hamilton's Naked-bellied Tomb Bat, Kordofan Sheathtail-bat. French: Taphien de Hamilton. German: Hamiltons Grabfledermaus. Italian: Tafozòo di Hàmilton.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing uncertainties as to its extent of occurrence, status, trends and ecological requirements (Mickleburgh *et al.*, 2008x; IUCN, 2009; Mickleburgh *et al.*, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019b). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008x; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004x; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats facing this species are unknown. It could be declining due to habitat loss through agriculture, but the data to confirm this are lacking (Mickleburgh *et al.*, 2008x; IUCN, 2009; Mickleburgh *et al.*, 2019b).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008x) [in IUCN (2009)] and Mickleburgh *et al.* (2019b) report that no specific conservation measures are in place. It probably occurs in some protected areas. The distribution and ecological requirements of this species require further investigation.

GENERAL DISTRIBUTION:
Taphozous hamiltoni is not well known, and there are very few records. It is known mainly from east Africa (including records from Sudan, Somalia, Kenya, and Tanzania), and there is one additional record from southern Chad.

Native: Chad; Kenya; Somalia; Sudan; Tanzania; Uganda.

POPULATION:
Structure and Density
There is no information, as there are few records of this species (Mickleburgh *et al.*, 2008x; IUCN, 2009; Mickleburgh *et al.*, 2019b).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019b). 2008: Unknown (Mickleburgh *et al.*, 2008x; IUCN, 2009).

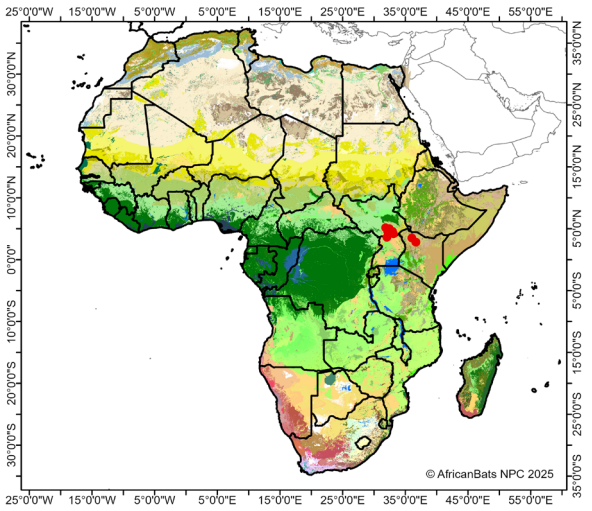

Figure 145. Distribution of *Taphozous hamiltoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, South Sudan, Sudan.

Taphozous hildegardeae Thomas, 1909

*1909. *Taphozous hildegardeæ* Thomas, Ann. Mag. nat. Hist., ser 8, 4 (20): 98. Publication date: 1 August 1909. Type locality: Kenya: Coast province: near Mombassa: Rabai. [Goto Description]. Holotype: NHMUK 1909.6.12.7: ad ♂, skull and alcoholic. Original number: 613. Collected and presented by Dr. and Mrs. Hinde, (see Thomas (1909a: 99). - Etymology: In honour of Mrs. Hildegarde Beatrice Hinde, wife of the Dr. Sydney Hinde, collector of the type specimen (see Colket and Wilson, 1998: 3; Lanza *et al.*, 2015: 213).
? *Taphozous (Taphozous) hildegardeae:* (Name Combination).
? *Taphozous hidegardeae:* (Alternate Spelling).
? *Taphozous hildegardeae:* (Current Combination, Current Spelling).

TAXONOMY:
See Colket and Wilson (1998, Mammalian Species, 597).

COMMON NAMES:
Chinese: 肯尼亚墓蝠. Czech: hrobkovec východoafrický. English: Hildegarde's Tomb Bat. French: Taphien de Hildegarde. German: Hildegardes Grabfledermaus. Italian: Tafozòo di Hildegàrde.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (VU B2ab(i,ii,iii) ver 3.1 (2001)) because its area of occupancy (AOO) is estimated at 48 km² (based on 12 known roost caves across its distribution), a severely fragmented population, and continuing decline in the extent and quality of its cave roost and forest habitat, leading to the reduction of its EOO and area of occupancy (AOO) (Webala *et al.*, 2020).

Assessment History
Global
2019: EN B2ab(i, ii, iii) ver 3.1 (2001) (Webala *et al.*, 2020). 2008: VU B1ab(iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2008y; IUCN, 2009). 2004: VU C1 ver 3.1 (2001) (Mickleburgh *et al.*, 2004r; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is endemic to Kenya and Tanzania, with a small geographic range. Disturbance, including tourism and recreational activities of the coral caves on which it depends, and loss of forest habitat along the coastal strip, could result in population declines (Mickleburgh *et al.*, 2008y; IUCN, 2009; Sagot and Chaverri, 2015: 1670; Webala *et al.*, 2020). Because the roost sites in coral caves are on unprotected community lands, at least in Kenya, this in itself is a threat because the future of these caves is uncertain. The land on which these caves are located are at risk of being converted to farmlands and the caves being closed off or destroyed.

CONSERVATION ACTIONS:
Webala *et al.* (2020) suggest It may occur in some protected areas in Tanzania. In Kenya it occurs on unprotected community lands (Makori, 2015a; Musila *et al.*, in press; P. Webala, *personal observation* in Webala *et al.* (2020)) and therefore stricter conservation of roosting and breeding sites is needed, and positive community engagement. Potential to protect these species through gating important maternity roosts and restoring degraded habitat within close proximity to these important roosts. Webala *et al.* (2020) suggests the following research are needed include: better understanding of the species distribution, including confirmation of records on Zanzibar and Pemba Islands and current survey to update historical records, baseline and monitoring data to understand population size and trends, including roost use throughout the year, and more information on significant threats and potential mitigation strategies.

GENERAL DISTRIBUTION:
Taphozous hildegardeae is found on Pemba and Unguja [=Zanzibar] islands (Tanzania), and along the coast of south-east Kenya and north-east Tanzania (from the Lower Tana River south to Dar es Salaam). It has so far been recorded from fewer than ten coastal localities but is probably present in some places where it has not yet been discovered.

The two central Kenya records collected by Harrison (1962), are questioned due to their location by Kock (1974a), as these points are not along the East African coast. The questioned locations do, however, coincide with coastal vegetation along the Tana River, which could afford this species suitable habitat (Colket and Wilson, 1998). Benda *et al.* (2025: 77) [referring to Monadjem et al. (2024)] mention that these inland records should rather be assigned to *Taphozous perforatus*. They also indicate that the only inland records for *T. hildegardeae* in eastern Africa are from Pangani (Kenya) and Kilulu (Tanzania) which are situated at 15 - 30 km from the coastline.

Native: Kenya; Tanzania.

ROOST:
McWilliam (1982: 208) found *T. hildegardeae* roosting in the larger caves of his study area (coastal Kenya), where they were found in smaller chambers or "erosion domes".

DIET:
In Kenya, McWilliam (1982: 248) reported that *T. hildegardeae* almost exclusively fed on large (> 10 mm) Lepidoptera and Orthoptera.

POPULATION:
Structure and Density
The overall global population is thought to be declining due to cave roost and forest degradation and loss (Webala *et al.*, 2020). Large colonies roosting at Makuruhu and Kaboga Caves near Watamu town in Kilifi County has been estimated to include over 21,240 and 3,800 individuals, respectively (Makori, 2015a; Musila *et*

al., in press; P. Webala, *unpublished data* in Webala *et al.* (2020)). Another coral cave, called Kuruwitu, just a few kilometres north of Mombasa has about 2,000 individuals (P. Webala, *unpublished data* in Webala *et al.* (2020)). The Fikirini/Mdenyenye Caves in Kwale County, south coast of Kenya are estimated to have over 20,000 (P. Webala, *unpublished data* in Webala *et al.* (2020)). A few individuals in the hundreds are also resident at the historical Shimoni Slave Cave on Kenya's south coast.

Therefore, Kenyan populations at northern and southern coastal Kenya are probably stable at the moment. However, as these caves are unprotected on private and community lands they are at great risk of development and loss (Webala *et al.*, 2020). Two large populations in coastal Kenya were estimated at about 1,000 to 2,000 individuals (McWilliam and Happold, 2013). During a survey in Kenya and Tanzania in 1988, population estimates from three caves surveyed yielded more than 1,500 individuals (1,000+, 300+, 130+) (Susan M. Pont, *pers. obs.,* in Mickleburgh *et al.*, 2008y [in IUCN, 2009]).

Trend
2019: Decreasing (Webala *et al.*, 2020). 2008: Decreasing (Mickleburgh *et al.*, 2008y; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
For Kenya, McWilliam (1988b: 433) indicates that male *T. hildegardeae* have a bimodal reproductive cycle that corresponds to the rainfall-induced seasonality in the coastal area. He also mentioned, however, that the second period (during the short rains in October-December), did not result in reproduction, indicating that the male cycle might be a relic of ancestral polyoestry.

MATING:
T. hildegardeae has a polygonous mating system, where a successful male can father at least seven young per year (McWilliam, 1982: 258).

PARASITES:
HEMIPTERA
Cimicidae
Loxaspis miranda Rothschild, 1912, described from specimens collected at Kilidini,near Mombasa, Kenya, Haeselbarth *et al.* (1966: 9) suggests that these are from *T. hildegardeae*.

DIPTERA
Streblidae
Brachytarsina alluaudi (Falcoz, 1923) in Kenya and probably Tanzania (Haeselbarth *et al.*, 1966: 101).

Nycteribiidae
Verrett *et al.* (2022: 8) and Dick *et al.* (2023: 77) reported *Pencillidia fulvida* (Bigot, 1885) in Kenya.

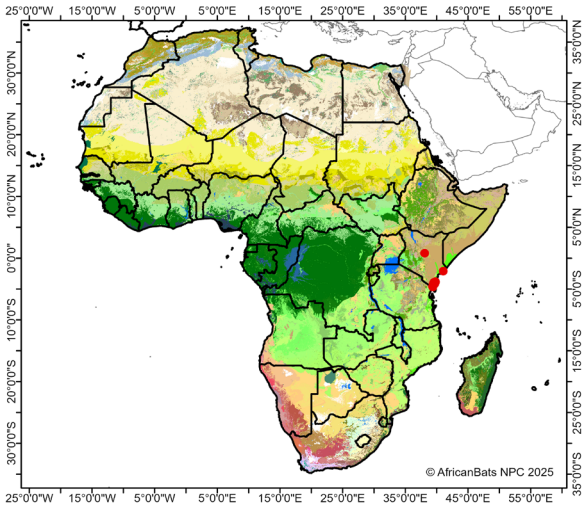

Figure 146. Distribution of *Taphozous hildegardeae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Tanzania.

†*Taphozous incognita* (Butler & Hopwood, 1957)

*1957. *Saccolaimus incognita* Butler and Hopwood, Fossil Mammals of Africa, Insectivora and Chiroptera from the Miocene rocks of Kenya, 13: 29, fig 9. Publication date: 1957. Type locality: Kenya: Koru. Holotype: BMGD M.14222. The left half of a rostrum lacking much of the bone but showing the interior of the orbit and part of the crowns of P4 and M2.
1978. *Taphozous incognita:* Butler, Evolution of African Mammals, 65. (Name Combination, Current Combination).

TAXONOMY:
Most similar to the extant *Taphozous nudiventris* (Butler and Hopwood, 1957; Butler, 1984; Lim, 2007).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Miocene (Burdigalian [Brown *et al.*, 2019: Suppl.] - 23.03 Mya) of the Legete Formation in Kenya (Lim, 2007), Koru (Butler, 1978).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Taphozous mauritianus E. Geoffroy St.-Hilaire, 1818

*1818. *Taphozous mauritianus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 127. Publication date: 1818. Type locality: Mauritius: "Mauritius". Holotype: MNHN ZM-MO-1997-1845: ad ♀, skull and alcoholic. Rode (1941: 243) mentions this specimen with numbers "199" and "A.381". Previously mentioned as MNHN A.381 - 199. - Comments: Mahoney and Walton (1988a: 116) in Grubb *et al.* (1998: 72) considered the date of Geoffroy's publication to be 1813. Gardner and Hayssen (2004: 12) mention that the correct date should be 1818, not 1813 as mentioned on the publication itself. - Etymology: From the masculine scientific Latin adjective *mauritiànus*, meaning "Maurician", as the type specimen was collected on the island of Mauritius (see Lanza *et al.*, 2015: 215). (Current Combination).

1841. *Taphozous leucopterus* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome Seconde, 2 (14): 284, pl 60, fig 7. Publication date: 1841. Type locality: South Africa: "Interior of South Africa". [Goto Description]. - Comments: Kock (1969a: 71), Meester *et al.* (1986: 31) and Dengis (1996: 1) mention "1838; Tijdschrift voor natuurlijke geschiedenis en physiologie, Amsterdam 5: 12".

1879. *Taphozous Dobsoni* Jentink, Notes Leyden Mus., 1 (1): 123, note 32. Publication date: April 1879. Type locality: Madagascar: Mahambo [17 29 00 S 49 28 00 E]. [Goto Description]. Holotype: RMNH MAM.30344: ad ♂, skull and alcoholic. Collected by: Jean Baptiste Audebert; collection date: 1876.

1900. *Taphozous maritianus var. Cinerascens:* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 77. Publication date: August 1900. Type locality: Angola: Benguela [12 34 S 13 24 E, 160 m]. (Lapsus).

1978. *Taphozous mauvitanius:* Arata and Johnson, Ebola Virus Haemorrhagic Fever, 135. (Lapsus).

2017. *T[aphozous] mauritiana:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 5. Publication date: 6 April 2017.

2020. *Taphozous mauritianum:* Sow, Seye, Faye, Benoit, Galan, Haran and Brévault, Crop Prot., 132 (105127): 4. Publication date: 5 March 2020. (Lapsus).

2021. *Taphazous mauritianus:* Thiombiano, Boungou, Kangoyé, Kaleme, Sinare, Soubeiga, Sawadogo, Ouéda and Kabre, J. Entomol. Zool. Stud., 9 (3): 30. (Lapsus).

? *Taphozous (Taphozous) mauritianus:* (Name Combination).

? *Taphozous mauritianus mauritianus:* (Name Combination).

Taxonomy:



Figure 147. *Taphozous mauritianus* caught at Sudwala Caves Resort, Mpumalanga, South Africa.

Koopman (1975) believed that a number of subspecies that have been described are of doubtful value.
See Dengis (1996, Mammalian Species, 522).

Common Names:

Afrikaans: Witlyfvlermuis. Azande (DRC): Fulo. Castilian (Spain): Murciélago de las Tumbas. Chinese: 南非墓蝠. Czech: hrobkovec mauricijský, netopýr mauricijský, netopýr hrobkový. English: Mauritian Tomb Bat, Tomb Bat, Taphozous bat of Mauritius. French: Taphien de l'Ile Maurice, Taphien de l'Ile de France, Taphien de Maurice, Chauve-souris mauritienne des tombeaux, Chauve-souris des tombes. German: Mauritius-Grabfledermaus. Italian: Tafozòo mauriziàno. Kinyarwanda: Mokombe. Kiluba (DRC): Katutu. Kinande (DRC): Kahazo-komule, Kakorokombe. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego das sepulturas das Mauricias. Swahili: Popo. Tshokwe (Angola): Kanga.

Etymology of common name:

The specimen from which the species was described came from the island of Mauritius (see Taylor, 2005: 274).

Palaeontological or archaeological records:

Evans and Mourad (2018: 81; Fig. 4, 5) provide images of wall paintings of bats, which look like *Taphozous*, on the walls of an Egyptian tomb at Beni Hassan, dating back from the Middle Kingdom (c. 2050 - 1650 BC).

Conservation status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Hutson *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017bb).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bb). 2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008f; IUCN, 2009). 2004: LC ver 3.1 (2001)

(Mickleburgh *et al.*, 2004bl; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016u). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).
Sáo Tomé: EN (Rainho *et al.*, 2022: 607).

MAJOR THREATS:
Overall, this species is not significantly threatened. It is locally hunted (by children) in parts of its range (Hutson *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017bb).

CONSERVATION ACTIONS:
Hutson *et al.* (2008f) [in IUCN (2009)] and Monadjem *et al.* (2017bb) report that this species is known from protected areas within Madagascar including Zombitse National Park and Ankarafantsika National Park, as well as from many protected areas on the African continent.

GENERAL DISTRIBUTION:
Taphozous mauritianus is found throughout much of subsaharan Africa and is also on several islands (including the Tanzanian island of Unguja [=Zanzibar] [see O'Brien, 2011: 287]), Bioko and Pagalu (Equatorial Guinea), and Sao Tomé and Príncipe). The most northerly records are from the border area between Senegal and Mauritania and at the head of the Nile River in Sudan. It is present throughout southern and eastern Madagascar, but it usually only occurs at lower altitudes and there are no records from the central plateau or above 900 m. It is known from Aldabra (von Brandis (2004: 135), Mauritius, the Comoros and Réunion. Records from the Western Cape region in southern Africa are unverified, with known records extending as far south as Mossel Bay. It is also recorded in an isolated location in the Northern Cape, near Hartwater (Taylor, 2000; Skinner and Chimimba, 2005). In the RSA, the species' distribution is linked with land use/land cover (Babiker Salata, 2012: 50).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,454,841 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 532; Taylor *et al.*, 2018b: 62); Benin (Capo-Chichi *et al.*, 2004: 162); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 535); Burkina Faso (Thiombiano *et al.*, 2021: 26); Cameroon; Central African Republic; Chad; Comoros (Louette, 2004; Goodman *et al.*, 2010c: 125; Hume and Middleton, 2011: 33); Congo (Bates *et al.*, 2013: 335); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 535); Côte d'Ivoire; Equatorial Guinea (Annobón, Bioko); Eswatini (Monadjem *et al.*, 2010d: 535, Monadjem *et al.*, 2021: 5); Ethiopia; Gabon; Gambia (Emms and Barnett, 2005: 50); Ghana; Kenya; Madagascar; Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 29; Monadjem *et al.*, 2010d: 535); Mauritius; Mayotte (Ramasindrazana *et al.*, 2015a: 109); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 535); Namibia (Monadjem *et al.*, 2010d: 535); Nigeria; Réunion; São Tomé and Príncipe (Juste and Ibáñez, 1993c: 906; Rainho *et al.*, 2010a: 35); Senegal; Seychelles [Aldabra]; Sierra Leone; Somalia; South Africa (Monadjem *et al.*, 2010d: 535); Sudan; Tanzania; Togo; Uganda; Zambia (Ansell, 1967; Ansell, 1969; Ansell, 1978;Ansell, 1986; Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 535); Zimbabwe (Monadjem *et al.*, 2010d: 535).

Presence uncertain: Burundi; Guinea; Guinea-Bissau; Liberia; Mali; Mauritania; Rwanda.

GEOGRAPHIC VARIATION:
Krutzsch (2000: 114) [referring to Rosevear (1965), Smithers and Lobão Tello (1976) and Happold (1987)] indicates that geographic variation is evident in the gular sac in this species. In Nigeria and Mozambique, it is only present in males, while in West Africa the males have a functioning sac and females have a vestigial pouch.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Fenton (1992: 49) indicates that the grizzled dorsal pelage contributes to the bat's camouflage while resting on natural surfaces. In the resting position, the striking white venter is completely concealed.

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 2 specimens: Fa: 60.25 mm, mass: 27.0 g, wing loading: 13.3 N/m^2, aspect ratio: 5.8.

ECHOLOCATION:
See Taylor (1999b), and Taylor (2000: 63).

Rainho *et al.* (2010a: 21) and Rainho *et al.* (2022: 605) reported the calls of 5 individuals from São Tomé: F_{min}: 24.2 ± 0.7 (23.4 - 25.2) kHz, F_{max}: 31.9 ± 0.6 (31.4 - 32.5) kHz, F_{maxE}: 28.3 ± 0.2 (28.1 - 28.4) kHz, duration: 14.8 ± 1.7 (12.8 - 16.8) ms and interpulse interval: 77.4 ± 6.4 (70.7 - 86.4) ms.

For 10 calls of specimens from Soutpansberg and Waterberg, South Africa, Taylor *et al.* (2013b: 18)

recorded the following parameters: F_{max}: 29.0 ± 1.17 (27.8 - 31.1) kHz, F_{min}: 25.3 ± 1.49 (22.1 - 27.9) kHz, F_{knee}: 28.3 ± 1.29 (27.0 - 30.2) kHz, F_{char}: 26.2 ± 0.94 (24.9 - 27.9) kHz, duration: 2.9 ± 0.64 (2.0 - 3.6) ms.

Weier *et al.* (2020: Suppl.) reported on seven calls from the Okavango River Basin with the following characteristics: F_{max}: 28.71 ± 2.38 kHz, F_{min}: 23.88 ± 2.10 kHz, F_{knee}: 26.96 ± 1.67 kHz, F_{char}: 24.96 ± 1.72 kHz, slope: 79.41 ± 58.64 OPS, duration: 3.06 ± 0.94 ms.

From western Uganda, Monadjem *et al.* (2011: 32) report the following values: F_{min}: 13.13 kHz, F_{max}: 13.48 kHz, F_{char}: 13.43 kHz, F_{knee}: 13.18 kHz, duration: 9.1 ms. They also indicate (p. 33) that the F_{peak} of 25.6 [actually 25.9] kHz reported by Schoeman and Jacobs (2008: Table S1) is probably for an harmonic.

Barataud and Giosa (2013: 150) reported on 57 sequences from Réunion with F_{start}: 26 ± 5.8 kHz, F_{end}: 21.8 ± 6.7 kHz, bandwidth: 4.2 ± 3.7 kHz, $F_{fund\ max}$: 14 ± 1 khz, $M_{1har\ max}$: 27.1 ± 1.6 kHz and duration: 13 ± 3.7 ms.

For Swaziland, Monadjem *et al.* (2017c: 179) recorded the following parameters: F_{min}: 25.1 ± 0.72 (24.3 - 25.9) kHz, F_{knee}: 28.6 ± 0.60 (28.1 - 29.5) kHz, F_{char}: 25.9 ± 1.20 (24.3 - 27.2) kHz, and duration: 2.7 ± 0.27 (2.4 - 3.0) kHz.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 14 bats: F_{max}: 28.35 ± 2.05 kHz, F_{min}: 22.97 ± 6.79 kHz, F_{knee}: 27.43 ± 1.74 kHz, F_{char}: 26.05 ± 1.61 kHz, slope: -215.69 ± 1248.24 OPS, duration: 5.71 ± 3.76 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Tabls S1) had a duration of 6.13 ± 1.57 ms, F_{min}: 25.07 ± 0.68 kHz, F_{max}: 25.92 ± 0.93 kHz, F_{knee}: 25.76 ± 0.89 kHz and F_{char}: 25.19 ± 0.71 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 25.9 kHz and duration: 7.4 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 24 *Taphozous mauritianus* calls from the Kruger Park (RSA): F_{min}: 25.7 ± 2.2 (23.7 34.7) kHz, Duration: 3.0 ± 0.5 (2.1 3.8) ms, F_{max}: 33.2 ± 8.0 (26.9 40.2) kHz, F_{knee}: 30.1 ± 3.7 (24.6 42.5) kHz, F_{char}: 27.9 ± 2.5 (24.3 35.9) kHz, 69 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 22 - 29 kHz, F_{max}: 29 - 31 kHz, F_{char}: 25 - 28 kHz, F_{knee}: 27 - 30 kHz and duration 3 ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 27.90 ± 2.50 kHz, F_{max}: 33.20 ± 8.00 kHz, F_{min}: 25.70 ± 2.20 kHz.

Parker (2022: 20) reported the following data from 232 passes at Mountain Zebra National Park (RSA): F_{min}: 24.90 ± 3.84 kHz, F_{char}: 26.48 ± 3.62 kHz and F_{max}: 29.78 ± 5.25 kHz.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 27.90 ± 2.50 kHz, F_{max}: 33.20 ± 8.00 kHz and F_{min}: 25.70 ± 2.20 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

Molecular Biology:

Karyotype

Rautenbach *et al.* (1993) reported for specimens from South Africa, 2*n* = 42, FN = 64, BA = 24, a metacentric X chromosome, and a submetacentric Y chromosome.

Protein / allozyme - Unknown.

Habitat:

Open savanna and forest edges in the wetter northern and eastern parts of the subcontinent (Taylor, 2000: 62).

On São Tomé, Castro-Fernandes *et al.* (2024: 2) reported this species to be an open-space forager.

Habits:

Fenton and Griffin (1997: 248) recorded one call above 24 kHz, which they attributed to *T. mauritianus* at an altitude of 500 - 550 m above a *Brachystegia* woodland in Zimbabwe.

Roost:

In the Durban area, Taylor *et al.* (1999: 67) found most of the roosts (72 %) being associated with the outer walls of houses at a height between 2 and 12 metres. The colony size varied from 1 to 5.

In a rural area on Madagascar; Rakotondramanana *et al.* (2017: 133) found a colony roosting on the trunk of a palm tree (*Cocos nucifera*), under dried fronds. They left the roost about 30 minutes after sunset. Ravelomanantsoa *et al.* (2019: 110) report it also roosting in *Tamarindus indica*.

In Malawi, O'Malley *et al.* (2020: 1) found that roosts in building were selected both on building and landscape level: the occupied buildings were

situated closer to woodlands than random buildings (709 versis 1847 m); these buildings generally had exposed roof beams, and the roosts were situated on larger areas and taller (brick) walls. O'Malley *et al.* (2020: 3) also indicated that day roosts are commonly found in the open, but away from direct sunlight, either on outer walls of buildings, cliff faces or large tree trunks.

DIET:
They feed primarily on moths (Allen *et al.*, 1917); termite alates such as *Macrotermes falciger* (Happold and Happold, 1988), and other insects (Smithers, 1971). See also (Taylor, 2000: 62; 2005: 275).

In Senegal, Sow *et al.* (2020: 4) used molecular analyses to identify the presence of *Heliocheilus albipunctella* de Joannis) (Lepidoptera, Noctuidae) in the faeces of *T. mauritianus*.

For Madagascar, Goodman *et al.* (2022: 1903) [referring to Razafimalala (2017)] mentioned the following volume percentages: Hymenoptera (45 %), Lepidoptera (30 %), and, to a much lesser extent, Coleoptera, Homoptera, Diptera, Orthoptera, and Odonata. Immature animals were found to eat more Lepidoptera than adults.

PREDATORS:
Demeler (1981: 133) found remains of *T. mauritianus* in pellets of *Bubo africanus* in the Yankari Game Reserve (Nigeria).

Mikula *et al.* (2016: Supplemental data) mention Wahlberg's eagle (*Hieraaetus wahlbergi* (Sundevall, 1851)) as a diurnal avian predator.

Goodman *et al.* (2015c: 78) found the remains of one individual in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar. Malan *et al.* (2022: 167) reported six individuals in pellets from this hawk in the RSA.

Goodman *et al.* (2022: 1903) mentioned predation by *Tyto alba* (Scopoli, 1769) in southwestern Madagascar.

POPULATION:
Structure and Density
Taphozous mauritianus is not rare and is easy to find. It usually roosts under covering vegetation on the outer bark of trees (Hutson *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017bb).

Trend
2016: Unknown (Monadjem *et al.*, 2017bb). 2008: Unknown (Hutson *et al.*, 2008f; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Kaudern (1914: 12) reported that he received a female with a very small foetus from villagers in Fenerive (Madagascar) on 6 January 1912.

Krutzsch (2000: 113) mentioned that *T. mauritianus* is monoestrous in parts of its range and polyoestrous in others.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births from October to December and from February to March.

In Malawi, births were reported in November-December and March-April (Happold and Happold, 1990b: 564).

PARASITES:
HEMIPTERA
Polyctenidae
Eoctenes intermedius (Speiser, 1904) from the DRC (Haeselbarth *et al.*, 1966: 16; Szentiványi *et al.*, 2022: 5).

DIPTERA
Nycteribiidae
Tripselia blainvillii (Leach, 1817) distributed over the Madagascan region and tropical Africa from west to east between lat. 10° north and south (Haeselbarth *et al.*, 1966: 113). Hutson (2004a: 129) mentions that *Basilia (Tripselia) blainvilli* (Nycteribiidae) is a widespread parasite of *Taphozous mauritianus*. (synonyms: *Nycteribia (Acrocholidia) fryeri*, *Tripselia fryeri*).

SIPHONAPTERA
Ischnopsyllidae
Chiropteropsylla brockmani Rothschild, 1915 widespread (Haeselbarth *et al.*, 1966: 192).

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Taphozous mauritianus*: Astroviruses, Paramyxoviruses and Rotaviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in one individual from Limpopo Province, South Africa, none were tested positive (0/1).

In their overview table, Maganga *et al.* (2014a: 8) reported that no viruses were ever found in this bat species.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burundi, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Guinea-Bissau, Kenya, Madagascar, Malawi, Mauritius, Mozambique, Namibia, Nigeria, Réunion, Rwanda, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

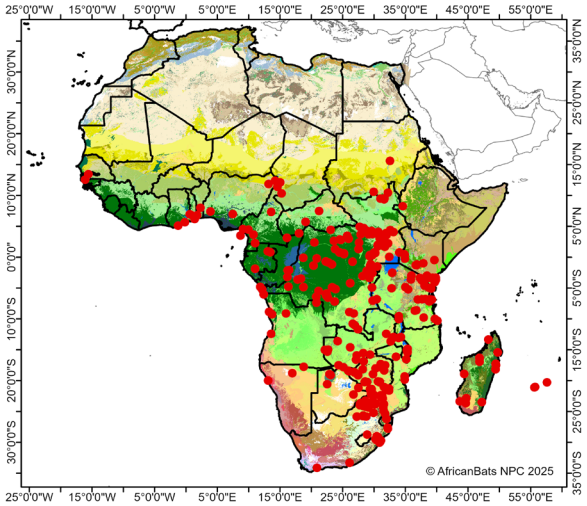

Figure 148. Distribution of *Taphozous mauritianus*.

Taphozous nudiventris Cretzschmar, 1830

*1830-1831. *Taphozous nudiventris* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 70, pl 27b. Publication date: 1830-1831. Type locality: Egypt: Giza province: Giza [30 01 N 31 13 E]. [Goto Description]. Lectotype: SMF 4310: ad ♂, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1824. Old catalog II.J.1.a; see Mertens (1925: 20), Qumsiyeh (1985: 26). Paralectotype: RMNH MAM.35962: mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell. Paralectotype: RMNH MAM.35964: ad, mounted skin (skull not removed). Collected by: Wilhem Peter Edward Simon Rüppell. - Comments: Kock (1969a: 83) mentioned the type locality as "Egypt, Nubia" and indicates that Giza is the type locality of the lectotype. Corbet and Hill (1992: 87) only mention "Egypt". Allen (1939a: 67) mentioned 1826 as year of description, whereas Kock (1969a: 83) mentioned 1830. Grubb *et al.* (1998: 73) mentions "1830, vel 1831". - Etymology: From the masculine Latin adjective *nùdus*, meaning "naked" and the masculine Latin substantive *vènter*, meaning"belly", as the fur stops short of the end of the body both dorsally and ventrally (see Lanza *et al.*, 2015: 221). (Current Combination).

1841. *Taphozous nudiventer:* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome Seconde, 2 (14): 280, pl 60, figs 10 - 12. Publication date: 1841. - Comments: Lapsus (Allen, 1939a: 67).
. (Lapsus).

1877. *Nycticejus serratus* Heuglin, Reise in Nordost Afrika, 2: 35. Publication date: 1877. Type locality: Sudan: ?Abyssinia: on the Araschkol and nearby mountains: "Sherq el Aqabah" [14 15 N 32 10 E]. [Goto Description]. - Comments: According to Simmons (2005) this is an enigmatic taxon, which is variously referred to either *Taphozous nudiventris* (e.g. Allen, 1939a: 67; Koopman, 1993a) or *Scotophilus nigrita leucogaster* (Allen, 1939a) [implying that it might either be *S. dinganii* or *S. leucogaster*], but which may not represent either of those species. Kock (1969a: 83) includes it with a question mark in the synonymy of *Taphozous nudiventris*, and Happold (2013bm: 434) mentions it as a possible synonym of that species.

1885. *Taphozous perforatus var. assabensis* Monticelli, Ann. Accad. O. Costa de Aspir. Nat. Napoli, ser 1, 1: 78, pl 7. Type locality: Eritrea: Assab [13 01 N 42 43 E]. - Comments: Allen (1939a: 67) indicates that Monticelli considered it a synonym of *perforatus*, but Senna (1905), who examined the type, says it is *T. nudiventris*. The type specimen was collected by prof. G.B. Licata.

1964. *T(aphozous) mudiuemtris:* Walker, Mammals of the World, I: 241. (Lapsus).

2013. *Taphozous nudiuentris:* Liu, Wang, Zhang, Li, He, Huang, Jiang, Murphy and Shi, Proc. R. Soc. Lond., B 281 (1776): 20132950 3 (for 2014). Publication date: 18 December 2013. (Lapsus).

? *Liponycteris nudiventris:* (Name Combination).

? *Taphozous (Liponycteris) nudiventris:* (Name Combination).

? *Taphozous nudiventris nudiventris:* (Name Combination).

TAXONOMY:
Simmons (2005) assigns four subspecies to *Taphozous nudiventris*: *T. n. kachhensis* Dobson, 1872; *T. n. magnus* Wettstein 1913; *T. n. nudaster* Thomas, 1915; and *T. n. zayidi* Harrison, 1955.

Uvizl *et al.* (2019: 31) consider *zayidi* to be a junior synonym of *T. n. nudiventris*, and also indicate that there is need for further investigation to ascertain the position of the other subspecies.

The enigmatic taxon *T. n. serratus* Heuglin, 1877 has been variously referred to either *Taphozous nudiventris* (e.g., Allen, 1939a, Koopman, 1993a) or *Scotophilus leucogaster* (e.g., Allen, 1939a; Koopman, 1993a), although it might not represent either of these species. See Felten (1962), Hayman and Hill (1971), Harrison and Bates

(1991), Bates and Harrison (1997) and Barkley (1984) for further information on this taxon.

COMMON NAMES:
Albanian: Pipistreli i varrezave barkzhveshur. Arabian: Khafash Abu Bouz, Khaffash. Armenian: Մերկփոր պարկաթև. Azerbaijani: Ilpaqqarın məzar yarasası. Basque: Hilobi-saguzar gibelsoil. Belarusian: Marĺьнік галабруxі. Bosnian: Golotrbušni grobni šišmiš. Breton: Logodenn-dall kof noazh ar bezioù. Bulgarian: Голокоремен прилеп. Castilian (Spain): Murciélago de cola libre y vientre desnudo. Catalan (Spain): Ratpenat de tomba de carpó nu. Chinese: 裸腹墓蝠. "Congolese": Kubukubo, Papo. Croatian: Golotrbi grobni šišmiš. Czech: Netopýr lysobřichý, Hrobkovec lysobřichý. Danish: Nøgenrumpet gravflagermus. Dutch: Kaalbuikgrafvleermuis. English: Naked-bellied Tomb Bat, Naked-rumped Tomb Bat, Egyptian sheath-tailed bat, Naked-rumped bat, Naked-bellied Taphozous. Estonian: Paljaskõht-kääpanahkhiir. Finnish: Arohautalepakko. French: Taphien à croupe nue, Taphien à ventre nu. Frisian: Kealbûktimpelflearmûs. Galician (Spain): Morcego de tumba de cú espido. Georgian: შიშველმუცელა ქარქაშკუდა. German: Nacktbäuchige Tempelfledermaus, Nacktbauch-Grabfledermaus. Greek: Άτριχη ταφονυχτερίδα. Hebrew: Ashman Gadol. Hungarian: Csupaszhasú sírlakó-denevér. Irish Gaelic: Ialtóg nochtphrompach thuama. Italian: Pipistrello delle tombe a ventre nudo, Tafozòo nudivèntre. Latvian: KailvĒdera sikspārnis. Lithuanian: Plikapilvis maišiasparnis. Luxembourgish: Plakegbauchege Griewerflatterer. Macedonian: Торбокрилест лилјак. Maltese: Farfett il-Lejl Għieri. Montenegrin: Golotrbušni grobni slijepi miš. Norwegian: Nakengumpflaggermus. Polish: Grobownik gołobrzuchy. Portuguese: Morcego-de-ventre-nú. Rhaeto-Romance: Pipistrel da fossa a venter niv. Romanian: Liliacul cu burtă golaşa. Russian: Мешкокрыл голобрюхий. Serbian: Голотрби гробнички м[ј]ешкокрилаш [=Golotrbi grobnički m[j]eškokrilaš]. Scottish Gaelic: Ialtag nochd-thònach thuaim. Slovak: Hladkonos holobruchý. Slovenian: Golotrebušni mavzolejnik. Swedish: Nakengumpsfladdermus. Tamil: திறந்த ரம்ப்டு கல்லறை வௌவால், Iṟanta Rampṭu Kallaṟai Veḷ

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Bates *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bq).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bq). 2008: LC ver 3.1 (2001) (Bates *et al.*, 2008; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bp; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is tolerant of a certain level of human disturbance. Loss of some roosts (e.g., in buildings) and use of pesticides probably impact some populations negatively, but overall it is not significantly threatened (Bates *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bq).

CONSERVATION ACTIONS:
Bates *et al.* (2008) [in IUCN (2009)] and Monadjem *et al.* (2017bq) report that there are international legal obligations for protection through the Bonn Convention (Eurobats) in areas to which this applies. However, through most of its range, no specific conservation measures are place for this species. It occurs in many protected areas across its wide range. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
Taphozous nudiventris has a much larger range than previously believed. It has been recorded throughout the southern desert and sub-desert belt of western and central Palaearctic, from Morocco, through the Saharan region across northern Africa to Egypt and north through the Middle East to southern Turkey, and the more arid areas of the Indian subcontinent. The most southerly record is from northern Tanzania. There are two isolated records from Myanmar (the southernmost locality being in the general vicinity of Bago (Pegu) Yoma (Bates *et al.*, 2000)).

In South Asia this species is presently known from Afghanistan (Kabul, Kandahar and Nangarhar provinces), Bangladesh, India (Andhra Pradesh, Bihar, Delhi, Gujarat, Karnataka, Madhya Pradesh, Maharashtra, Rajasthan, Sikkim, Tamil Nadu, Uttar Pradesh and West Bengal) and Pakistan (Punjab and Sind) (Molur *et al.*, 2002).

Native: Afghanistan; Algeria (Horáček *et al.*, 2000: 104); Burkina Faso (Kangoyé *et al.*, 2015a: 614); Cape Verdian Islands (Tranier and de Naurois, 1985: 304; Borloti *et al.*, 2020: 2); Chad; Congo (The Democratic Republic of the); Djibouti (Pearch *et al.*, 2001: 396); Egypt; Eritrea (Lavrenchenko *et al.*, 2004b: 138); Ghana; Guinea-Bissau (Castella *et al.*, 2000; Rainho and Ranco, 2001: 38); India; Iran, Islamic Republic of; Iraq; Israel; Jordan; Kenya; Macronesian Islands (Cape Verd islands (Tranier and de Naurois, 1985; de Naurois, 1994; Hazevoet, 1995; Masseti, 2010); Mauritania; Morocco (Dbiba *et al.*, 2025: 6); Myanmar; Niger; Nigeria; Pakistan; Palestinian Territory, Occupied; Saudi Arabia; Senegal; Somalia; Sudan; Syrian Arab Republic; Tanzania; Togo; Tunisia (Dalhoumi *et al.*, 2023: 1); Turkey; United Arab Emirates (Anonymus, 2008: 38); Yemen.

Presence uncertain: Ethiopia; Kuwait; Libyan Arab Jamahiriya; Oman; Qatar; Uganda; Western Sahara. The records from Lebanon were revoked by Benda and Engelberger (2016: 17).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 22.4 Pa, aspect ratio 9.5 and tip shape index of 1.14 for a wingspan of 46 cm and a wing area of 219 cm^2 and a body mass of 50 g.

ECHOLOCATION:
In Jordan, Benda *et al.* (2010b: 204) registered the following parameter for 17 calls: F_{start}: 26.1 ± 1.0 (24.4 - 27.6) kHz, F_{end}: 22.2 ± 0.6 (20.3 - 22.9) kHz, F_{peak}: 24.5 ± 0.5 (23.6 - 25.3) kHz, Pulse duration: 15.4 ± 2.6 (11.0 - 19.5) ms, and Inter-pulse interval: 363.9 ± 115.1 (188.0 - 571.0) ms.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 23.38 kHz, F_{start}: 24.39 kHz, F_{end}: 22.8 kHz, Band width: 1.59 kHz, and duration: 12.99 ms.

From Israel, Hackett *et al.* (2016: 223) reported the following parameters for 74 calls: Pulse duration: 12.99 ± 3.50 ms, F_{start}: 24.39 ± 1.55 (22.3 - 25.3) kHz, F_{end}: 22.80 ± 1.29 (20.4 - 26.3) kHz, F_{peak}: 23.38 ± 1.31 (21.3 - 26.3) kHz.

MOLECULAR BIOLOGY:
Karyotype
Đulić (1984), Yaseen *et al.* (1994), Hood and Baker (1986), Asan and Albayrak (2007) reported $2n$ = 42, FN = 64, BA = 24. However, Robbins (1983b: 35) reported $2n$ = 42 and FN = 68 and Sreepada *et al.* (1995) $2n$ = 42, FN = 66, BA = 26 for specimens from India. In Turkey, Karataş and Sözen (2003: 359) and Arslan and Zima (2014: 7) reported $2n$ = 42, FNa = 64, FN = 68, a meta-/submetacentric X and an acrocentric Y chromosome. The autosomal chromosomes consist of 12 metacentric and submetacentric pairs and 8 acrocentric pairs.

Genetics
See Hoofer and Van Den Bussche (2003).

Capanna *et al.* (1968: 240) already pointed out that there was a cytotaxonomic difference between the Vespertilioninae and the Miniopterinae, especially in the average length of the aploid female set.

Platt *et al.* (2016: 9) analysed the genome data for *M. natalensis* and compared it with that of several other vesper bats and they concluded that *Helitrons* and hATs were introduced into the genome of the Vespertilionidae after their divergence from *Miniopterus*.

HABITAT:
Although *T. nudiventris* has a medium to high wing loading and flexible roost requirements, which could be advantageous for urban life, Marsden *et al.* (2023: 7) found no evidence that it is an urban resident.

Becker *et al.* (2025: 2) indicate that *Taphozous nudiventris* occupies eight distinct habitat types as defined by the IUCN.

HABITS:
Lučan and Šálek (2012: 235) report on the mobbing behaviour of *T. nudiventris* on a barn owl (*Tyto alba*) in the Dakhla Oasis in Egypt. The bats were able to detect the owl when it was on route to their roost, but it could not be determined how the bats were able to do this. There were no alarm or distress calls from other bats, so possibly visual cues or acoustic signals (e.g., sounds made by the feathers of the flying owl) might be involved.

ROOST:
Davis (2007: 10) found that in the United Arab Emirates, they may roost in groups of 200 to 1,000+ individuals. During late pregnancy and lactation, the females form separate groups.

Węgiel *et al.* (2024: 3) reported this species (400 bats) from undamaged domed tombs at the Old Dongola archaeological site (Sudan), and also indicated that none of the damaged tombs housed bats. An additional colony of about 40 bats was found in an old mosque.

DIET:
Benda *et al.* (2012a: 282) report that the most important food categories in Syria, Sudan, Oman and Turkey are Coleoptera (Scarabaeidae) and Orthoptera. Desai *et al.* (2012) [in Benda *et al.*, 2012a: 282] found seasonal changes in the food composition of these bats in Gujarat (India): Coleoptera and Orthoptera prevailed in winter, while Isoptera, Lepidoptera, Orthoptera, Neuroptera and Hymenoptera (Vespoidea) were most consumed in summer.

PREDATORS:
In Algeria, Djilali *et al.* (2016: 161) found remains of 2 *T. nudiventris* specimens in 516 preys captured by the Short-eared Owl (*Asio flammeus* (Pontoppidan, 1763)).

In Sudan, Tryjanowski *et al.* (2024: 2) found remains of this bat in scats of the striped polecat (*Ictonyx striatus* (Perry, 1810)).

POPULATION:
Structure and Density
It is common in some places, and less so in others. It is an uncommon species in the western part of its range: colonies in Africa and the Mediterranean region are generally restricted to a few individuals, although large colonies (dozens to hundreds) have been found in eastern Africa (Bates *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bq). The species is common in its range in South Asia, however, a declining trend in its population has been observed in recent years (Bates and Harrison, 1997).

Trend
2016: Stable (Monadjem *et al.*, 2017bq). 2008: Stable (Bates *et al.*, 2008; IUCN, 2009). *T. nudiventris* populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

REPRODUCTION AND ONTOGENY:
Kurta and Kunz (1987: 82) report that, at birth, the young has a forearm length of about 34.4 % of that of the mother (27.5 against 80.0 mm).

In the United Arab Emirates, Davis (2007: 10) indicates that they arrive in their summer roosts in March, and a single young is born in mid-April. Young are carried by their mothers until 8 weeks of age.

In Gujarat (India), Desai *et al.* (2012: 33) found that pregnancy lasted for 87 days and parturition occurred in August/September. The young reached their full adult size in nine months, when females become sexually mature. The males only become mature at the age of 20 months.

MATING:
In Gujarat (India), Desai *et al.* (2012: 33) report that copulation and fertilization takes place during the last week of March and the first week of April.

PARASITES:
Duszynski (2002: 20) indicates that *T. nudiventris* might be a host for *Eimeria dukei* Lavier, 1927, but as Černá and Ryšavý (1976) did not provide any proof about the parasite, the identification might be wrong, given the fact that eimerians are reasonably host specific.

HEMIPTERA
Cimicidae
Leptocimex vespertilionis Ferris and Usinger, 1957 known only from the Sudan (Zeidab, Khartoum, Wad Medani) (Haeselbarth *et al.*, 1966: 13).

ACARI
Argasidae
Sándor *et al.* (2021a: 4) mentioned *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933), *Chiropterargas confusus* (Hoogstraal, 1955), and *Carios vespertilionis* Latreille, 1802.

Dermanyssidae
Zumpt and Till (1954: 49) mentions that Hirst (1926) described *Steatonyssus sudanensis* from a "*Liponycteris nudiventris*" from near Khartoum, Sudan, but that this mite hasn't been found since.

Rosensteiniidae
Fain (1979: 125) mentioned a *Nycteriglyphus camerounensis* Fain, 1972 and *Nycterilichus longitarsis* Fain, 1972.

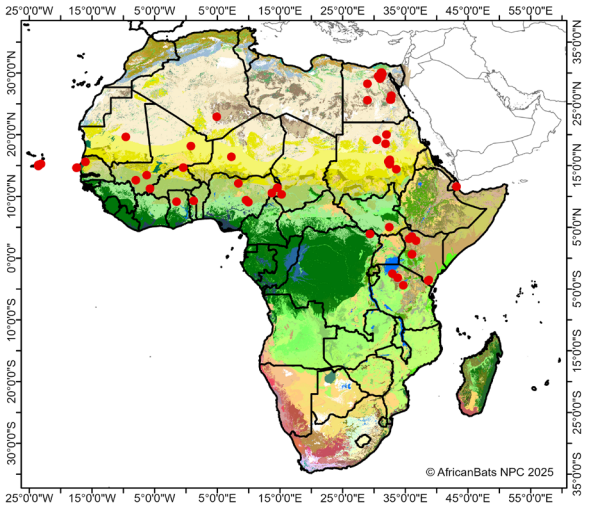

Figure 149. Distribution of *Taphozous nudiventris*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Algeria, Burkina Faso, Cameroon, Cape Verde, Congo (Democratic Republic of the), Djibouti, Egypt, Ethiopia, Ghana, Kenya, Mali, Mauritania, Niger, Nigeria, Senegal, Somalia, South Sudan, Sudan, Tanzania, The Gambia, Togo.

Taphozous perforatus E. Geoffroy St.-Hilaire, 1818

*1818. *Taphozous perforatus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 126. Publication date: 1818. Type locality: Egypt: Kom Ombo [24 26 N 32 57 E]. Holotype: MNHN ZM-MO-1986-1100: ad, alcoholic (skull not removed). Numbers "198" and "A.372" in Rode (1941: 243), who indicates the type might be a male. Previously mentioned as A.372. Paratype: MNHN ZM-AC-1880-236: complete skeleton. Collected by: Etienne Geoffroy-Saint-Hilaire. Paratype: MNHN ZM-AC-A6801: skull only. Collected by: Etienne Geoffroy-Saint-Hilaire. Paratype: MNHN ZM-MO-1985-272: alcoholic (skull not removed). Collected by: Etienne Geoffroy-Saint-Hilaire. - Comments: Allen (1939a: 66) mentioned "Egypt" only as type locality. Restricted to Ombos (=Kom Ombo), between Edfu and Aswan by Kock (1969a: 74): see Meester *et al.* (1986: 32). Mahoney and Walton (1988a: 116) in Grubb *et al.* (1998: 72) considered the date of Geoffroy's publication to be 1813. Gardner and Hayssen (2004: 12) mention that the correct date should be 1818, not 1813 as mentioned on the publication itself. - Etymology: From the masculine scientific Latin adjective *perforàtus*, meaning "perforated", since the tail, as in all Emballonuridae, seems to perforate the uroparagium (see Lanza *et al.*, 2015: 227). (Current Combination).

1877. *Taphozous maritimus* Heuglin, Reise in Nordost Afrika, 2: 25. Publication date: 1877. Type locality: Sudan: Suakin [19 06 N 37 22 E].

1915. *Taphozous perforatus hædinus* Thomas, J. Bomb. nat. Hist. Soc., 24: 62. Publication date: 30 September 1915. Type locality: Kenya: Northern Guaso Nyiro: Chanler Falls [=Chandler's Falls] [00 47 N 38 04 E, 2 000 ft]. Holotype: NHMUK 1912.7.1.46: ad ♂, skin only. Collection date: 3 September 1911; original number: 756.

2014. *Taphozous perforates:* Kohl and Kurth, Viruses, 6 (8): 3115. Publication date: 13 August 2014. (Lapsus).

2023. *Taphozous perforattus:* Al Obaid, Shuraim, Al Boug, Al Jbour, Neyaz, Aloufi and Amr, Diversity, 15 (6): 5. Publication date: 24 May 2023. (Lapsus).

2024. *Taphazois perforatus:* Gippoliti, J. Vertebr. Biol., 73 (23110): 2. Publication date: 5 April 2024. (Lapsus).

? *Taphozous (Taphozous) perforatus:* (Name Combination).

? *Taphozous perforatus haedinus:* (Name Combination).

TAXONOMY:

Harrison (1958b, 1962) regards *sudani* as a separate species, but is not followed in this by subsequent authors (Rosevear, 1965; Kock, 1969a; Hayman and Hill, 1971; Koopman, 1975). Hayman and Hill (1971) make no attempt to recognize subspecies within *perforatus*, but Kock (1969a) recognizes three, *perforatus*, *sudani* and *haedinus*. Koopman (1975) does not agree entirely with the geographic limits suggested by Kock but appears to accept the validity of the names proposed. Simmons (2005) recognized three subspecies: *haedinus* Thomas, 1916; *sudani* Thomas, 1915; and *senegalensis* Desmarest, 1820.

Uvizl *et al.* (2019: 30) could not find any genetic structuring to distinguish *haedinus* from *perforatus* and reject the recognition of subspecies in the Middle East and north-eastern Africa. However, they did not examine material from the type locality, nor from any other East African locality, and therefore do not draw any conclusions about the subspecific status of *haedinus*. A genetic sequence obtained by Benda *et al.* (2025: 31) from a Kenyan bat did not differ from the sequences from other African regions. Therefore, they reject the subspecific status of *haedinus* and consider it a junior synonym of *perforatus*..

Uvizl *et al.* (2019: 30) also indicate that *T. perforatus* is probably of Asian origin, and its occurrence in the Middle East and Africa is the result of a rapid westward expansion, which is illustrated by the lack of genetic structure across its populations.

Benda *et al.* (2025: 73-76) mention that the intraspecific taxonomy of this species is rather controversial and that the subspecific status of *senegalensis* and *sudani* still needs to be confirmed by genetic molecular analyses.

COMMON NAMES:

Afrikaans: Egiptiese witlyfvlermuis. Arabian: Khafash abu bouz saghir, Khaffash. Chinese: 埃及墓蝠. Czech: hrobkovec egyptský, wečerník senegalský, wečerník prowrtaný, netopýr slujový. Dutch: Egyptische grafvleermuis. English: Geoffroy's Tomb Bat, Egyptian Tomb Bat, Tomb Bat, Perforated Taphozous bat, African Taphozous. French: Taphien perforé, Taphien des tombeaux, Chauve-souris des tombes egyptiennes. German: Ägyptische Grabfledermaus. Hebrew: Ashman Katan. Italian: Tafozòo perforàto. Portuguese: Morcego das sepulturas do egipto.

ETYMOLOGY OF COMMON NAME:

The specimen from which this species was described was taken by Geoffroy Saint-Hilaire from a royal tomb in Egypt (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Kock *et al.*, 2008d; IUCN, 2009; Monadjem *et al.*, 2017bo; Monadjem *et al.*, 2020c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bo; Monadjem *et al.*, 2020c). 2008: LC ver 3.1 (2001) (Kock *et al.*, 2008d; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004aa; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: NT D2 ver 3.1 (2001) (Richards *et al.*, 2016b). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
Kock *et al.* (2008d) [in IUCN (2009)], Monadjem *et al.* (2017bo) and Monadjem *et al.* (2020c) report that human disturbance has been highlighted as a threat to *T. perforatus*, but overall it is unlikely that this species is significantly threatened across its very wide range. In South Asia it is threatened by clearing of thorn forests for agricultural purposes, from mining and stone quarrying. Roost disturbance due to human interference and development of old buildings for tourism purposes is also considered serious threats (C. Srinivasulu *pers. comm.*, Molur *et al.*, 2002).

In Egypt, Mansour *et al.* (2017: 109) found that liver and kidney tissues of these bats contained 0.39 µg/g wet weights of DDTs (its usage was prohibited in Egypt in 1980) and 0.11 µg/g wet weights of PCBs (banned worldwide in 1990s). These values showed variations between sexes and seasons.

CONSERVATION ACTIONS:
Kock *et al.* (2008d) [in IUCN (2009)], Monadjem *et al.* (2017bo) and Monadjem *et al.* (2020c) report that this species is present in many protected areas, and no direct conservation measures are currently needed for the species as a whole. The species has not been recorded from any protected areas in Pakistan or India. Being a poorly understood species in the region, more studies on distribution, abundance, reproduction and ecology are recommended (Molur *et al.*, 2002).

GENERAL DISTRIBUTION:
Taphozous perforatus occurs widely throughout northern and sub-Saharan Africa, the Arabian Peninsula, and Asia, east to the Indian Subcontinent. In sub-Saharan Africa, records extend along the Nile and east to Ethiopia and northern Somalia, and west to Mauritania, Senegal, Gambia, Guinea-Bissau, Ghana, Burkina Faso, Benin, Niger, and northern Nigeria, and south to Kenya (including Lamu island), Tanzania, Democratic Republic of Congo, Zimbabwe, and Botswana. In southwest Asia, it has been recorded from Israel, Saudi Arabia, Yemen and Oman. In South Asia, this species is presently known to be widely distributed from southern Pakistan (Roberts, 1977) and western India (Gujarat, Madhya Pradesh and Rajasthan) (Bates and Harrison, 1997, Molur *et al.*, 2002) and recently reported from central Eastern Ghats in Andhra Pradesh (Chakraborty *et al.*, 2004). It has been recorded up to 200 m.

Native: Benin; Botswana (Monadjem *et al.*, 2010d: 535); Burkina Faso (Kangoyé *et al.*, 2015a: 614); Cameroon (Bakwo Fils *et al.*, 2022: 21117); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 535) ; Djibouti (Pearch *et al.*, 2001: 394); Egypt (Benda *et al.*, 2008f: 1); Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Gambia; Ghana; Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 37); India; Iran, Islamic Republic of; Israel; Kenya; Mali; Mauritania; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 535); Niger; Nigeria; Oman; Pakistan; Saudi Arabia; Senegal; Somalia; Sudan; Tanzania; Togo; Uganda; Yemen (Benda *et al.*, 2011b: 30); Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 535); Zimbabwe (Monadjem *et al.*, 2010d: 535).

Presence uncertain: Angola; Côte d'Ivoire; Eritrea; Guinea; Namibia (Cotterill, 2004a: 260); Palestinian Territory, Occupied; United Arab Emirates; Zambia.

DETAILED MORPHOLOGY:
Tongue
El-Mansi *et al.* (2019: 24) identified two type of papillae: mechanical, subdivided into two types of conicals (small and large), and filiform (pronged and crown-shaped) papillae; and gustatory, subdivided into vallate (containing about 10 ovoid taste buds) and fungiform types.

ECHOLOCATION:
In Jordan, Benda *et al.* (2010b: 204) registered the following parameters: F_{start}: 31.4 ± 1.5 (29.6 - 34.4) kHz, F_{end}: 27.6 ± 0.6 (26.6 - 28.8) kHz, F_{peak}:

29.2 ± 0.6 (28.5 - 30.0) kHz, duration: 12.4 ± 4.2 (5.8 - 19.7) ms, and interpulse interval: 225.1 ± 110.4 (58.0 - 426.0) ms.

Two sets of data from Iran were presented by Benda *et al.* (2012a: 182): **1**: F_{start}: 31.4 ± 1.6 (30.0 - 34.2) kHz, F_{end}: 29.1 ± 1.7 (28.1 - 31.8) kHz, and F_{peak}: 30.4 ± 2.1 (28.9 - 33.4) kHz; **2** (hand released): F_{start}: 35.9 ± 0.5 (35.3 - 36.6) kHz, F_{end}: 29.9 ± 0.5 (29.4 - 30.8) kHz, F_{peak}: 32.5 ± 0.3 (32.1 - 33.0) kHz, duration: 4.8 ± 0.3 (4.5 - 5.2) ms, and interpulse interval: 47.3 ± 26.8 (12.5 - 81.3) ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 32.5 kHz, F_{start}: 35.9 kHz, F_{end}: 29.9 kHz, Band width: 6 kHz, and duration: 4.8 ms.

Götze *et al.* (2016: 2) mentioned that *T. perforatus* doesn't shift the frequency of their echolocation signals (jamming avoidance response - JAR) in the presence of conspecifics.

Molecular Biology:

Karyotype

Đulić (1984) and Yaseen *et al.* (1994) reported 2*n* = 42, FN = 64, BA = 24, a metacentric X chromosome and an acrocentric Y chromosome. Volleth *et al.* (2020b: 258, 260) reported 2*n* = 42 and FNa = 66, containing 12 bi-armed, one subtelocentric and seven acrocentric autosomal pairs, a medium-sized metacentric X and a Y chromosome with the same size as the smallest autosomal, which was too small to determine the shape.

Other

Mansour *et al.* (2016: 66) investigated the presence of heavy metals in bats from two caves in the Saqqara region of Egypt and found that cobalt was not detected in winter and spring, and at very low concentration in the other seasons (ca. 0.01 µg/g tissue). High concentrations were found for Fe, Ca, Mg, and to some extent also Al and Zn, whereas Ba, Cu and Mn were found at relatively lower concentrations, and Cr, Cd, Mo, Ni and Pb were detected at very low concentrations. Ba, Cd, Co, Cr, Mo, Ni and Pb were not detected in kidney tissue. Kidneys of males showed higher concentrations of Mg than those of females.

Roost:

Węgiel *et al.* (2024: 3) reported this species (60 bats) from undamaged domed tombs at the Old Dongola archaeological site (Sudan), and also indicated that none of the damaged tombs housed bats.

Diet:

Rydell and Yalden (1997: 72) report that *T. perforatus* mainly feeds on Lepidoptera (moths - 56 % by volume), but also that Isoptera (14 %), Coleoptera (10 %) and Orthoptera (8 %) are major food categories. Furthermore, Hemiptera, Neuroptera, Hymenoptera and Diptera are eaten.

Predators:

Mikula *et al.* (2016: Supplemental data) mention the Fox kestrel (*Falco alopex* (Heuglin, 1861)) and the Lanner falcon (*Falco biarmicus* Temminck, 1825) as avian predators.

Population:

Structure and Density

It is common in parts of its African range but is less common elsewhere. It is found in small colonies (between six to eight individuals) in the southern African subregion (Skinner and Chimimba, 2005). In South Asia the abundance, population size and trends for this species are not known, and the species has only been recorded from a few localities (Bates and Harrison, 1997).

Trend

2016: Stable (Monadjem *et al.*, 2017bo; Monadjem *et al.*, 2020c). 2008: Stable (Kock *et al.*, 2008d; IUCN, 2009).

Reproduction and Ontogeny:

Krutzsch (2000: 113) indicates that *T. perforatus* is a polyoestrous species, although he also mentions (lower on the same page) that it is monoestrous in parts of its range and polyoestrous in others.

Parasites:

HAEMOSPORIDA

Nycteria medusiformis Garnham and Heisch, 1953 was reported from various countries by Perkins and Schaer (2016: Suppl.).

ARACHNIDA

Argasidae

Sándor *et al.* (2021a: 4) mentioned the presence of *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933), *Chiropterargas confusus* (Hoogstraal, 1955), and *Reticulinasus salahi* (Hoogstraal, 1953).

DIPTERA

From Iran, Benda *et al.* (2012a: 275) report on the presence of *Raymondia huberi* Frauenfeld, 1855 (Streblidae). They also indicate that this bat fly occurs in a broad area from East Africa to the Middle East. Other parasites reported by Benda *et al.* (2012a: 276) from the north African part of the bat's range are: *Argas boueti* Roubaud et Colas-Belcour, 1933, *Chiropteropsylla aegyptia*

(Rothschild, 1903), and *C. brockmani* Rothschild, 1915.

Dick *et al.* (2023: 74) mentioned that the nycteribiid fly *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817) has been found on *Taphozous perforatus* from Egypt.

HEMIPTERA
Polyctenidae
Eoctenes intermedius (Speiser, 1912) was reported from the DRC and Egypt by Szentiványi *et al.* (2022: 5).

VIRUSES:
In bats from Saudi Arabia, Mishra *et al.* (2019: 5) found evidence for the presence of the following viruses: Bat astrovirus, Bat Coronavirus, Bat mastadenovirus, Bat papillomavirus, Chuvirus, Rotavirus.

Astroviridae
El Taweel *et al.* (2020: 8) found viruses belonging to the genus Mamastrovirus in bats from Egypt.

Bunyaviridae
Willoughby *et al.* (2017: Suppl.) report the presence of Kaeng Khoi orthobunyavirus.

Coronaviridae - Coronaviruses
Gortazar and Segalés (2013: 954) indicate that recently a virus was identified from a Saudi-Arabian *T. perforatus* specimen that showed 100 % nucleotide identity with MERS-CoV (Middle East Respiratory Syndrome) in a conserved portion of its CoV genome, suggesting that this species might be the host for the MERS-CoV virus [=*Betacoronavirus cameli*].

Flaviviridae
Flavivirus
Dakar bat virus was isolated from the pooled bat organs and salivary glands of this species in 1974 (Williams *et al.*, 1964; Kemp *et al.*, 1974). Reported in this species by de Jong *et al.* (2011: 10), Luis *et al.* (2013: Suppl.), Blitvich and Firth (2017: 3), Willoughby *et al.* (2017: Suppl.).

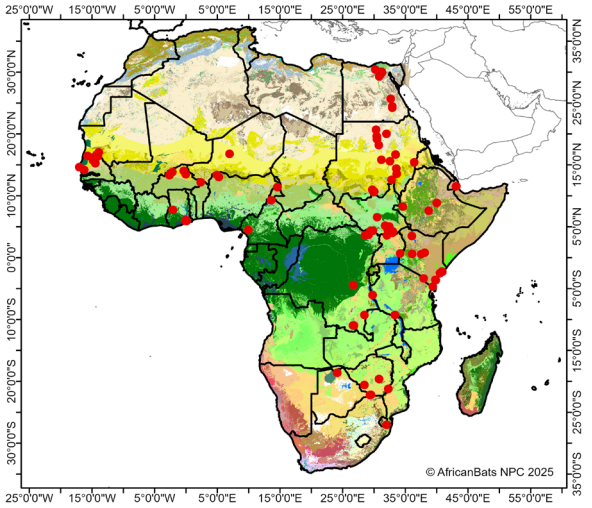

Figure 150. Distribution of *Taphozous perforatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Burkina Faso, Cameroon, Congo (Democratic Republic of the), Djibouti, Egypt, Ethiopia, Ghana, Kenya, Mauritania, Niger, Nigeria, Senegal, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Taphozous perforatus perforatus E. Geoffroy St.-Hilaire, 1818

*1818. *Taphozous perforatus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 126. Publication date: 1818. Type locality: Egypt: Kom Ombo [24 26 N 32 57 E]. Holotype: MNHN ZM-MO-1986-1100: ad, alcoholic (skull not removed). Numbers "198" and "A.372" in Rode (1941: 243), who indicates the type might be a male. Previously mentioned as A.372. Paratype: MNHN ZM-AC-1880-236: complete skeleton. Collected by: Etienne Geoffroy-Saint-Hilaire. Paratype: MNHN ZM-AC-A6801: skull only. Collected by: Etienne Geoffroy-Saint-Hilaire. Paratype: MNHN ZM-MO-1985-272: alcoholic (skull not removed). Collected by: Etienne Geoffroy-Saint-Hilaire. - Comments: Allen (1939a: 66) mentioned "Egypt" only as type locality. Restricted to Ombos (=Kom Ombo), between Edfu and Aswan by Kock (1969a: 74): see Meester *et al.* (1986: 32). Mahoney and Walton (1988a: 116) in Grubb *et al.* (1998: 72) considered the date of Geoffroy's publication to be 1813. Gardner and Hayssen (2004: 12) mention that the correct date should be 1818, not 1813 as mentioned on the publication itself. - Etymology: From the masculine scientific Latin adjective *perforàtus*, meaning "perforated", since the tail, as in all Emballonuridae, seems to perforate the uroparagium (see Lanza *et al.*, 2015: 227). (Current Combination).

1820. *Taphozous senegalensis* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 130. Publication date: 1820. Type locality: Senegal: "Senegal". - Comments: Based on "le lérot-volant" of Daubenton, Mém. Acad. Paris, p. 366, 1759 (see Allen, 1939a: 66).

1958. *Taphozous perforatus swirae* Harrison, Durban Mus. Novit., 5 (11): 144. Publication date: 15 December 1958. Type locality: Nigeria: N Nigeria: Sokoto [13 02 N 05 16 E]. Holotype: NHMUK 1967.1226: ad, skin and skull. Collected by: Mrs. Pamela Swire; collection date: 26 August 1958. Skin made up by D.L. Harrison, formerly in HZM collection 12.2690. - Comments: Grubb *et al.* (1998: 72) mention the locality as Sokoyo. Considered a valid subspecies by Grubb *et al.* (1998: 73), but see Kock (1969a: 80 - 81).

? *Taphozous perforatus perforatus:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Burkina Faso, Egypt, Ethiopia, Ghana, Kenya, Mauritania, Niger, Nigeria, Senegal, South Sudan, Sudan, Tanzania, Uganda.

Taphozous perforatus sudani Thomas, 1915

*1915. *Taphozous Sudani* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 561. Publication date: 1 June 1915. Type locality: Sudan: Equatoria Province: Upper Nile, N of Lado: Mongalla [05 10 N 31 50 E, 500 m]. [Goto Description]. Holotype: NHMUK 1902.7.4.2: ad ♂. Collected by: W.L.S. Loat Esq. Presented/Donated by: W.L.S. Loat Esq. - Etymology: Referring to the country where the type specimen was collected.

1962. *Taphozous sudani australis* Harrison, Occ. Pap. Nat. Mus. S. Rhod., 26B: 763. Type locality: Zimbabwe: Junction between Limpopo and Shashi rivers [22 12 S 29 23 E]. [Goto Description]. Holotype: [Unknown] |TS18|: ad ♂. Collected by: M.P. Stuart Irwin *et al.*; collection date: 5 May 1960; original number: 9932. Rhodesian School Exploration Society Sentinel Ranch Expedition. - Comments: Homonym of *T. australis* Gould, 1854, from Australia (Harrison, 1964a; Kock, 1969a: 74; Meester *et al.*, 1986: 32; Simmons, 2005).

1964. *Taphozous sudani rhodesiae* Harrison, Arnoldia Rhod., 1 (3): 2. - Comments: Renaming of *australis* Harrison, 1962, preoccupied.

? *Taphozous perforatus sudani:* (Current Combination, Current Spelling).

PARASITES:
ACARI
Myobiidae
Fain (1973: 297, 299; 2003: 42) reported *Ugandobia barnley* (Radford, 1951), *Ugandobia garambensis* Fain, 1973 and *Ugandobia vachoni* Fain, 1973 on bats from the DRC and Congo.

HEMIPTERA
Polyctenidae
Eoctenes intermedius (Speiser 1904) from the Congo (Haeselbarth *et al.*, 1966: 16).

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Congo (Democratic Republic of the), South Sudan, Tanzania, Uganda.

†Genus ***Vespertiliavus*** Schlosser, 1887

*1887. *Vespertiliavus* Schlosser, Beitr. Pal. Geol. Österr.-Ung, 6: 70; pl I, figs 37, 40, 44, 45, 47, 48, 50-60,.

†***Vespertiliavus aenigma*** (Ravel, 2016)

*2016. *?Vespertiliavus aenigma* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 384, figs 14, 15. Publication date: 30 September 2016. Type locality: Tunisia: Kassérine governorate: Djebel Chambi National Park: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: From the Latin *aenigma*, meaning enigma, puzzle or riddle, referring to the original morphology of the specimens, which makes it difficult to assign them systematically (see Ravel *et al.*, 2016: 384).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Timeframe: Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

†***Vespertiliavus kasserinensis*** (Ravel, 2016)

*2016. *Vespertliavus kasserinensis* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 377, figs 11 - 13. Publication date: 30 September 2016. Type locality: Tunisia: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: The name refers to the city of Kasserine, at the foot of Djebel Chambi (see Ravel *et al.*, 2016: 377).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Timeframe: Late lower Eocene (Ypresian - Centeno-Cuadros *et al.*, 2019: Suppl.) to early middle Eocene.

Family NYCTERIDAE Van der Hoeven, 1855

*1855. *Nycteridae* Van der Hoeven, Handboek Dierkunde, 2nd ed, 2: 1028. - Comments: Type genus: *Nycteris* Cuvier and Geoffroy, 1795. - Etymology: The family gets its name from the Greek name for a bat, *Nycteris* (see Taylor, 2005). (Current Combination).

1866. *Nyctericina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 91. Publication date: 1 February 1866.

1910. *Petaliidæ* Miller, Proc. Biol. Soc. Wash., 22: 90 [Goto Description]. - Comments: Type genus: *Nycteris* Cuvier and Geoffroy, 1795. Replacement name for Nycteridae Dobson, 1875, due to the fact that Miller (1910) considered the name for the type genus (*Nycteris* Geoffroy 1803) to be antedated by *Nycteris* Borkhausen, 1797).
1984. *Nycteridídae:* Butler, Palaeovert., 14 (3): 117, 185. Publication date: 15 November 1984. (Emendation).
2015. *Nycteriidae:* Anti, Owusu, Agbenyega, Annan, Badu, Nkrumah, Tschapka, Oppong, Adu-Sarkodie and Drosten, Emerg. Inf. Dis., 21 (8): 1419. Publication date: August 2015. (Lapsus).
2018. *Nicteridae:* Malekani, Musaba, Gembu, Bugentho, Toengaho, Badjedjea, Ngabu, Mutombo, Laudisoit, Ewango, Van Cakenberghe, Verheyen, Asimonyo, Masudi, Bongo and Ngbolua, Nat. Conserv. Res., 3 (1): 68. Publication date: January 2018. (Lapsus).

Taxonomy:

Koopman (1993a) mentions Van der Hoeven (1855) as author whereas Corbet and Hill (1992: 88) mention Dobson (1875e: 348).

Flower (1900: 344), Sclater (1901: 120), Medway (1978: 19), Sigé and Legendre (1982), Kock *et al.* (2002b: 82), Hand and Archer (2005: 376), and Lanza *et al.* (2015: 232) use the name Nycteridídae, but we follow Gunnell and Simmons (2005: 212), who state (when referring to the Tanzanycteridae): "This family is a new taxon named by Gunnell *et al.* (2003) for *Tanzanycteris*. They spelled the family name Tanzanycteridídae, but we follow Simmons and Geisler (1998: 133, footnote 13), who argued that all bat family group names based on generic epithets ending with the Greek root -nycteris should be spelled the same way, i.e., -nycteridae rather than -nycteridídae."

Simmons and Geisler (1998: 133) state: "Despite Russell and Sigé (1970)'s argument about the nature of the greek root of -nycteris, we think that it is counterproductive to spell some family-group names in one fashion and others differently. Because Nycteridae is widely accepted as the spelling of the family-group name based on *Nycteris*, we argue that all family-group names based on genera ending in -nycteris should be spelled in the same fashion."

Currently (Simmons and Cirranello, 2024a) recognized genus in the family Nycteridae: ***Nycteris*** G. Cuvier and E. Geoffroy, 1795.
Additionally, there is a fossil genus: *Khoufechia* Ravel, 2016.

Common Names:

Afrikaans: Langoor-vlermuise. Czech: rýhonosovití, nykteridovití. Dutch: Spleetneusvleermuizen. English: Slit-faced bats, Hollow-faced bats, Hispid bats, Long-eared bats. Finnish: Valkopäälepakot. French: Nyctéridés, Chauve-souris à face creuse, Nyctères. German: Schlitznasenfledermäuse, Schlitznasen-Fledermäuse, Schlitznasen. Norwegian: Hullneser, striflaggermus.

Palaeontological or archaeological records:

Shi and Rabosky (2015: 1537) calculated the family-level stem age and crown age to be respectively 52.8 and 17.9 MYA.

The split off from the Emballonuridae occurred according to Amador *et al.* (2016: 22) some 51 MYA, and the diversification within the family started about 33 MYA.

Ravel *et al.* (2016: 415, 418) indicate that *Koufechia gunnelli* represents the basal taxon of the Nycteridae. They also suggest that the family originated in Africa in the Lower Eocene and migrated to Europe in the Oligocene, and even more recently to Asia.

Detailed morphology:

Vomeronasal complex
Smith *et al.* (2024: 13) confirmed a previous observation by Bhatnagar (1980) that VNCs are absent in these bats, but that there are cartilaginous projections, which lead to a nearly separate bar on the animal's right side, and disappear into a mass of bone on the left side.

Molecular Biology:

Karyotype
The karyotype of the various species in this family has a 2*n* value between 34 and 42 (Sotero-Caio *et al.*, 2017: 5).

Parasites:

BACTERIA
Esteves *et al.* (2022: 1) indicate that the Nycteridae - together with the Rhinonycteridae - are the bat families that are most heavily infected by (*Leptospira* bacteria.

Viruses:

Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 14 % of the species belonging to this family are confirmed viral carriers.

Filoviridae
Although no Ebolaviruses have been reported from representatives of this family, Shapiro *et al.* (2020b: 1) indicated that the outbreaks or spillover events of Ebola occurred in areas with

high species richness of nycterid bats (and low levels of both anthropogenic disturbance and human population density). They also suggested that more research is required to investigate the role of the Nycteridae in Ebola spillover to humans as up until now the presence of *Ebolavirus* was only examined in one single species: *Nycteris hispida*, which turned out to be negative for this virus.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa".

†Genus ***Khoufechia*** Ravel, 2016

*2016. *Khoufechia* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 391. Publication date: 30 September 2016. - Etymology: From the Arabian "*Khouféche*", a term to designate abat (see Ravel *et al.*, 2016: 391).

TAXONOMY:
Ravel *et al.* (2016: 358) indicate that this genus has a basal position within the Nycteridae.

†***Khoufechia gunnelli*** Ravel, 2016

*2016. *Khoufechia gunnelli* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 391, figs 18 - 20. Publication date: 30 September 2016. Type locality: Tunisia: Kassérine governorate: Djebel Chambi National Park: Chambi [35 14 03 N 08 45 29 E, 630 m]. - Etymology: In honour of Gregg Gunnell for his numerous contributions to the study of African paleogene bats (see Ravel et al., 2016: 394). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe: Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

Genus ***Nycteris*** E. Geoffroy and G. Cuvier, 1795

*1795. *Nycteris* E. Geoffroy and G. Cuvier, Mag. Encyclop. , 1 année 2: 186. - Comments: Type: *Vespertilio hispidus* Schreber, 1774. Notice that the order of the authors is "Geoffroy and Cuvier" and not "Cuvier and Geoffroy" as most offten mentioned. - Etymology: From the Greek "*νυκτορισ*", meaning "nocturnal", or from the feminine Greek substantive "*νυκτερίς*" (nykterís), "bats" (see Lanza *et al.*, 2015: 234). (Current Combination).
1803. *Nicteris:* Desmarest, Nouveau Dictionnaire d'Histoire Naturelle, 15: 501. (Lapsus).
1813. *Nycterus:* G. Fischer, Zoognosia, ed. iii, I: 18. (Lapsus).
1838. *Petalia* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 494. Publication date: 1 February 1838. - Comments: Type species: *Nycteris Javanicus* E. Geoffroy Saint-Hilaire, 1813.
1845. *Nyctoris:* ?, London Encyclopedia, 22: 738. (Lapsus).
1866. *Nycterops* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 83. Publication date: May 1866 [Goto Description]. - Comments: Type species: *Nycterops pilosa* Gray, 1866 (=*Vespertilio hispidus* Schreber, 1774). - Etymology: Derived from Nycteris and the Greek "*οψ*", meaning aspect (see Palmer, 1904: 465).
1866. *Pelatia:* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 83. Publication date: May 1866. (Lapsus).
1977. *Petelia:* Lekagul and McNeeley, Mammals of Thailand, 107. (Lapsus).
1998. *Nyteris:* Van Cakenberghe and De Vree, Bonn. zool. Beitr., 48 (2): 123. (Lapsus).
? *Nycteris sp. DMR-2017*
? *Nycteris sp.:*

TAXONOMY:
Meester *et al.* (1986) state that Andersen (1912b) divided *Nycteris* into four groups, three of which, viz. *hispida*, *aethiopica* (= *macrotis* - Koopman, 1965, 1975) and *thebaica*, occur in Southern Africa. The fourth group (*arge*) is limited to the African forest block.

Ellerman and Morrison-Scott (1951 1: 106), Corbet and Hill (1992: 88) mention *Nycteris* to be a *nomen nudum*, which was validated by Opinion 111 (Anonymus, 1929) [See also Stiles (1914: 66)]. Revised by Van Cakenberghe and De Vree (1985, 1993a, 1993b, 1999a). A key is provided by Gray *et al.* (1999: 1, Mammalian Species, 612).

Using mitochondrial and nuclear DNA, Demos *et al.* (2019b) distinguished at least 16 lineages in African *Nycteris*, 10 of which were wholly or partly occurring in East Africa, which made them suspect that more lineages will be found in Central and West Africa. Their analyses confirmed the four species groups recognized within the genus. They distinguish the following putative species: *arge* 1, *arge* 2, *grandis, hispida/aurita*, cf. *hispida/aurita, macrotis* 1, *macrotis* 2, *macrotis* 3, *nana* 1, *nana* 2, *thebaica* 1, *thebaica* 2, *thebaica* 3, *thebaica* 4, *thebaica 5*,

thebaica 6, cf. *thebaica* 1, cf. *thebaica* 2, cf. *thebaica* 3.

Based on morphometric and cyt-*b* analyses, Demos *et al.* (2021: 30) concluded that *N. madagacariensis* G. Grandidier, 1937 is a junior synonym of *Nycteris macrotis* Dobson, 1876. Furthermore, their review of the Grandidier's notes and itinerary suggests that the type specimens were not collected on Madagascar, but rather on coastal East Africa (northern Tanzania or Kenya).

Simmons and Cirranello (2023b: 26;2024a:26) assigned *aurita, grandis, hispida, macrotis, parisii* and *woodi* (as well as the extralimital *javanica* and *tragata*) to the subgenus *Nycteris*. Furthermore, they assigned *gambiensis, intermedia, major, nana* and *thebaica* to an "unnamed" subgenus, and did not assign a subgenus to *arge* ("unassigned")..

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Nycteris*: ***arge*** Thomas, 1903; ***aurita*** (K.Andersen, 1912); ***gambiensis*** (K. Andersen, 1912); ***grandis*** Peters, 1865; ***hispida*** (Schreber, 1774); ***intermedia*** Aellen, 1959; *javanica* E. Geoffroy Saint-Hilaire, 1813 – Java, Nusa Penida (near Bali) and Kangean Isl (Indonesia) (Simmons, 2005: 392); ***macrotis*** Dobson, 1876; ***major*** (K. Andersen, 1912); ***nana*** (K. Andersen, 1912); ***parisii*** (De Beaux, 1924); ***thebaica*** E. Geoffroy Saint-Hilaire, 1818; *tragata* (K. Andersen, 1912) – Burma, Thailand, western Malaysia, Sumatra, Borneo (Simmons, 2005: 394); ***woodi*** K. Andersen, 1914.

COMMON NAMES:
Czech: rýhonosi, šerowecové, dutonosecové, nykteridy. English: Hollow-faced bats, Slit-faced bats. French: Nyctères. German: Schlitznasen-Fledermäuse, Schlitznasen. Italian: Nitterìdi, Nicterìdi. Kiluba (DRC): Kasusu. Kiande (DRC): Kakorokombe.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery (2007: 619) reported on the presence of *Nycteris* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa. The approximate fossil date for the genus was reported by Shi and Rabosky (2015: 1532) to be about 5.332 million years ago.

DENTAL FORMULA:
All of the recent *Nycteris* species examined by Czaplewski and Baker (2022: 269) possessed deep carnassiform notches (CN) on the cristid obliqua, but never on the postcristid. They suggest these notches increase the functional efficiency at sectioning chitin.

ECHOLOCATION:
One call from a non-identified *Nycteris* from Zambia was reported by Taylor-Boyd *et al.* (2025: 116): Interpulse interval: 68.5 ms; F_{max}: 71.3 kHz; Start slope: -17.7 kHz/ms; End slope: 16.5 kHz/ms; Ledge duration: 0.5 ms.

Fernandes *et al.* (2025: 6) remark that *Nycteris* species are sometimes not detected acoustically, most probably as a result of their short FM pulses that are often excluded as noise by the sound analysis software.

MOLECULAR BIOLOGY:
Genetics
In their study of the *FoxP2* gene, Li *et al.* (2007: 6) found that *Nycteris* shows the highest rate of non-synonymous change at exon 17, which they link with the evolution of nasal emission, multi-harmonic call structure and prey location by passive listening.

HABITS:
Rainho *et al.* (2023: 7) assigned the *Nycteris* bats in Meru county (Kenya) to a low-flying guild as they are flying at altitudes less than 3.5 m.

ROOST:
In the Ruaha National Park in Tanzania, Dorward *et al.* (2021: 1) reported bats belonging to this genus roosting in latrine cesspits.

In Kenya (Taita-Taveta county), Jackson *et al.* (2023: 5) mentioned four roosts in buildings of which one was shared with another species.

DIET:
Nsengimana *et al.* (2023: 8) analyzed fecal pellets of four sp. individuals from eastern Rwande and found none of these to contain Lepidoptera, but one species of *Conocephalus* Thunberg, 1815 (Orthoptera).

PARASITES:
HAEMOSPORIDA
Perkins and Schaer (2016: Suppl.) reported *Nycteria medusiformis* Garnham and Heisch, 1953 from various countries in Africa.

ACARI
Demodecidae
Fain (1960: 84) described *Stomatodex cornett* from a *Nycteris* sp. from Astrida (= Butare), Rwanda.

Myobiidae
Fain (1994: 1280) indicates that one species of *Ewingana* has been reported from a *Nycteris*, but this is possibly due to a museum contamination. Various species of the genus *Nycteris* do harbour one species of the monotypic genus *Nycterimyobia* (also see Fain, 1994: 1280).

DIPTERA
Nycteribiidae
Penicillida pachymela Speiser, 1901, from Somalia, Sudan, Kenya, Tanzania, the Congo, Guinea and the Cameroon Mts (Haeselbarth *et al.*, 1966: 114; Dick *et al.*, 2023: 78).

HEMIPTEA
Polyctenidae
Eoctenes nycteridis (Horváth, 1910) was reported by Szentiványi *et al.* (2022: 4).

VIRUSES:
Coronaviridae
None of the 18 Kenyan bats tested positive for CoV (Tao *et al.*, 2017: Suppl.). In Guinea, 1 out of 3 *Nycteris* specimens tested by Lacroix *et al.* (2020: 7) was positive for CoV. Widagdo *et al.* (2017: 1) indicate that MERS-CoV-like viruses were detected in 24.9 % of the Ghanaian *Nycteris* bats.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that one of two examined *Nycteris* specimens from Kenya tested positive for *Paramyxovirus* sequences.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 1 Tanzanian and 1 Kenyan *Nycteris* sp. specimen, but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Egypt, Ethiopia, Gabon, Ghana, Guinea, Kenya, Mozambique, Namibia, Nigeria, Senegal, Somalia, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Nycteris arge Thomas, 1903

*1903. *Nycteris arge* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (72): 633. Publication date: 1 December 1903. Type locality: Cameroon: SW Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1904.2.8.2: ad ♂, skull and alcoholic. Collected by: George Latimer Bates Esq. - Etymology: From the Greek "*argos*" meaning shiny, bright, nimble, swift, rapid. (Current Combination).
1910. *Petalia arge:* Thomas and Wroughton, Trans. Linn. Soc. Lond., 19 (5) (63): 488. (Name Combination).
2002. *Nycteris argae:* Fenton and Bogdanowicz, Can. J. Zool., 80: 1008. (Lapsus).
2014. *Nycteris arge 2:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris arge 1:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 ((4): 1023. Publication date: 20 August 2019.
? *Nycteris arge complex sp. 1 TD-2019*
? *Nycteris arge complex sp. 2 TD-2019*

TAXONOMY:
Formerly included *intermedia* (Hayman and Hill, 1971: 19), but see Van Cakenberghe and De Vree (1985).

arge species group (Van Cakenberghe and De Vree, 1985; Simmons, 2005: 391).

COMMON NAMES:
Castilian (Spain): Murciélago de Cara Hueca. Chinese: 淡色凹脸蝠. Czech: rýhonos guinejský. English: Bates's Slit-faced Bat, Nimble Slit-faced Bat. French: Nyctère de Bates. German: Bates' Schlitznasen-Fledermaus. Kiluba (DRC): Katutu. Tshokwe (Angola): Kafukufuku.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bf; IUCN, 2009; Monadjem *et al.*, 2017ar).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ar). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bf; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004by; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It parts of its range it is presumably threatened by conversion of forest to agricultural land, and the logging of roost trees (Mickleburgh *et al.*, 2008bf; IUCN, 2009; Monadjem *et al.*, 2017ar).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bf) [in IUCN (2009)] and Monadjem *et al.* (2017ar) reported that in view of the species wide range, it is presumably present in some protected areas. Further studies are needed into the distribution and threats to this species.

GENERAL DISTRIBUTION:
Nycteris arge is widely distributed over much of West and Central Africa. It ranges from Sierra Leone in the west, through West Africa and the Congo Basin to western Uganda, southern Sudan, western Kenya, northern Tanzania and Burundi. It is distributed as far south as southern parts of the Democratic Republic of the Congo and northern Angola.

Amori *et al.* (2016: 217) [referring to Grubb *et al.* (1998: 74)] pointed out that the record from Togo (reported until ACR, 2015) is actually from Ghana.

Native: Angola (Hayman, 1963; Simmons, 2005: 391; Monadjem *et al.*, 2010d: 547); Burundi; Cameroon (Simmons, 2005: 391); Central African Republic (Lunde *et al.*, 2001: 537); Congo (Bates *et al.*, 2013: 335); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Simmons, 2005: 391; Monadjem *et al.*, 2010d: 547); Côte d'Ivoire; Equatorial Guinea [= Bioko] (Simmons, 2005: 391); Gabon; Ghana (Decher and Fahr, 2007: 12 - 13); Guinea (Fahr *et al.*, 2006a: 72); Kenya (Webala *et al.*, 2004: 171; Simmons, 2005: 391); Liberia (Monadjem and Fahr, 2007: 50); Nigeria; Rwanda; Sierra Leone (Simmons, 2005: 391); Sudan (Simmons, 2005: 391); Tanzania; Uganda (Kityo and Kerbis, 1996: 60).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 11 specimens: Fa: 45.23 ± 0.880 mm, mass: 10.9 ± 0.94 g, wing loading: 5.9 ± 0.50 N/m^2, aspect ratio: 4.8 ± 0.49.

Ferreira *et al.* (2020a: 88) reported on a piebald *Nycteris arge* that was captured in Equatorial Guinea and had distinct white patches on its body and normally pigmented eyes. 90

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Eisenberg and Wilson (1978: 743) indicate that *N. arge* has a relatively larger cranial volume than its congeners, which they link to differences in feeding strategy and habitat selection.

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 3.15 - 4.28 mm in length; the shaft is long, slender, parallel-sided and essentially straight; the base is expanded and round; in lateral profile it is sometimes angled ventrally while the tip is simple, with only a small expansion (Thomas *et al.*, 1994: 19).

Brain
Tambusso and Fariña (2015: Suppl.) mention a brain mass of 0.36 g for an average body mass of 10.6 g.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Monadjem *et al.* (2011)] mention a wing loading value of 5.9 Pa, aspect ratio 4.8 for a wingspan of 30 cm and a wing area of 181 cm^2 and a body mass of 11 g.

ECHOLOCATION:
From western Uganda, Monadjem *et al.* (2011: 32) reported two different sets of data for two calls each: F_{min}: 21.55 kHz, F_{max}: 22.11 kHz, F_{char}: 21.88 kHz, F_{knee}: 21.77 kHz, duration: 4.1 ms; F_{min}: 46.43 kHz, F_{max}: 47.83 kHz, F_{char}: 47.23 kHz, F_{knee}: 47.23 kHz, duration: 5.9 ms. The authors indicate that these different data might represent harmonics.

Tanshi *et al.* (2022a: 332) mention that the echolocation calls are multi-harmonic steep FM sweeps, which span a range between 13 and 107.7 kHz.

A sound file is available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003656_DPFCVGLACA.WAV

MOLECULAR BIOLOGY:
Karyotype
Ngene *et al.* (2025: 6) reported 2n = 40 and FN = 78 for Nigerian bats.

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
R.B. Woosnam [in Thomas and Wroughton, 1910: 488] reported it to be flying low over the water of the Aruwimi River.

Monadjem *et al.* (2016y: 367) recorded this species widely from forested habitats between 400 and 1,000 m in the Mount Nimba area.

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008bf; IUCN, 2009; Monadjem *et al.*, 2017ar).

Trend
2016: Stable (Monadjem *et al.*, 2017ar). 2008: Stable (Mickleburgh *et al.*, 2008bf; IUCN, 2009).

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2015a: 381) found *Nycteria* cf. *eradi* parasites in *N. arge* from Sierra Leone. Landau *et al.* (2012: 142) and Perkins and Schaer (2016: Suppl.) mention this parasite as *Nycteria eradi* Rosin, Landau *et al.*, 1978.

HEMIPTERA
Polyctenidae
Eoctenes nycteridis (Horváth 1910) from Liberia, Congo, Ruanda-Urundi, Tanzania, Uganda and Eritrea (Haeselbarth *et al.*, 1966: 17; Szentiványi *et al.*, 2022: 6).

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested [as *N. argae*] between 1986 and 1999, for antibody to SARS-CoV in sera in one individual from Oriental Province, DRC, none tested positive (0/1).

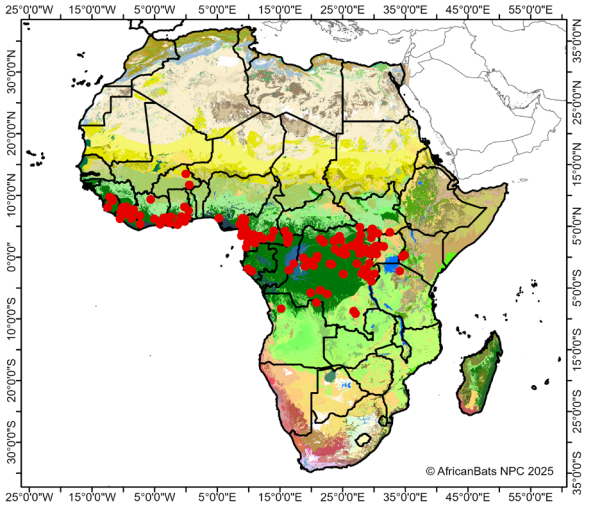

Figure 151. Distribution of *Nycteris arge*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Sierra Leone, South Sudan, Tanzania, Uganda.

Nycteris aurita (K. Andersen, 1912)

*1912. *Petalia aurita* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 547. Publication date: 1 November 1912. Type locality: Kenya: Kilifi [03 38 N 39 51 E]. [Goto Description]. Holotype: NHMUK 1889.1.11.1: ad ♀, skull and alcoholic. Collected by: G.D. Trevor-Roper. Presented/Donated by: G.D. Trevor-Roper. - Etymology: From the feminine Latin adjective *aurìta*, meaning "long-eared" (see Lanza *et al.*, 2015: 236).
1924. *Nycteris aurita:* de Beaux, Atti Sic. Lig. Sci. Lett., ns, 3 (1): ???. (Name Combination, Current Combination).
1957. *Nycteris hispida aurita:* Ansell, Ann. Mag. nat. Hist., ser 12, 10: ???. (Name Combination).
2019. *Nycteris cf. hispida/aurita:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1021. Publication date: 20 August 2019.
2019. *Nycteris hispida/aurita:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Syst. Evol. Res., 57 (4): 1021. Publication date: 20 August 2019.
? *Nycteris hispida/aurita complex sp. TD-2019*
? *Nycteris hispida:* (Name Combination).

GENERAL COMMENTS:
Lanza *et al.* (2015: 236) pointed out that we erroneously mentioned Kitui as type locality for this taxon, whereas this should be Kilifi.

TAXONOMY:
Nycteris aurita is often considered as a synonym or subspecies of *N. hispida* (Blyth, 1863: 391), but see Van Cakenberghe and De Vree, 1993b).

hispida species group Van Cakenberghe and De Vree, 1993b; Simmons, 2005: 391).

COMMON NAMES:
Chinese: 安氏凹脸蝠. Czech: rýhonos východoafrický. English: Andersen's Slit-faced Bat. French: Nyctère d'Andersen, Nyctère à longues oreilles. German: Andersens Schlitznasen-Fledermaus. Italian: Nitterìde orecchiùta, Nicterìde orecchiùta.

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population (it is common where it has been recorded), and because its savanna habitat is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017f).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017f). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008r; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004n; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known, however, it is likely that there are no major threats to the species, as it has been recorded from an extensive habitat that is not severely declining (Mickleburgh *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017f).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008r) [in IUCN (2009)] and Monadjem *et al.* (2017f) report that it is not known if there are any direct conservation measures in place, or if the species is present within any protected areas. Further studies are needed into the distribution, natural history and possible threats to this little-known species.

GENERAL DISTRIBUTION:
Nycteris aurita is known from scattered records in East Africa. It has been recorded from northern Somalia in the north of its range, through southern Ethiopia and Sudan, into Kenya and Tanzania in the south.

Native: Ethiopia (Lavrenchenko *et al.*, 2004b: 147; Simmons, 2005: 391); Kenya (Simmons, 2005: 391); Somalia (Simmons, 2005: 391); Sudan; Tanzania (Simmons, 2005: 391), United Republic of; Uganda; Zambia.

POPULATION:
Structure and Density
There is little information available on the abundance of this species, but it seems to be common where it has been recorded (Mickleburgh *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017f).

Trend
2016: Unknown (Monadjem *et al.*, 2017f). 2008: Unknown (Mickleburgh *et al.*, 2008r; IUCN, 2009).

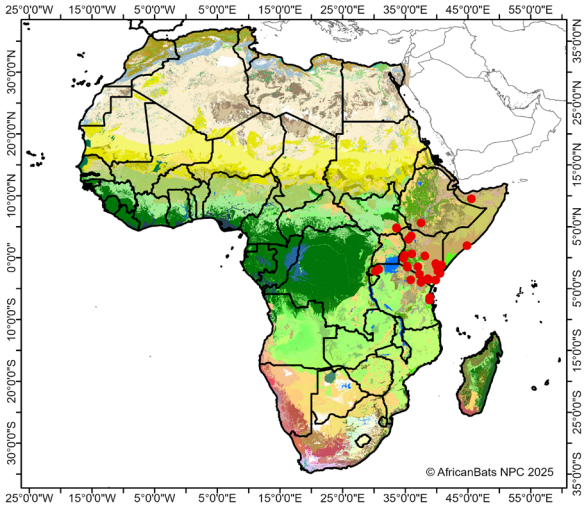

Figure 152. Distribution of *Nycteris aurita*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Kenya, Rwanda, Somalia, South Sudan, Tanzania.

Nycteris cf. parisii De Beaux, 1924

2016. *Nycteris cf. parisii* Kruskop, Benda, Vasenkov and Lavrenchenko, Lynx, 47: 60.

TAXONOMY:
Due to the lack of molecular genetic analyses, Kruskop *et al.* (2016: 60) indicate that taxonomic composition and species delimitations in the *N. woodi* complex are rather uncertain. Van Cakenberghe and De Vree (1985) suggested that *parisii* and *benuensis* are synonyms of *N. woodi*, but based on bacular morphology, Thomas *et al.* (1994) suggested that *parisii* is specifically different from *woodi*. Kruskop *et al.* (2016: 60) state that the shape of the baculum of the specimens they report on, is more like that of *woodi*, and not like that of *parisii* which would be the species involved if the complex contains more than one species.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

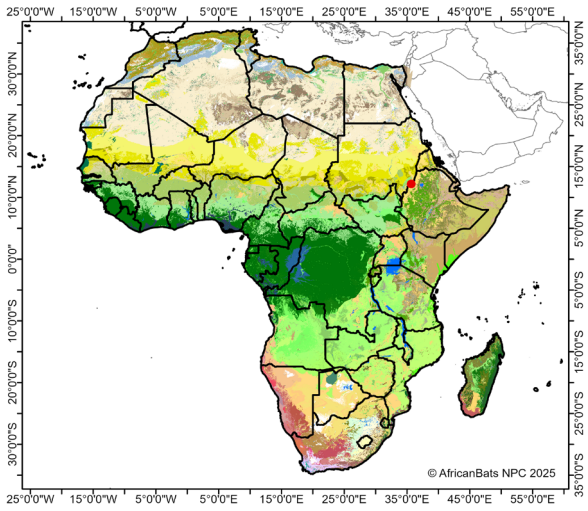

Figure 153. Distribution of *Nycteris* cf. *parisii*.

Nycteris gambiensis (K. Andersen, 1912)

*1912.	*Petalia gambiensis* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 548. Publication date: 1 November 1912. Type locality: Senegal: Dialocote [13 25 N 13 20 W]. [Goto Description]. Holotype: NHMUK 1911.6.10.10: ad, skin and skull. Collected by: G.F. Owen; collection date: 7 May 1910; original number: A5.
1923.	*P[etalia (Nycteris)] th[ebaica] gambiensis:* de Beaux, Atti Soc. ital. Sci. nat., 62: 96. (Name Combination).
1929.	*Nycteris thebaica gambiensis:* Ingoldby, Ann. Mag. nat. Hist., ser 10, 3: 514. (Name Combination).
1939.	*Nycteris gambiensis:* G.M. Allen, Bull. Mus. comp. Zool., 83: 69. (Name Combination, Current Combination).
1975.	*[Nycteris] gambianus:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 381. (Lapsus).
2007.	*Nycteris cambiensis:* Nel and Markotter, Crit. Rev. Microbiol., 33 (4): 308. (Lapsus).
2021.	*Nycteris gambianus:* Coertse, Geldenhuys, le Roux and Markotter, Viruses, 13 (4): 4. Publication date: 29 March 2021. (Lapsus).

TAXONOMY:
Reviewed by Van Cakenberghe and De Vree (1999a).

thebaica species group (Van Cakenberghe and De Vree, 1999a; Simmons, 2005: 392).

COMMON NAMES:
Czech: rýhonos západoafrický. English: Gambian Slit-faced Bat. French: Nyctère de Gambie. German: Gambia Schlitznasen-Fledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Bergmans and Fahr, 2008; IUCN, 2009; Monadjem *et al.*, 2017ah).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ah). 2008: LC ver 3.1 (2001) (Bergmans and Fahr, 2008; IUCN, 2009). 2004: LC ver 3.1 (2001) (Bergmans and Fahr, 2004; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species overall. It is threatened in parts of its range by habitat loss, often resulting from conversion of savanna to agricultural use (Bergmans and Fahr, 2008; IUCN, 2009; Monadjem *et al.*, 2017ah).

CONSERVATION ACTIONS:
Bergmans and Fahr (2008) [in IUCN (2009)] and Monadjem *et al.* (2017ah) report that there appear to be no direct conservation measures in place for this species, and it is not known if it occurs in any protected areas. There is a need to protect roosts of this species, and to better determine the eastern limits of the species range.

GENERAL DISTRIBUTION:
Nycteris gambiensis is a West African species which ranges from Senegal and the Gambia, through most of West Africa, as far east as central Nigeria. There is a single uncertain record from Cameroon which requires verification.

A record from Sierra Leone is in error (J Fahr *pers. comm.* in Simmons, 2005: 392)

Native: Benin (Simmons, 2005: 392); Burkina Faso (Simmons, 2005: 392; Kangoyé *et al.*, 2015a: 615); Côte d'Ivoire (Simmons, 2005: 392); Gambia (Simmons, 2005: 392); Ghana (Simmons, 2005: 392); Guinea (Simmons, 2005: 392; Decher *et al.*, 2016: 264); Guinea-Bissau (Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 43; Simmons, 2005: 392); Mali; Mauritania; Niger; Nigeria (Simmons, 2005: 392); Senegal (Simmons, 2005: 392); Togo (Simmons, 2005: 392).
Uncertain: Cameroon; Sierra Leone (Simmons, 2005: 392).

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 2.88-3.42 mm in length; the shaft is slender and parallel-sided; the base is expanded and in lateral view is angled ventrally, while the tip is simple with a slight expansion (Thomas *et al.*, 1994:22).

POPULATION:
Structure and Density
It can be a locally common species (Bergmans and Fahr, 2008; IUCN, 2009; Monadjem *et al.*, 2017ah).

Trend
2016: Unknown (Monadjem *et al.*, 2017ah).
2008: Unknown (Bergmans and Fahr, 2008; IUCN, 2009).

PARASITES:
CESTODA
Hymenolepididae
Jenzen and Howell (1983: 135) referred to Edungbola (1981) , who mentioned *Vampirolepsis kerivoulae* (Hübscher, 1937) from a bat from Nigeria

VIRUSES:
Willoughby *et al.* (2017: Suppl.) report the following viruses: Chobar Gorge virus, Lagos bat lyssavirus, Saboya virus.

Coronaviridae - Coronaviruses
Betacoronavirus
Annan *et al.* (2013: 457) reported that 46 out of 185 (24.9 %) *N.* cf. *gambiensis* specimens tested in Ghana were found to be positive for 2c *Betacoronavirus*. They also found that juvenile bats and lactating females were more likely to be infected than adult males and non-lactating females.

Flaviviridae
Flavivirus
de Jong *et al.* (2011: 10) and Luis *et al.* (2013: suppl.) reported Saboya virus occurring on this species. Calderon *et al.* (2016: 8) also mention Sokuluk virus.

Reoviridae
Orbivirus
Fomede virus
Reported in the CDC's Arbovirus Catalogue, to have been isolated in 1978 from the Republic of Guinea, from the brain and internal organs of *N.* cf. *gambiensis*. Reported by de Jong *et al.* (2011: 11) and Luis *et al.* (2013: suppl.).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Lagos bat virus
Isolated in Guinea (Institute Pasteur, 1985). Coertse *et al.* (2021: 4) mention this was the only time LBV was found in an insectivorous bat.

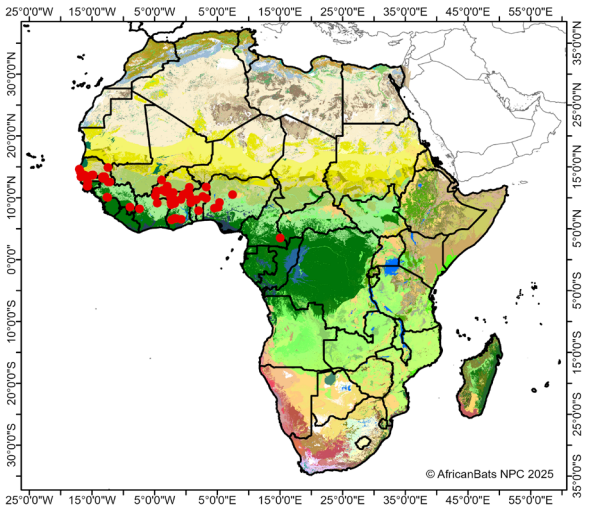

Figure 154. Distribution of *Nycteris gambiensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Guinea, Guinea-Bissau, Nigeria, Senegal, The Gambia, Togo.

Nycteris grandis Peters, 1865

*1865. *Nycteris grandis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 351, 358. Type locality: Ghana: vicinity of Elmina [05 05 N 01 21 W]. [Goto Description]. Holotype: RMNH MAM.27348: ad, skin only. Collected by: Colonel C.J.M. Nagtglas; collection date: 1863. Previously (before 2025), we had this specimen mentioned as "paralectotype". However, the online catalog mentions this specimen as "holotype", which agrees with Peters (1865a: 359), who mentions a single specimen in the RMNH collection. - Comments: Grubb *et al.* (1998: 76) mention the type locality as 'Usually given as "Guinea" but the type, in the Leiden Museum, was collected in 1863 by Nagtglas, and ascribed to Côte d'Or (Jentink, 1888b: 170). The type locality may be further restricted to the vicinity of Elimina [Ghana] which is the only definite locality Jentink cited for any of the Nagtglas material'. The publicatiion covers a meeting held on 13 July 1865. - Etymology: From the Greek "*grandis*" meaning magnificent (Brown, 1991; Jaeger, 1972, both in Hickey and Dunlop, 2000: 3). (Current Combination).

1866. *Nycteris Baikii* J. E. Gray, in: Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 672 (for 1866). Type locality: "Africa": West Africa: Baikie. - Comments: Meester *et al.* (1986: 34) mention "Gray in Peters" as author. Nomen nudum.

1912. *Petalia grandis:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): ???. (Name Combination).

1923. *Nycteris marica* Kershaw, Ann. Mag. nat. Hist., ser 9, 12 (70): 534. Publication date: 1 October 1923. Type locality: Tanzania: Kilosa: Tindiga [06 55 S 37 20 E]. [Goto Description]. Holotype: NHMUK 1923.8.2.1: ad, skin and skull. Collected by: Professor Arthur Loveridge; collection date: 24 January 1922.

1925. *Nycteris proxima* Lönnberg and Gyldenstolpe, Ark. Zool. Stockholm, 17B (9): 1. Publication date: 14 May 1925. Type locality: Congo (Democratic Republic of the): Semliki valley: Kartoushi [00 44 N 29 34 E]. [Goto Description]. Holotype: NRM 100755: ad ♂. Collection date: 11 May 1921; original number: 813. See Lönnberg and Gyldenstolpe (1925: 2).

1938. *[Nycteris] narica:* Frechkop, Exploration du Parc National Albert, 50. (Lapsus).

1938. *[Nycteris] praxima:* Frechkop, Exploration du Parc National Albert, 50. (Lapsus).

1981. *N[ycteris] g[randis] marica:* Kock, Senckenb. biol., 61 (5/6): 325. (Name Combination).

1991. *Nycteris graudis:* Baker, Honeycutt and Van den Bussche, Bull. Am. Mus. Nat. Hist., 206: 46. (Lapsus).

2016. *Nycteris grande:* Bhatnagar, Smith, Rai and Frahm, Anat. Rec., 299: 495. Publication date: 21 January 2016. (Lapsus).

TAXONOMY:



Figure 155. *Nycteris grandis*, Zanzibar Island.

Reviewed by Van Cakenberghe and De Vree (1993b). *N. marica* is sometimes recognized as a distinct savanna subspecies, but this does not seem justified based on morphology (Van Cakenberghe and De Vree, 1993b; Hickey and Dunlop, 2000; Simmons, 2005: 392).

hispida species group (Van Cakenberghe and De Vree, 1993b; Simmons, 2005: 392).

COMMON NAMES:

Afrikaans: Groot spleetneusvlermuis. Chinese: 魁凹脸蝠. Czech: rýhonos velký, nycteris velká. English: Large Slit-faced Bat. French: Grande nyctère. German: Große Schlitznase, Große Schlitznasen-Fledermaus. Portuguese: Morcego grande orelhudo.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bg; IUCN, 2009; Monadjem *et al.*, 2017g).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017g). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bg; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cd; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

In general, there appear to be no major threats to this species as a whole. It is threatened in parts of its range by habitat loss, particularly the logging of large trees used for roosting. Some populations may be threatened by overharvesting for subsistence food (Mickleburgh *et al.*, 2008bg; IUCN, 2009; Monadjem *et al.*, 2017g).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008bg) [in IUCN (2009)] and Monadjem *et al.* (2017g) report that in view of the

species wide range, it is presumably present in a number of protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Nycteris grandis is broadly distributed in sub-Saharan Africa. It ranges from Senegal, through West and Central Africa, to southern Sudan, southeastern Kenya and eastern Tanzania, with scattered records as far south as Zambia, Zimbabwe and Mozambique. Also found on the islands of Zanzibar and Pemba (Simmons, 2005: 392). It is a lowland species.

Native: Benin; Burkina Faso (Kangoyé *et al.* (2012: 6025; 2015a: 615); Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Congo (Bates *et al.*, 2013: 335); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547); Côte d'Ivoire; Equatorial Guinea (Fahr and Ebigbo, 2003: 128); Gabon; Ghana; Guinea; Kenya (Simmons, 2005: 392); Liberia (Fahr, 2007a: 103); Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 815; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547); Mozambique (Smithers and Lobão Tello, 1976; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547; Monadjem *et al.*, 2010c: 381); Nigeria; Senegal (Simmons, 2005: 392); Sierra Leone; Sudan; Tanzania (Stanley and Goodman, 2011: 43) (including the islands of Pemba and Unguja [O'Brien, 2011: 289]); Togo (Capo-Chichi *et al.*, 2004: 162); Uganda (Kityo *et al.*, 2009b: 137); Zambia (Ansell, 1969; Ansell, 1986; Monadjem *et al.*, 2010d: 547); Zimbabwe (Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Hickey and Dunlop (2000).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Hickey and Dunlop (2000).

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 3.45-3.54 mm in length and is small in relation to body size; the shaft is stout and deep, unlike that of any other *Nycteris* examined, the base is narrow and in lateral profile is usually angled ventrally, while the tip is squared, with a pronounced ventral projection (Thomas *et al.*, 1994: 21).

Other
For a description of the skull, ears and tragus, and wingshape and aspect ratio see Hickey and Dunlop (2000).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 11.4 Pa, aspect ratio 5.2 for a wingspan of 38 cm and a wing area of 277 cm^2 and a body mass of 32 g.

SEXUAL DIMORPHISM:
N. grandis is not sexually dimorphic in size (Hickey and Dunlop, 2000: 1).

ECHOLOCATION:
See Taylor (1999b) and Hickey and Dunlop (2000).

Keeley *et al.* (2018: 14) indicate that echolocation calls range between 17 and 114 kHz. Tanshi *et al.* (2022a: 332) mention multi-harmonic calls with a range between 32 and 83 kHz.

MOLECULAR BIOLOGY:
Karyotype
Porter *et al.* (2010) reported for a single male Gabonese specimen as $2n = 42$, with 34 biarmed and 6 acrocentric autosomes, with an X as a large subtelocentric and the Y is a small acrocentric.

Ngene *et al.* (2025: 6) reported $2n = 40$ (p. 6) and 42 (p. 11), and FN = 80 (p. 6) and 82 (p. 11) for Nigerian bats.

HABITAT:
This species has been recorded from a variety of lowland habitats, ranging from lowland tropical moist forest (often found near to swampy sites) to drier savanna areas and Miombo woodland (Rosevear, 1965; Fenton *et al.*, 1990; Hickey and Dunlop, 2000; Skinner and Chimimba, 2005). Kangoyé *et al.* (2015a: 615) report it from a gallery forest in Lera, Burkina Faso.

In the Mount Nimba area, Monadjem *et al.* (2016y: 367) recorded this species from forested and forest edge habitats between 400 and 700 m.

HABITS:
See Hickey and Dunlop (2000).

ROOST:
Nycteris grandis generally roosts in hollow trees, but is also found in manmade structures such as houses (Fenton *et al.*, 1990; 1993), disused water towers (Fenton *et al.*, 1990; 1993) and culverts (Rosevear, 1965). They may also roost in hollow

fallen logs, and holes or small caverns in rocks (Rosevear, 1965; Hickey and Dunlop, 2000).

Happold and Happold (2023: 107) mention they can roost singly, in twos or in small groups, and some of these groups can consist of one male and several pregnant or lactating females, possibly making up harems.

DIET:
Fenton *et al.* (1981: 463; 1990: 2, 4) found that in the Mana Pools National Park, in Zimbabwe, *N. grandis* primarily fed on frogs (e.g., *Ptychadena anchietae, P. mossambica, P.* spp., *Xenopus laevis*), bats (e.g., *Nycteris thebaica, Rhinolophus* cf *darlingi*, "*Pipistrellus* cf. *nanus*", *Hipposideros* cf. *caffer*), arthropods, but sometimes also captured birds (*Cisticola fulvicapilla, Apalis flavida*) and fish (*Tilapia rendalli*, *Barbus* sp., *Alestes* sp.).

Based on various publications by Brock Fenton, Gual-Suárez and Medellín (2021: Suppl.) mention the following prey items: Arachnida: Pholcidae and Solifugae. Insects: Coleoptera: *Cybister senegalensis, Heteronitis castelnaui, Onitis* sp., Tenebrionidae; Dictyoptera; Hemiptera; Homoptera: *Platypleura brevis, Platypleura marshalli, Platypleura quadraticollis*; Hymenoptera; Lepidoptera: *Achaea trapezoids, Acherontia atrops, Hypopyra capensis, Pandesma robusta, Polydesma* sp., *Sarangesa motozi, Pachypasa truncate, Agrius convolvuli, Euchloron megaera, Nephele comma, Omomantis zebrata*; Mantodea: *Polyspilota aeruginosa*; Neuroptera; Odonata; Orthoptera: *Aiolopus* sp., *Arantia* sp., *Gryllacris* sp., *Brachytrupes membranaceus*, *Gryllotalpa* sp., *Lobosceliana brevicornis*, *Sia pinguis*, *Conocephalus* sp., *Horatosphaga* sp., *Zabalius* sp.; Trichoptera. They also mention as variety of vertebrates: Fish: *Tilapia rendalli, Barbus* sp., *Alestes* sp.; Frogs: *Hyperolius marmoratus, Chiromantis xerampelina, Xenopus laevis, Ptychadena anchietae, Ptychadena mossambica*; Birds: *Apalis flavida, Cisticola fulvicapilla* and Nectariniidae; and even other bats: *Rhinolophus darlingi, Rhinolophus landeri, Hipposideros caffer, Hipposideros ruber, Neoromicia capensis* and *Neoromicia nanus*.

Tomita (2025: Suppl.) [referring to Bayefsky-Anand, 2005: 95] reported an unidentified cicada as prey item for *Nycteris grandis*, but Bayefsky-Anand (2005: 95) identified two species: *Oxypleura quadraticollis* (Butler, 1874) and *Brevisana brevis* (Walter, 1850) [=Shrill thorntree cicada]. She also identified two species of antlion: *Palpares tristis* Hagen, 1853 and *Syngenes debilis* (Gerstaecker, 1885).

Gual-Suárez and Medellín (2021: 1) considered *Nycteris grandis* to be the only carnivorous bat in Africa and based on its ecology and the seasonality of its habits it was assigned to the group of seasonal predominantly gleaning carnivores (which further included *Megaderma lyra* and *Macroderma gigas*).

Happold and Happold (2023: 106) mention that small vertebrates make up to 80 % of the diet by weight, where frogs were the main prey (in numbers) in March-May, bats in June-July and arthropods in December-February, but this composition can change from year to year.

Vleut *et al.* (2019: 11) [referring to Fenton *et al.* (1990: 4)] mention that these bats can commute up to 2.2 km to their hunting grounds.

POPULATION:
Structure and Density
It appears to be a rare, or rarely recorded, species. The species occurs in small colonies, but is usually found only as single animals or in pairs (Mickleburgh *et al.*, 2008bg; IUCN, 2009; Monadjem *et al.*, 2017g).

Trend
2016: Decreasing (Monadjem *et al.*, 2017g).
2008: Decreasing (Mickleburgh *et al.*, 2008bg; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
See Hickey and Dunlop (2000).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 115), referring to Verschuren (1957), indicates that *N. grandis* is polyoestrous with two or more (continuous) cycles per year, a postpartum oestrus and often no anoestrus.

Stanley and Goodman (2011: 43), referring to Verschuren (1957), report on a pregnant female collected on 31 July 1993 in the East Usambara Mountains (Tanzania).
Pakenham (1984: 28) reported a pregnant female on Zanzibar in December.

PARASITES:
Little information is available regarding parasites of *N. grandis* (Hickey and Dunlop, 2000).

HAEMOSPORIDA
Schaer *et al.* (2015a: 381) found two different forms of *Nycteria* sp. parasites in *N. grandis* from Sierra Leone. Karadjian *et al.* (2016: 9834) mentioned *Nycteria medusiformis* and *Nycteria* sp. from the DRC. *Nycteria* sp. parasites were

also found in the single bat from Cameroon examined by Tsague *et al.* (2021: 3).

Keymer (1971) reported "broad trypanosomes" from four of six specimens collected from Zambia.

HEMIPTERA
Polyctenidae
Eoctenes nycteridis (Horváth, 1910) from Liberia, Congo, Ruanda-Urundi, Tanzania, Uganda and Eritrea (Haeselbarth *et al.*, 1966: 17; Szentiványi *et al.*, 2022: 6).

SIPHONAPTERA
Pulicidae
Echidnophaga aethiops Jordon and Rothschild, 1906 locality not mentioned (Haeselbarth *et al.*, 1966: 135).

VIRUSES:
Circoviridae
Vidovszky *et al.* (2023: Suppl.) reported Bat associated cyclovirus 12 from a bat in the DRC.

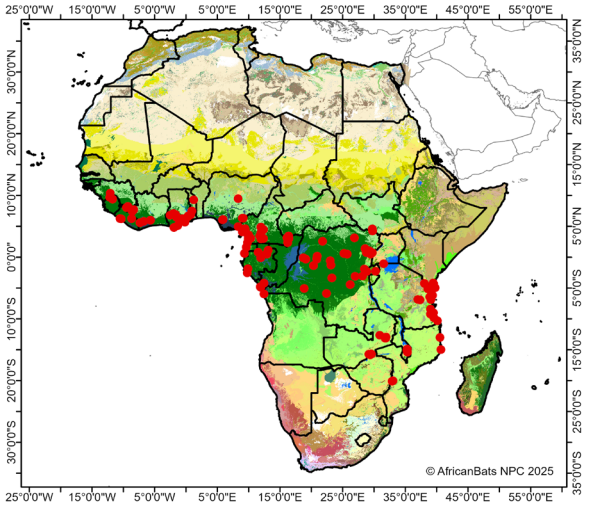

Figure 156. Distribution of *Nycteris grandis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mozambique, Nigeria, Rwanda, Sierra Leone, Tanzania, Togo, Zambia, Zimbabwe.

Nycteris hispida (Schreber, 1774)

*1774. *Vespertilio hispidus* Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, 1 (8): pl 56 + 1 (9): 169, 188. Publication date: 1774. Type locality: Senegal: "Senegal". [Goto Description]. - Etymology: From the masculine Latin adjective *hispidus*, meaning "shaggy", referring to the bristly hair around the facial slit (see Lanza *et al.*, 2015: 242).

1813. *Nycteris Daubentonii* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 20: 19. Publication date: August 1813. Type locality: Senegal: "Senegal". [Goto Description].

1840. *Nycteris hispida:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 3: ???. (Name Combination, Current Combination).

1843. *Nycteris poensis* J. E. Gray, Catalogue of the species of mammals of the British Museum, 24. Publication date: 13 May 1843. Type locality: Equatorial Guinea: Bioko [formerly Fernando Po] [ca. 03 21 N 08 40 E]. [Goto Description]. Holotype: NHMUK 1855.12.26.252: ad ♀, skin and skull. Presented/Donated by: Captain E. Downes R.N. Intended specimen = *Rhinolophus martini* Fraser: see Meester *et al.* (1986: 33). - Comments: Considered a nomen nudum by Dobson (1878: 162) and Allen (1939a: 69).

1843. *Rhinolophus Martini* Fraser, Proc. zool. Soc. Lond., 1843, V (cxxi): 25. Publication date: July 1843. Type locality: Equatorial Guinea: Bioko [formerly Fernando Po] [ca. 03 21 N 08 40 E]. [Goto Description].

1852. *Nycteris villosa* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 48, pl 11. Publication date: 1852. Type locality: Mozambique: Inhambane [24 00 S 35 28 E]. [Goto Description]. Holotype: ZMB 394/85665: ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008) [skull: ZMB 394 + skeleton: ZMB 85665]. - Comments: Considered a valid subspecies by Taylor (1998: 33).

1866. *Nycterops pilosa* J. E. Gray, Proc. zool. Soc. Lond., 1866, I (vi): 83. Publication date: May 1866. Type locality: "Africa": "Africa".

1878. *Nycteris hispida villosa:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 163. Publication date: 15 June 1878. (Name Combination).

1883. *Nycteris hispidus:* Rochebrune, Act. Soc. Linn. Bordeaux, 37: 93. (Name Combination).

1910. *Petalia hispida:* Thomas and Wroughton, Trans. Linn. Soc. Lond., 19 (5) (63): 488. (Name Combination).

1917. *Nycteris pallida* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 425. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 49144: ad ♂. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 1 March 1912; original number: 1858. Paratype: RMCA 12390: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 22 Novermber 1911; original number: formerly AMNH 49119. Topotype: MCZ 17226: ♂, alcoholic (skull not removed). Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 9 March 1912.

1935. *[Nycteris hispida] martini:* Braestrup, Vidensk. Meddr dansk naturh. Foren., 99: 88. (Name Combination).

1935. *N[ycteris] h[ispida] pallida:* Braestrup, Vidensk. Meddr dansk naturh. Foren., 99: 88. (Name Combination).

1935. *Nycteris hispida hispida:* Braestrup, Vidensk. Meddr dansk naturh. Foren., 99: 88. (Name Combination).

2019. *Nycteris cf. hispida/aurita:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1021. Publication date: 20 August 2019.

2019. *Nycteris hispida/aurita:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Syst. Evol. Res., 57 (4): 1021. Publication date: 20 August 2019.
2019. *Nycteris hispidar:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).
? *Nycteris cf. hispida/aurita TD-2019*

TAXONOMY:



Figure 157. *Nycteris hispida*, Zanzibar Island.

Koopman (1975: 377, 378) includes *aurita* and *pallida*. Van Cakenberghe and De Vree (1993b) consider *aurita* as a separate species.

hispida species group (Van Cakenberghe and De Vree, 1993b; Simmons, 2005: 392).

COMMON NAMES:
Afrikaans: Harige spleetneusvlermuis, Harige Langoorvlermuis. Chinese: 粗毛凹脸蝠. Czech: rýhonos štětinatý, šerowec senegalský. English: Hairy Slit-faced Bat, Hairy Long-eared Bat. French: Nyctère hérissée, Nyctère hirsute. German: Rauhaarschlitznase, Gemeine Schlitznasen-Fledermaus, Haarige Schlitznasenfledermaus. Italian: Nitterìde irsùta, Nicterìde irsùta, Nitterìde ìspida, Nicterìde ìspida. Kiluba (DRC): Katutu. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego orelhudo piloso. Tshokwe (Angola): Kafukufuku.

ETYMOLOGY OF COMMON NAME:
Although this species is not hairier than any of the other slit-faced bats, the name is applied to it as a translation of the specific name *hispida*, which is from the Latin *hispidus*, meaning hairy or bristly, referring to the bristly hair around the facial slit (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008s; IUCN, 2009; Monadjem *et al.*, 2017h).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017h). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008s; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004m; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016c). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species. It is locally threatened in parts of its range by habitat loss, largely through the conversion of forest to agricultural use (Mickleburgh *et al.*, 2008s; IUCN, 2009; Monadjem *et al.*, 2017h).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008s) [in IUCN (2009)] and Monadjem *et al.* (2017h) report that in view of the species wide range it is presumably present in a number of protected areas (including the Udzungwa Mountains National Park of Tanzania (Stanley *et al.*, 2005b)). No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
This species has a wide range, encompassing much of sub-Saharan Africa, with the exception of the Horn of Africa and parts of southern Africa. There is an apparently disjunct population in western Mauritania close to the border with Senegal, and an isolated record from central Mali. Also recorded from the island of Unguja [=Zanzibar] (Simmons, 2005: 392; O'Brien, 2011: 289).

The records from Cape of Good Hope are probably invalid (Cotterill, 1996a).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 710,458 km^2.

Native: Angola (Crawford-Cabral, 1989; Hayman, 1963; Simmons, 2005: 392; Monadjem *et al.*,

2010d: 547); Benin (Capo-Chichi *et al.*, 2004: 162); Botswana (Archer, 1977; Cotterill, 2004a: 261; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547); Burkina Faso (Kangoyé *et al.*, 2015a: 615); Burundi; Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Chad; Congo (Bates *et al.*, 2013: 336); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 547); Côte d'Ivoire; Equatorial Guinea [= Bioko] (Simmons, 2005: 392); Ethiopia (Lavrenchenko *et al.*, 2004b: 132); Gabon; Gambia (Simmons, 2005: 392; Emms and Barnett, 2005: 50); Ghana; Guinea (Fahr *et al.*, 2006a: 72); Guinea-Bissau (Bocage, 1892a; Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 41); Kenya; Liberia (Fahr, 2007a: 103); Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 815; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547); Mali; Mauritania (Simmons, 2005: 392); Mozambique (Smithers and Lobão Tello, 1976; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547; Monadjem *et al.*, 2010c: 381); Namibia (Monadjem *et al.*, 2010d: 547); Niger; Nigeria; Rwanda; Senegal (Adam and Hubert, 1976; Simmons, 2005: 392); Sierra Leone; Somalia (Simmons, 2005: 392); South Africa (Monadjem *et al.*, 2010d: 547); Sudan; Tanzania (Stanley *et al.*, 2005b); Togo; Uganda (Kityo and Kerbis, 1996: 60); Zambia (Ansell, 1973; Ansell, 1974; Ansell, 1986; Monadjem *et al.*, 2010d: 547); Zimbabwe (Monadjem *et al.*, 2010d: 547).

Detailed morphology:

Baculum

The baculum ranges from 3.33 - 4.16 mm in length, the shaft is long, slender and variably ventrally curved, the base is expanded and in lateral profile is angled ventrally, while the tip is sometimes angled ventrally, it has a projection on the ventral aspect varying between individuals from a slight swelling to a pronounced hook (Thomas *et al.*, 1994: 20).

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 5.4 Pa, aspect ratio 4.8 and tip shape index of 2.02 for a wingspan of 27 cm and a wing area of 146 cm^2 and a body mass of 8 g.

Echolocation:

In Benin, the bat's call was categorized as a FMd (Frequency modulation downward) sonotype by Roemer *et al.* (2021: Suppl.).

Tanshi *et al.* (2022a: 332) reported mulit-harmonic calls with a frequency range of 81 - 132 kHz and F^{max} > 100 kHz.

See also Taylor *et al.* (2005).

Molecular Biology:

Karyotype

Lee *et al.* (1989) reported 2*n* = 42, FN = 78, BA = 38, and a metacentric X and Y.

Habitat:

Nycteris hispida has been recorded from a wide variety of habitats, ranging from lowland tropical moist forest, into moist savanna, dry savanna, papyrus swamps and marsh.

R.B. Woosnam [in Thomas and Wroughton, 1910: 488] reported it to be most numerous among the acacia trees on the plains around the south end of the Ruwenzori range.

Monadjem *et al.* (2016y: 367) recorded *N. hispida* sparsely in open savanna on the Liberian side of Mount Nimba.

Roost:

Colonies roost in hollow trees, dense bushes, caves, holes in termite colonies and similar habitats.

Predators:

Mikula *et al.* (2016: Supplemental data) mention *N. hispida* to be taken by the Western marsh harrier (*Circus aeruginosus* (Linnaeus, 1758)).

Population:

Structure and Density

Colonies range in size from individual and pairs of animals to up to 20 bats. This is a very common bat (Mickleburgh *et al.*, 2008s; IUCN, 2009; Monadjem *et al.*, 2017h).

Trend

2016: Stable (Monadjem *et al.*, 2017h). 2008: Stable (Mickleburgh *et al.*, 2008s; IUCN, 2009).

Reproduction and ontogeny:

Krutzsch (2000: 94) reports that the testes are probably permanently scrotal in *N. hispida*, according to Matthews (1941). The specieis's reproductive cycle is polyoestrous with two or more (continuous) cycles per year, a postpartum oestrus and often no anoestrus. Matthews (1941) also noticed that copulation followed shortly after parturition.

In Burkina Faso, Kangoyé *et al.* (2015a: 615) captured females carrying young during the month of September.

From Sierra Leone, Weber *et al.* (2019: 25) reported a lactating female with a young attached on 25 May.

Pakenham (1984: 28) caught a sucking young on 18 November on Zanzibar.

PARASITES:

BACTERIA

Obodoechi *et al.* (2021: 3) investigated the antimicrobial resistance of *E. coli* bacteria recovered from Nigerian bats. 70 % of these showed resistance to one of the antimicrobial agents they tested.

PROTOZOA

Kassahun *et al.* (2015: 168) examined one *N. hispida* specimen from Awash-Methara (Ethiopia) and found it infected by *Leishmania major* Friedlin (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 4).

Based on the original description, Austen and Barbosa (2021: 7) and Sato and Mafie (2022: 2) mention the presence of *Trypanosoma (Megatrypanum) heybergi* from the DRC.

Thiombiano *et al.* (2023: 4) reported one *Nycteris hispida* (only one was examined) from Burkina Faso infected by *Trypanosoma* cf. *livingstonei*.

ACARI

Trombiulidae

Vercammen-Grandjean and Fain (1958: 30) described *Trombigastia (Trombigastia) nycteris* from *N. hispida hispida* from the Astrida region (= Butare), Rwanda (Stekolnikov, 2018a: 120).

HEMIPTERA

Polyctenidae

Eoctenes nycteridis (Horváth, 1910) from Liberia, Congo, Ruanda-Urundi, Tanzania, Uganda and Eritrea (Haeselbarth *et al.*, 1966: 17; Szentiványi *et al.*, 2022: 6).

SIPHONAPTERA

Ischnopsyllidae

Lagaropsylla idea Smit, 1957, primary host being molossids but recorded from this taxon (Haeselbarth *et al.*, 1966: 190).

VIRUSES:

Circoviridae

Porcine circovirus 3 was reported by Vidovszky *et al.* (2023: Suppl.) from a *Nycteris* cf. *hispida* from the DRC.

Coronaviridae - Coronaviruses

SARS-CoV

One fecal sample was tested by Pfefferle *et al.* (2009) in Ghana in February 2008, and this was found to be negative for coronavirus (CoV) RNA.

Hantaviridae (formerly included in Bunyaviridae)

Hantavirus

Weiss *et al.* (2012b: 160) report the presence of a new hantavirus, named Magboi virus [MGBV], in one *N. hispda* specimen collected at the Magboi River, Gola National Park, Sierra Leone. Arai *et al.* (2019b: 2) and Arai and Yanagihara (2020: 7) tentatively included this virus in the genus *Loanvirus*.

Paramyxoviridae

Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen they examined from Ghana did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

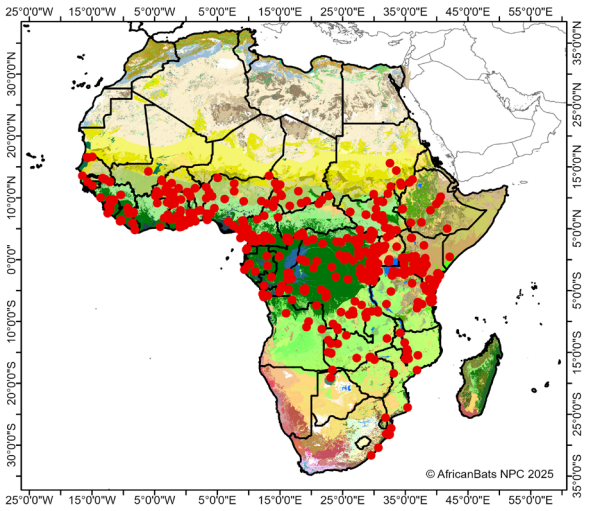

Figure 158. Distribution of *Nycteris hispida*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Lesotho, Liberia, Malawi, Mali, Mauritania, Mozambique, Namibia, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Nycteris intermedia Aellen, 1959

*1959. *Nycteris intermedia* Aellen, Archs Sci. Genève, 12 (2): 218. Type locality: Côte d'Ivoire: NW of Abidjan: Adiopodoumé [05 19 N 04 08 W, 0 - 30 m]. [Goto Description]. Holotype: MHNG 923.094: ad ♀, skull and alcoholic. Collected by: Dr. Villy Aellen; collection date: 20 July 1953; original number: A1437. Paratype: MHNG 923.095: ad ♀, skull and alcoholic. Collected by: Dr. Villy Aellen; collection date: 24 July 1953; original number: A1438. Paratype: MHNG 923.096: ad ♀, skull and alcoholic. Collected by: Dr. Villy Aellen; collection date: 19 August 1953; original number: A1439. Paratype: ad ♀; alcoholic and skull; Collector: Villy Aellen; Original number: Collection date:. Paratype: MHNG 923.097: ad ♀, skull and alcoholic. Collected by: Dr. Villy Aellen; collection date: 24 July 1953; original number: A1440. - Etymology: Referring to its intermediary size between *Nycteris arge* and *Nycteris nana*. (Current Combination).

TAXONOMY:

Formerly included in *N. arge*, but Van Cakenberghe and De Vree (1985) regard this as a distinct species (Simmons, 2005: 392).

COMMON NAMES:

Czech: rýhonos prostřední. English: Intermediate Slit-faced Bat. French: Nyctère d'Aellen, Nyctère moyen. German: Intermediäre Schlitznasenfledermaus, Intermediäre Schlitznasen-Fledermaus.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in some protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bh; IUCN, 2009; Monadjem *et al.*, 2017au).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017au). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bh; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bm; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

The species is threatened in parts of its range by deforestation including loss of roosting trees (Mickleburgh *et al.*, 2008bh; IUCN, 2009; Monadjem *et al.*, 2017au).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008bh) [in IUCN (2009)] and Monadjem *et al.* (2017au) report that there do not appear to be any direct conservation measures in place, however, the species has been recorded from some protected areas (e.g., Comoe National Park and Tai National Park both in Côte d'Ivoire). Further research is needed into the distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:

Nycteris intermedia is broadly distributed in sub-Saharan Africa, ranging from Liberia in the west, to western Tanzania in the east, with records as far south as northeastern Angola. The species appears to be known from around 27 localities. It is typically a lowland species.

Native: Angola (Van Cakenberghe *et al.*, 1999; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 547); Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Congo (The Democratic Republic of the); Côte d'Ivoire (Simmons, 2005: 392); Equatorial Guinea; Gabon; Ghana; Guinea (Denys *et al.*, 2013: 282); Liberia (Simmons, 2005: 392); Tanzania (Simmons, 2005: 392).

MOLECULAR BIOLOGY:

Karyotype

Denys *et al.* (2013: 282) report the karyotype for one female from the Guinean Mount Nimba area as: $2n = 34$, NFa = 62, including 15 pairs of large to small metacentric and submetacentric chromosomes and one middle-sized acrocentric pair. The X chromosome is submetacentric.

POPULATION:

Structure and Density

This species appears to be relatively rare. It is usually found as small groups of animals (Mickleburgh *et al.*, 2008bh; IUCN, 2009; Monadjem *et al.*, 2017au).

Trend

2016: Decreasing (Monadjem *et al.*, 2017au). 2008: Decreasing (Mickleburgh *et al.*, 2008bh; IUCN, 2009).

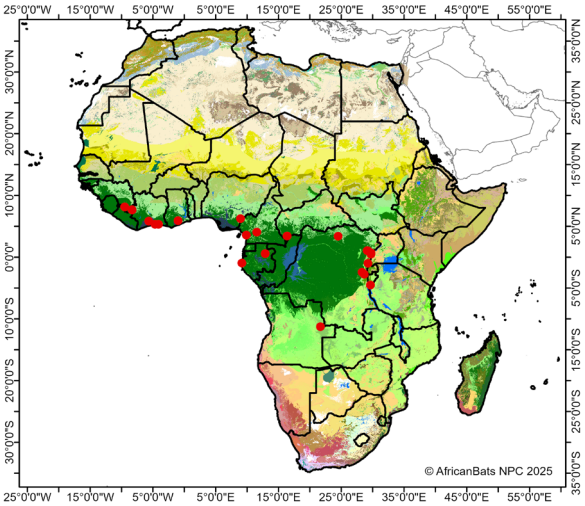

Figure 159. Distribution of *Nycteris intermedia*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Angola, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Ghana, Guinea, Liberia, Nigeria, Tanzania.

Nycteris macrotis Dobson, 1876

*1876. *Nycteris macrotis* Dobson, Monograph of the Asiatic Chiroptera and catalogue of the species of bats in the collection of the Indian Museum Calcutta, 80. Type locality: Sierra Leone: "Sierra Leone". [Goto Description]. Holotype: NHMUK 1866.2.2.2: sad ♂, skull and alcoholic. - Etymology: From the Greeek adjective "*μακρός*" (macròs), meaning "long, large" and the neuter Greek substantive "*οὖς*" (genitive *ώu0964\ός*"; "*ûs*", "*ōtós*"), meaning "ear", although the ear of the species is not of especially outstanding size (see Lanza *et al.*, 2015: 244). (Current Combination).

1878. *Nycteris æthiopica* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, xxxviii, 162, 165, pl 11, fig 3. Publication date: 15 June 1878. Type locality: Sudan: Kordofan province: Sennaar [15 35 N 33 38 E, 425 m]. [Goto Description]. Holotype: NHMUK 1847.5.27.32: ad, skin and skull. Collected by: Theodor Kotschy.

1901. *Nycteris aethiopica aethiopica:* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 30.

1901. *Nycteris aethiopica luteola* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 30. Publication date: 1 July 1901. Type locality: Kenya: Kitui [01 22 S 38 01 E, 3 500 ft]. [Goto Description]. Holotype: NHMUK 1901.5.6.4: ad ♀, skin and skull. Collected by: Dr. Sidney Langford Hinde; collection date: 14 February 1901.

1912. *P[etalia] macrotis:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 548. (Name Combination).

1912. *P[etalia]. ?thiopica luteola:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 549. (Name Combination).

1912. *P[etalia]. ?thiopica ?thiopica:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 549. (Name Combination).

1917. *Nycteris major* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 427. - Comments: Not of Andersen (1912b).

1922. *Nycteris oriana* Kershaw, Ann. Mag. nat. Hist., ser 9, 10 (56): 179. Publication date: 1 August 1922. Type locality: Malawi: Shiré valley: Chiromo [16 32 S 35 09 E, 60 m]. [Goto Description]. Holotype: NHMUK 1922.4.25.3: ad ♀, skin and skull. Collected by: Rodney Carrington Wood Esq. Collection date: 7 June 1918; original number: 312.

1923. *Nycteris luteola:* Loveridge, Proc. zool. Soc. Lond., 1923, II: 396.

1937. *Nycteris madagascariensis* G. Grandidier, Bull. Mus. natn. Hist. nat., Paris, sér 2, 9: 353. Publication date: November 1937. Type locality: Madagascar: N of Diego-Suarez [=Antsiranana]: Rodo valley, N of Pirkana: Ankarana, near the [12 05 S 49 05 E]. [Goto Description]. Holotype: MCZ 45433: skull and alcoholic. Collection date: June 1910. Formerly Grandidier collection; see Helgen and McFadden (2001: 142). Demos *et al.* (2021: 21) indicated that this is an unsexed specimen. Paratype: MCZ 45434: ad ♀, skull and alcoholic. Formerly Grandidier collection; see Helgen and McFadden (2001: 142). - Comments: Based on a review of Grandidier's notes and itinary, Demos *et al.* (2021: 30) conclude that the type specimens were not collected on Madagascar, but on the east coast of the African mainland (possibly either northern Tanzania or Kenya). Mitochondrial material from the type specimen also place this specimen within the continental populations. - Etymology: Referring to the island of Madagascar, where the species occurs.

1939. *Nycteris æthiopica guineensis* Monard, Arq. Mus. Bocage, 10: 66, fig 4. Publication date: March 1939. Type locality: Guinea-Bissau: Mansoa [12 04 N 15 19 W]. [Goto Description]. Syntype: [Unknown] |TS501|: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 1937; original number: 284. Syntype: [Unknown] |TS502|: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 1937; original number: 282. Syntype: MHNG 1326.005: ad ♂, skull and alcoholic. Collected by: Dr. Albert Monard; collection date: 14 December 1937; original number: 283. Syntype: MHNG 861.052: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 14 December 1937; original number: 283. Syntype: NMBA 5271: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 17 Decembre 1937; original number: 319. Syntype: RMCA 15310: ad ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 1937; original number: 285. - Comments: Monard (1939: 66) mentions a larger series: 282 (♀), 283 (♂), 284 (♂), 285 (♀), 319 (♂).

1939. *Nycteris æthiopica guineensis f. aurantiaca* Monard, Arq. Mus. Bocage, 10: 68. Publication date: March 1939. Type locality: Guinea-Bissau: Pitche [12 20 N 13 57 W]. [Goto Description].

1942. *Nycteris aethiopica oriana:* G.M. Allen and Loveridge, Bull. Mus. comp. Zool., 89 (4): 150, 161.

1953. *Nycteris macrotis macrotis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 54. (Name Combination).

1953. *Nycteris macrotis oriana:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 54. (Name Combination).
1960. *Nycteris macrotis luteola:* Harrison, J. East Afr. Nat. Hist. Soc., 23 (7) (104): 288. Publication date: December 1960. (Name Combination).
1965. *Nycteris vinsoni* Dalquest, J. Mamm., 46 (2): 254, 256. Publication date: May 1965. Type locality: Mozambique: 212 km SSW Beira, S bank Save river: Zinave [21 26 S 33 52 E]. [Goto Description]. Holotype: KU 105221: ad ♀, skin and skull. Collected by: Prof. Dr. Walter Woelber Dalquest; collection date: 8 October 1963; original number: MWUC 18739. See Jones and Genoways (1969: 130). - Etymology: In honour of J. Vinson, who sponsored an expedition to Mozambique during which the first specimens were collected (see Dalquest, 1965; Taylor, 2005).
1969. *Nycteris macrotis aethiopica:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 97. (Name Combination).
2011. *Nycteris macrotus:* Altringham, Bats, Plate 12. (Lapsus).
2018. *Nycteris macrotis lutreola:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Lapsus).
2019. *Nycteris macrotis 1:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris macrotis 2:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris macrotis 3:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
? *Nycteris aethiopica:* (Alternate Spelling).
? *Nycteris macrotis complex sp. 1 TD-2019*
? *Nycteris macrotis complex sp. 2 TD-2019*
? *Nycteris macrotis complex sp. 3 TD-2019*
? *Nycteris marcrotis oriana:* (Name Combination).

Taxonomy:

Meester *et al.* (1986) indicate that both Koopman (1965, 1975, 1982) and Kock (1969a) included the extralimital [to southern Africa] *aethiopica* Dobson, 1878, and *luteola* Thomas, 1901, as subspecies in this species. While Hayman and Hill (1971) treat *macrotis* and *aethiopica* as separate species, they confirm that the distinction is by no means certain.

N. macrotis macrotis Dobson, 1876 may include also *Plecotus aethiopicus* Fitzinger, 1866, from the White Nile, a *nomen nudum* (Kock, 1969a).

Kock (1969a) regards *oriana* as a synonym of the extralimital *luteola*, but Ansell (1978) and Smithers (1983) treat it as a separate subspecies.

Includes *madagascariensis* Grandidier, 1937 (see Demos *et al.*, 2021: 30) and *vinsoni* Dalquest, 1965 (see next paragraph).

Nycteris vinsoni

Bronner *et al.* (2003) state that is was originally described from Mozambique (Dalquest, 1965). Kock (1969a) considered *Nycteris vinsoni* a synonym of *N. macrotis luteola*, based on the size and position of the second lower premolar. Hayman and Hill (1971) suggest that *N. vinsoni* is a variant of *N. aethiopica*, itself considered a member of the *N. macrotis* group (Koopman, 1965; Kock, 1969a). Koopman (1975) argued that the size and position of the second lower premolar is extremely variable, and instead recognised *vinsoni* as a distinct species closely related to *N. thebaica*, based on the presence of a pyriform tragus (and see Koopman, 1982). He later concluded that the tragus of the holotype is actually semilunate and therefore synonymised *vinsoni* under *N. macrotis oriana* (Koopman, 1992, 1993a). Swanepoel *et al.* (1980), Meester *et al.* (1986), Corbet and Hill (1992) and Simmons (2005: 394) retained *vinsoni* as a distinct species, a treatment endorsed by limited morphometric comparisons (Van Cakenberghe and De Vree, 1999a). However, Van Cakenberghe and De Vree (1999a: 132) and Simmons (2005: 394) consider it a member of the *thebaica* species group.

Simmons (2005: 393) recognises three subspecies - *aethiopica* Dobson, 1878; *luteola* Thomas, 1901; and *oriana* Kershaw, 1922.



Figure 160. *Nycteris macrotis*, Zanzibar Island.

Common Names:

Afrikaans: Groter spleetneusvlermuis. Chinese: 大耳凹脸蝠. Czech: rýhonos velkouchý, nykteris velkouchá. English: Large-eared Slit-faced Bat, Greater Slit-faced Bat, Big-eared slit-faced bat. French: Nyctère de Dobson, Nyctère à grandes

oreilles. German: Großohrige Schlitznasen-Fledermaus. Italian: Nitterìde di Dòbson, Nicterìde di Dobsòn. Malawian: Liputiputi, Ndemiya, Namzeze. Tshokwe (Angola): Kafukufuku.

ETYMOLOGY OF COMMON NAME:
Although the specific name *macrotis* is derived from the Greek "*makros*" and "*otis*" meaning large eared, the species' ears are in fact smaller than in species such as the Egyptian slit-faced bat (*N. thebaica*) (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008aa; IUCN, 2009; Monadjem *et al.*, 2017k).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017k). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008aa; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004at; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
In general, there are no major threats to this species. In parts of its range it is threatened by general habitat loss, presumably mostly through the conversion of land to agricultural use (Mickleburgh *et al.*, 2008aa; IUCN, 2009; Monadjem *et al.*, 2017k).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008aa) [in IUCN (2009)] and Monadjem *et al.* (2017k) report that in view of the species wide range it is presumably present in some protected areas (it has been found in at least one, i.e. Parc National du 'W' (Poché, 1975)). No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Nycteris macrotis is a widespread African species which ranges from Senegal in the west, to Somalia in the east, being recorded as far south as northern Botswana. Found on the island of Zanzibar (Simmons, 2005: 392). It has been recorded between sea level and 2,200 m asl.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,466,326 km^2.

Native: Angola (Hayman, 1963; Van Cakenberghe and De Vree, 1985; Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 547); Benin (Capo-Chichi *et al.*, 2004: 162); Botswana (Monadjem *et al.*, 2010d: 547); Burkina Faso (Kangoyé *et al.*, 2015a: 616); Burundi; Cameroon; Central African Republic; Chad; Congo (Bates *et al.*, 2013: 336); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Gallagher and Harrison, 1977; Van Cakenberghe and De Vree, 1985; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 547); Côte d'Ivoire; Equatorial Guinea; Ethiopia (Simmons, 2005: 392); Gabon; Gambia (Emms and Barnett, 2005: 50; Simmons, 2005: 392); Ghana; Guinea; Guinea-Bissau (Seabra, 1900a; Monard, 1939; Rainho and Ranco, 2001: 44); Kenya; Liberia (Fahr, 2007a: 103); Malawi (Happold *et al.*, 1988; Van Cakenberghe and De Vree, 1985; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 548); Mali (Meinig, 2000: 105); Mauritania (1st record: Benda *et al.*, 2011a: 267); Mozambique (Lopes and Crawford-Cabral, 1992; Simmons, 2005: 392; Monadjem *et al.*, 2010d: 548; Monadjem *et al.*, 2010c: 381); Niger; Nigeria; Rwanda; Senegal (Simmons, 2005: 392); Sierra Leone; Somalia; Sudan; Tanzania (including the island of Unguja [O'Brien, 2011: 289]); Togo; Uganda (Kityo and Kerbis, 1996: 60); Zambia (Ansell, 1967; Ansell, 1973; Ansell, 1978; Cotterill, 2002b: 6; Monadjem *et al.*, 2010d: 548); Zimbabwe (Simmons, 2005: 392; Monadjem *et al.*, 2010d: 548).

Presence uncertain: Namibia (Cotterill, 2004a: 261).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Fain (1953b: 102) reported on the exceptional yellowish-orange colour of some specimens from a cave near the Nyumba Mission (Rwanda). Other specimens from the save cave were uniformly orange or somewhat darker, or yellowish-brown with a few grey hairs, brownish-grey with orange-yellowish hairs, and brownish-grey with a pale belly without any yellowish or orange hairs. These colour differences were not found to be linked with either the sex or the age of the specimens

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 3.84 to 5.12 mm in length, the shaft is long, parallel-sided and usually straight, thickening towards the base, the base has two basal lobes of varying development, in lateral view it is sometimes

angled ventrally, while the tip is expanded and trifid with three variably developed processes (Thomas *et al.*, 1994: 21).

Brain
Based on specimens from Bénin, Amrein *et al.* (2007) reported that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus was found to be absent. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. Furthermore, Amrein *et al.* (2007) detected few DCX positive cells in the rostral migratory stream and the olfactory bulb. No NeuroD was detected in the hippocampal granule cells (Amrein *et al.*, 2007).

Femur
Louzada *et al.* (2019: 136) provided a detailed description of the femur, which has a well-developed medial ridge that begins on the shaft of the femur, a short and well-developed lateral ridge, and well-developed trochanters. The latter nearly reach the same level proximally. The femur is greatly sinusoidal, and the torsion of the proximal epiphysis is the most conspicuous of all the bat families they examined.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.1 Pa, aspect ratio 5.2 and tip shape index of 1.84 for a wingspan of 29 cm and a wing area of 159 cm^2 and a body mass of 12 g.

ECHOLOCATION:
Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 76.7 kHz and duration: 1.2 ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd (Frequency modulation downward) sonotype.

MOLECULAR BIOLOGY:
Karyotype
In the absence of data on a male of this species (only one female from Somalia), Lee *et al.* (1989) described the karyotype as having a diploid number of 2*n* = 40, FNa = 74, BA = 36, X = M, and suggested that the Y chromosome might be a small metacentric as in the other *Nycteris* species. Volleth *et al.* (2020a: 272) reported that a male from Benin had the following karyotype: 2*n* = 40, FNa = 76, with all of the chromosomes bi-armed, consisting of two large submetacentric pairs, 17 medium to small meta- to submetacentric, a medium-sized metacentric X and a very small metacentric Y. Based on the different FNa number, Volleth *et al.* (2020a: 276) suggest that the two specimens might belong to closely related but different species. They also suggest that the Somalian specimen might possibly belong to *Nycteris parisii*, "*aethiopica*", or "*Nycteris* cf. *parisii*" (sensu Kruskop *et al.*, 2016: 60).

HABITAT:
Monadjem *et al.* (2016y: 367) reported one specimen from the Mount Nimba area, which was recorded from a disturbed habitat close to a settlement at 500 m.

HABITS:
Mazur *et al.* (2019: 172) radio-tracked a number of *N. macrotis* specimens in Ghana, and found these to display regular activity patterns of approximately three foraging flights per night. After each foraging bout, they returned to their day roost without using any additional night roosts.

ROOST:
In the Parc National du 'W' in Niger Republic, 300 km west of Sokoto, they have been found roosting in thatched huts and others were found in abandoned mine shafts (Poché, 1975). Stanley *et al.* (2007c: 60) refer to Koopman (1975), who mentions that *N. macrotis* is known to roost in burrows in the ground made by aardvarks (*Orycteropus afer*) or porcupines (*Hystrix cristata*). Weber and Fahr (2006: 4) indicate that *N. macrotis* largely or exclusively depends on the availability of caves as day roosts in Guinea.

Webala *et al.* (2022: 2) report on a group of about 15 bats using a pit latrine as a day roost in Kenya.

Happold and Happold (2023: 109) indicate that *N. macrotis* usually roosts singly or in small groups, which generally include one adult male and one or more adult females, and sometimes also subadult females, which suggest a harem structure.

POPULATION:
Structure and Density
In the Parc National du 'W' in Niger Republic, 300 km west of Sokoto, they have been found roosting in groups of 10-20 individuals (Poché, 1975). Happold (1987) notes that they are solitary or live in small groups.

Trend
2016: Unknown (Monadjem *et al.*, 2017k). 2008: Unknown (Mickleburgh *et al.*, 2008aa; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 115) indicates that most nycterid species (including *N. aethiopica* = *N. macrotis*) are polyoestrous with two or more (continuous) cycles per year, a postpartum oestrus and often no anoestrus. In the DRC and Rwanda, Anciaux de Faveaux (1978c) reported copulations in August and October.

Happold and Happold (1990b: 566) reported that, in Malawi, young were born in the wet season and early dry season, suggesting an aseasonal or extended seasonal reproduction, and that females are not in reproductive synchrony.

Matthews (1937) [in Krutzsch (2000: 115)] noted that male *N. luteola* [= *N. macrotis*] collected at the time of post partum oestrus were reproductively functional. For the same "species", Martin and Bernard (2000: 32) reported that the corpus luteum is only present for the first half of pregnancy. Krutzsch (2000: 94) furthermore reports that the testes are probably permanently scrotal.

Pakenham (1984: 28) collected a very young animal and a juvenile on 4 November on Zanzibar.

PARASITES:
BACTERIA
15 out of 17 Nigerian *Nycteris macrotis* specimens that were examined by Kamani *et al.* (2021: 4) tested positive for *Leptospira borgpetersenii*.

PROTOZOA
Schaer *et al.* (2015a: 381) found *Nycteria* sp. parasites in *N. macrotis* from South Sudan. Based on older references, Austen and Barbosa (2021: 7) mentioned *Trypanosoma (Megatrypanum) mpapuense* from "*Nycteris aethiopica*" from Tanganyika and *Trypanosoma (Megatrypanuml) thomlasi* from the DRC. In northern Nigeria; Kamani *et al.* (2022a: Suppl.) found 11 out of 16 *Nycteris* cf. *macrotis* specimens to be infected by *Trypanosoma* cf. *livingstonei*. A single *N. macrotis* from Uganda was also reported with *T. livingstonei* by Babyesiza *et al.* (2025: 4).

HEMIPTERA
Polyctenidae
Eoctenes nycteridis (Horváth, 1910) from Liberia, Congo, Ruanda-Urundi, Tanzania, Uganda and Eritrea (Haeselbarth *et al.*, 1966: 17; Szentiványi *et al.*, 2022: 6).

ACARI
Macronyssidae
Orlova *et al.* (2020c: 951) mention the presence of *Steatonyssus after* Radovsky and Yunker, 1963 on bats frm Angola.

Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides nycteris* Fain, 1959 on the ears of bats from the DRC.

Trombiculidae
Stekolnikov (2018b: 280) examined one larva of *Trombigastia nycteris* Vercammen-Grandjean and Fain, 1958, which was collected from an unknown locality in Rwanda (the slide label refers to "Ada", which might refer to "Astrida" [=Butare]). Stekolnikov (2018a: 162; 2018b: 284) also reported on three larvae of *Microtrombicula nycteris* (Jadin, Vercammen-Grandjean and Fain, 1955), collected in Butare.

DIPTERA
Streblidae
Raymondi alulata Speiser, 1908 from Angola, the Congo, Malawi and Somalia (Haeselbarth *et al.*, 1966: 102). *Raymondia scopigera* Jobling, 1954 in Cameroon (Haeselbarth *et al.*, 1966: 103, host referred to *N. aethiopica*), Senegal and Sierra Leone (Shapiro *et al.*, 2016: 255).

VIRUSES:
Hermida Lorenzo *et al.* (2021: 6) reported unidentified viruses belonging to the Riboviria realm from Guinean bats.

Adenoviridae
Hermida Lorenzo *et al.* (2021: 6) mentioned the presence of unclassified Adenoviridae, Bat Mastadenovirus C and Canine Bat Mastadenovirus A in bats from Guinea.

Coronaviriddae
Joffrin *et al.* (2020: 6) reported Beta-C coronaviruses from Mozambican bats they identified as "*Nycteris thebaica*" (but were actually *N. macrotis* according to Demos *et al.*, 2019b).

Meyer *et al.* (2024: 4) found Ghanaian bats to be infected by CoV 2b and CoV 2c viruses.

Flaviviridae
In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against non-specific Flaviviruses.

Herpesviridae
Hermida Lorenzo *et al.* (2021: 6) reported Rhinolophus gammaherpesvirus from Guinean bats.

Retroviridae
Bat gammaretrovirus was reported by Hermida Lorenzo *et al.* (2021; 7) from bats from Guinea.

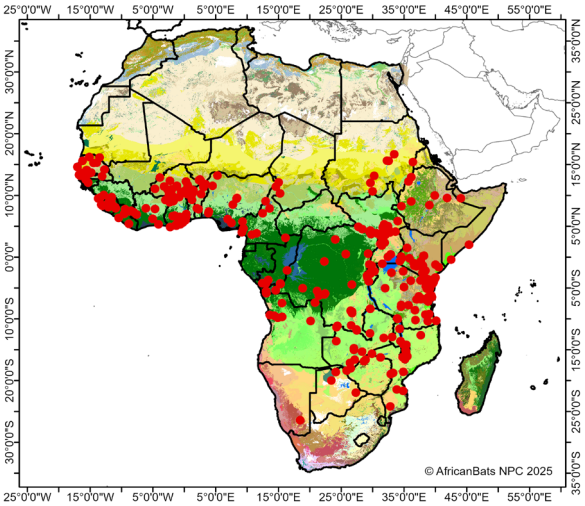

Figure 161. Distribution of *Nycteris macrotis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Nycteris major (K. Andersen, 1912)

*1912. *Petalia major* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 547. Publication date: 1 November 1912. Type locality: Cameroon: Ja River [ca. 03 00 N 13 00 E]. [Goto Description]. Holotype: NHMUK 1909.10.2.49: ad ♀, skull and alcoholic. Collected by: George Latimer Bates Esq. Collection date: 23 January 1906. - Etymology: From the Latin "*maior*" (see Kozhurina, 2002: 16).

1917. *Nycteris avakubia* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 426, fig 3. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Avakubi [01 18 N 27 32 E]. [Goto Description]. Holotype: AMNH 49403: ad ♂, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: September 1913; original number: 2623.

1917. *Nycteris major:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 427. Publication date: 29 September 1917. - Comments: The specimens assigned to this species by Allen (1917), however, belong to *Nycteris macrotis* (see Koopman, 1965). (Name Combination, Current Combination).

TAXONOMY:
Includes *avakubia* J.A. Allen, 1917 (see Koopman, 1965; Van Cakenberghe and De Vree, 1985; Simmons, 2005: 393).

arge species group (Van Cakenberghe and De Vree, 1985; Simmons, 2005: 393).

COMMON NAMES:
Czech: rýhonos kamerunský. English: Ja Slit-faced Bat, Dja Slit-faced Bat, Large Slit-faced Bat. French: Nyctère de Ja. German: Dja-Schlitznasenfledermaus, Dja Schlitznasen-Fledermaus.

SIMILAR SPECIES:
Eisentraut (1956b: 517) indicated that the claws of *N. major* are more robust than those of *N. arge*.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence in Central Africa, natural history, and threats. If the species is found to range more widely in Central Africa it is likely to meet the criteria for Least Concern, as the extent and quality of its habitat are probably not declining at a rate sufficient to justify listing in a higher category (Mickleburgh *et al.*, 2008bi; IUCN, 2009; Mickleburgh *et al.*, 2019j).

Assessment History
Global
2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019j). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008bi; IUCN, 2009). 2004: VU A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004cg; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species appears to need rather large trees, and is presumably threatened by deforestation resulting from logging activities and the conversion of forest to agricultural use (Mickleburgh *et al.*, 2008bi; IUCN, 2009; Mickleburgh *et al.*, 2019j).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bi) [in IUCN (2009)] and Mickleburgh *et al.* (2019j) report that although there appear to be no direct conservation measures in place, it has been recorded from the Tai National Park in Côte d'Ivoire. Further studies are needed into the distribution, natural history and threats to this somewhat enigmatic species. There is a need to monitor to presence of this species at its known localities.

GENERAL DISTRIBUTION:
Nycteris major is distributed in West and Central Africa, where it has been patchily recorded from Guinea, Liberia (at Voinjama) and Côte d'Ivoire in the west, and from Cameroon and the Democratic Republic of the Congo in Central Africa (at Avakubi), with the southern-most record from northern Zambia (close to the border with the Democratic Republic of the Congo).

Native: Benin (Capo-Chichi *et al.*, 2004: 162); Cameroon (Simmons, 2005: 393); Central African Republic; Congo (The Democratic Republic of the) (Simmons, 2005: 393); Côte d'Ivoire (Simmons, 2005: 393); Guinea; Liberia (Simmons, 2005: 393); Nigeria (Tanshi *et al.*, 2022a: 317); Zambia (Van Cakenberghe and De Vree, 1985; Simmons, 2005: 393; Monadjem *et al.*, 2010d: 548).

MOLECULAR BIOLOGY:
Karyotype
Ngene *et al.* (2025: 11) reported 2n = 40 and FN = 79 (♂) or FN = 80 (♀) for Nigerian bats.

PREDATORS:
Demeler (1981: 133) found remains of *N. major* in pellets of *Bubo africanus* (Temminck, 1821) in the Yankari Game Reserve (Nigeria). However, as *N. macrotis* was often mis-identified as *N. major* and the latter species was not yet reported from that area, the bat's identification still needs to be confirmed.

POPULATION:
Structure and Density
This appears to be an extremely rare species, which is only known from a dozen or so specimens. It is not difficult to catch and efforts have been made to locate more specimens (Mickleburgh *et al.*, 2008bi; IUCN, 2009; Mickleburgh *et al.*, 2019j).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019j). 2008: Unknown (Mickleburgh *et al.*, 2008bi; IUCN, 2009).

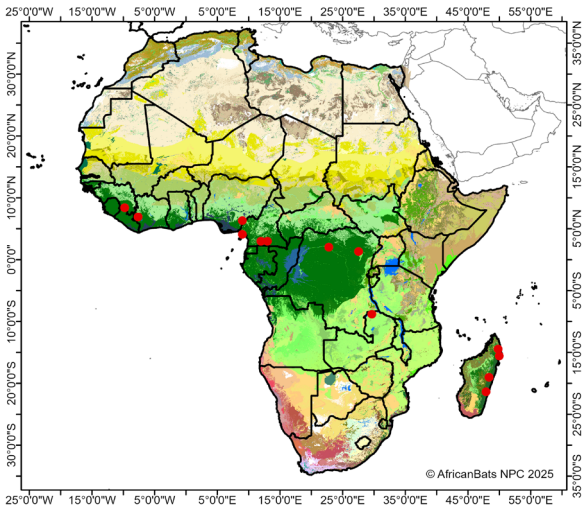

Figure 162. Distribution of *Nycteris major*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Liberia, Madagascar, Nigeria, Zambia.

Nycteris nana (K. Andersen, 1912)

*1912. *Petalia nana* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 547. Publication date: 1 November 1912. Type locality: Congo: [Rio Muni ?] Benito River [ca. 01 31 N 09 52 E]. [Goto Description]. Holotype: NHMUK 1900.2.5.46: ad ♂, skull and alcoholic. Collected by: George Latimer Bates Esq.

1926. *Nycteris nana:* Cabrera and Ruxton, Ann. Mag. nat. Hist., ser 9, 17: xxx. (Name Combination, Current Combination).

1936. *Nycteris nana tristis* G.M. Allen and Lawrence, Bull. Mus. comp. Zool., 79 (3): 47. Publication date: 30 January 1936. Type locality: Kenya: W Nyanza: Kakamega district: Kaimosi [00 08 N 34 51 E, 2 130 m]. [Goto Description]. Holotype: MCZ 31156: ad ♀, skin and skull. Collected by: Professor Arthur Loveridge; collection date: 13 February 1934. See Helgen and McFadden (2001: 142). (Name Combination).

1939. *Nycteris nana nana:* G.M. Allen, Bull. Mus. comp. Zool., 83: 70. (Name Combination).

2019. *Nycteris nana 1:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.

2019. *Nycteris nana 2:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.

2020. *Nycterus nana:* Shchelkanov, Dunaeva, Moskvina, Voronova, Kononova, Vorobyeva, Galkina, Yanovich, Gadzhiev and Shestopalov, S. Russia: ecol., dev., 15 (3): 23. Publication date: 27 August 2020. (Name Combination, Lapsus).
? *Nycteris cf. nana DMR-2017*
? *Nycteris nana complex sp. 1 TD-2019*
? *Nycteris nana complex sp. 2 TD-2019*

TAXONOMY:
Includes *tristis* Allen and Lawrence, 1936 (Koopman, 1975; Van Cakenberghe and De Vree, 1985; Simmons, 2005: 393).

arge species group (Van Cakenberghe and De Vree, 1985; Simmons, 2005: 393).

COMMON NAMES:
Chinese: 侏凹脸蝠. Czech: rýhonos drobný. English: Dwarf Slit-faced Bat. French: Nyctère naine. German: Kleinste Schlitznasen-Fledermaus, Zwerg-Schlitznasenfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bj; IUCN, 2009; Monadjem *et al.*, 2017av).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017av). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bj; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cc; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known, but it seems likely to be locally threatened by deforestation in parts of its range (Mickleburgh *et al.*, 2008bj; IUCN, 2009; Monadjem *et al.*, 2017av).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bj) [in IUCN (2009)] and Monadjem *et al.* (2017av) report that it is not known if the species is present within any protected areas. Further studies are needed into the distribution, general ecology and threats to this species.

GENERAL DISTRIBUTION:
Nycteris nana has been widely recorded in West and Central Africa, with some records from East Africa. It ranges from Côte d'Ivoire and Ghana in the west, through south Cameroon and Equatorial Guinea (Rio Muni), to the Democratic Republic of the Congo, Rwanda and Burundi, to Uganda and western Kenya. It ranges as far south as northern Angola. Generally, a lowland species, but can be found up to 2,100 m asl.

A record from Tanzania, represents *intermedia* (J. Fahr *pers. comm.* in Simmons, 2005: 393).

Native: Angola (Crawford-Cabral, 1989; Simmons, 2005: 393; Monadjem *et al.*, 2010d: 548); Cameroon; Central African Republic; Congo (The Democratic Republic of the) (Van Cakenberghe and De Vree, 1985; Monadjem *et al.*, 2010d: 548); Côte d'Ivoire (Simmons, 2005: 393); Equatorial Guinea (Simmons, 2005: 393); Ghana; Kenya (Simmons, 2005: 393); Rwanda; Sudan (Simmons, 2005: 393); Togo; Uganda.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Verschuren (1955) reported on an albino specimen caught in a hollow tree in the DRC.

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 2.10 to 3.36 mm in length, smaller than that of *N. arge*, the shaft is slender, parallel-sided and essentially straight, the base is expanded and rounded and in lateral profile is often angled ventrally, while the tip is simple, with only a small expansion (Thomas *et al.*, 1994: 20).

POPULATION:
Structure and Density
It is considered to be a rather rare bat, colony sizes tend to be small (Mickleburgh *et al.*, 2008bj; IUCN, 2009; Monadjem *et al.*, 2017av).

Trend
2016: Unknown (Monadjem *et al.*, 2017av). 2008: Unknown (Mickleburgh *et al.*, 2008bj; IUCN, 2009).

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2015a: 381) found *Nycteria* cf. *houini* in *N. nana* from South Sudan. Landau *et al.* (2012: 142) and Perkins and Schaer (2016: Suppl.) mentioned the parasite as *Nycterida houini* Rosin, Landau and Hugot, 1978, and also reported it from the Republic of Congo and Gabon.

VIRUSES:
Reoviridae
Orbivirus
Fomede virus
Reported in the CDC's Arbovirus Catalogue, to have been isolated in 1978 from the Republic of Guinea, from the brain and internal organs of *N.* cf. *nana*. Reported by de Jong *et al.* (2011: 11).

Chobar Gorge virus was mentioned by Luis *et al.* (2013: Suppl.) and Willoughby *et al.* (2017: Suppl.).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Kenya, South Sudan, Uganda.

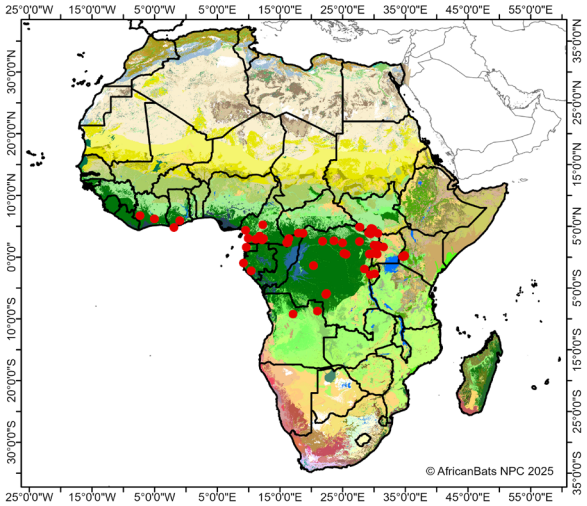

Figure 163. Distribution of *Nycteris nana*.

Nycteris parisii (de Beaux, 1924)

*1924. *Petalia parisii* de Beaux, Atti Soc. ital. Sci. nat., 62: 254 (for 1923). Publication date: February 1924. Type locality: Somalia: Balli [=Ballei Uen] [00 42 N 43 04 E]. [Goto Description]. Holotype: [Unknown] N 1449: ♀, skull and alcoholic. Collection date: 6 April 1922. See De Beaux (1924: 254), Allen (1939a: 70). - Etymology: In honour of Dr. Bruno Parisi, former head of the zoological section (1921 - 1927) and director (1928 - 1951) of the Museo Civico di Storia Naturale di Milano (see De Beaux, 1924: 255; Lanza *et al.*, 2015: 250).
1930. *Nicteris parisii:* Zammarano, Le colonie Italiane, 146. (Name Combination).
1939. *Nycteris parisii:* G.M. Allen, Bull. Mus. comp. Zool., 83: 70. Publication date: February 1939. (Name Combination, Current Combination).
1952. *Nycteris benuensis* Aellen, Mém. Soc. neuchât. Sci. nat., 8: 53. Type locality: Cameroon: Rei Bouba [ca. 08 37 N 14 09 E]. [Goto Description]. Holotype: MHNC 1481a: ad ♂. Collected by: MSS Cameroun; collection date: 16 September 1947. Paratype: MHNG 1326.002: ad. Collected by: Dr. Villy Aellen; collection date: 16 September 1947; original number: 1481b-514.
1971. *N[ycteris] p[arisii] benuensis:* Hayman and Hill, Mammals of Africa: Chiroptera, 18. (Name Combination).
1971. *N[ycteris] p[arisii] parisii:* Hayman and Hill, Mammals of Africa: Chiroptera, 18. (Name Combination).
2015. *[Nycteris] parissi:* Kaipf, Rudolphi and Meinig, NABU - Biodiversity Assessment in Kafa, Ethiopia, 13. (Lapsus).

TAXONOMY:
Included in *woodi* by Van Cakenberghe and De Vree (1985), Koopman (1993a: 162). Thomas *et al.* (1994: 22) elevated it to species rank (Simmons, 2005: 393).

Rosevear (1965: 173) included *N. parisii* in the *aethiopica* group. Included in the *macrotis* group (Simmons (2005: 393) based on Thomas *et al.* (1994: 22) being closely related to *N. macrotis*.

Simmons (2005: 393) recognises one subspecies *benuensis* Aellen, 1952.

COMMON NAMES:
Czech: rýhonos somálský. English: Parisi's Slit-faced Bat, Balli Slit-faced Bat, Parissi's Slit-faced Bat. French: Nyctère de Parisi. German: Parisis Schlitznasen-Fledermaus. Italian: Nitterìde di Parìsi, Nicterìde di Parìsi.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Mickleburgh *et al.*, 2008ap; IUCN, 2009; Mickleburgh *et al.*, 2019h).

Assessment History
Global
2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019h). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008ap; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004bf; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Mickleburgh *et al.*, 2008ap; IUCN, 2009; Mickleburgh *et al.*, 2019h).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ap) [in IUCN (2009)] and Mickleburgh *et al.* (2019h) report that it is not known if the species is present within any protected areas. Further studies are needed into the distribution, abundance, general ecology and threats to this species.

GENERAL DISTRIBUTION:
Nycteris parisii has been recorded from southern Somalia, south Ethiopia and from northern Cameroon, close the border with Nigeria. It is a low elevation species.

Nycteris parisii parisii may be distributed in East Africa and *N. p. benuensis* in West Africa.

Native: Cameroon (Aellen, 1952; Simmons, 2005: 393); Ethiopia (Hill, 1975; Simmons, 2005: 393); Somalia (Varty and Hill, 1988; Simmons, 2005: 393); Togo? (Amori *et al.*, 2016: 217).

DETAILED MORPHOLOGY:
Baculum
The shaft is long, parallel-sided and essentially straight, thickening towards the base, the base is expanded, in lateral profile it is angled ventrally, while the tip is expanded and trifid with three variably developed processes (Thomas *et al.*, 1994: 21).

POPULATION:
Structure and Density
The abundance of this species is not known, and only a few specimens have ever been collected. It was last recorded in the 1980s. Presumably this is a consequence of limited survey effort within the species known range (Mickleburgh *et al.*, 2008ap; IUCN, 2009; Mickleburgh *et al.*, 2019h).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019h).
2008: Unknown (Mickleburgh *et al.*, 2008ap; IUCN, 2009).

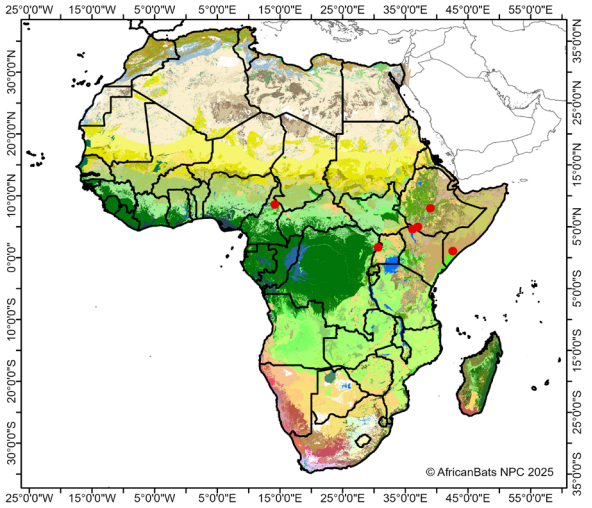

Figure 164. Distribution of *Nycteris parisii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Ethiopia, Somalia.

Nycteris thebaica E. Geoffroy St.-Hilaire, 1818

*1818. *Nycteris Thebaicus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 119, pl 1, No 2. Publication date: 1818. Type locality: Egypt: Qena province: Thebes (near Luxor) [ca.25 41 N 32 39 E]. [Goto Description]. Holotype: MNHN ZM-MO-1997-1800: ad ♀, skin only. Collected by: Etienne Geoffroy-Saint-Hilaire. Number 172 in Rode (1941: 235), who also mentioned number MNHN 142. Previously mentioned as MNHN 889. Paratype: MNHN ZM-AC-1880-974: complete skeleton. Paratype: MNHN ZM-AC-A6954: skull only. - Etymology: From the masculine Latin adjective *thēbàicus*, meaning "native or belonging to Thebes", the ancient capital of Upper Egypt, on the site of modern Luxor, the type locality of the species (see Lanza *et al.*, 2015: 254). (Current Combination).

1820. *Nycteris Geoffroyi* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 127. Publication date: 1820. Type locality: Senegal: 40 mi (= 60 km) east of Podor. [Goto Description]. - Comments: Included in *macrotis* by Kock (1969a: 93) [although with a question mark] and Meester *et al.* (1986: 35).

1829. *Nycteris affinis* A. Smith, Zool. Journ., 4 (16): 434. Publication date: May 1829. Type locality: South Africa: E Cape province: Grahamstown [33 17 S 26 31 E]. [Goto Description]. - Comments: Type locality originally as "South Africa", restricted to "Grahamstown, eastern Cape Province, South Africa" by Roberts (1951: 69): see Kock (1969a: 98), Meester *et al.* (1986: 35), Gray *et al.* (1999: 2).

1829. *Nycteris Capensis* A. Smith, Zool. Journ., 4 (16): 434. Publication date: May 1829. Type locality: South Africa: SW Cape province: Swellidam [34 01 S 20 26 E]. [Goto Description]. Lectotype: NHMUK 1863.2.21.6: ad ♂, skin only. Collected by: A. Smith. Paralectotype: RMNH MAM.35900: ad, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters. The RMNH catalog mentions this specimen as a syntype, but as the NHMUK specimen is designated as a lectotype, this specimen is to be considered a paralectotype. - Comments: The type locality was originally mentioned as "Interior of South Africa, as well as upon the Eastern Coase", and restricted to "Swellidam, SW Cape Province, South Africa" by Roberts (1951: 69): see Kock (1969a: 98), Meester *et al.* (1986: 35), Gray *et al.* (1999: 2). Ansell and Dowsett (1988: 31) mention the locality as "Swellendam"). Considered a valid subspecies by Taylor (1998: 33).

1834. *Nycteris thebaica:* A. Smith, S. Afr. Quart. J., 2: 59. (Current Spelling).

1840. *N[ycteris] albiventer* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 1: 439. Type locality: Sudan: Northern province: Dongola [19 10 N 30 27 E]. [Goto

Description]. - Comments: Type locality originally given as "Nubia" (see Kock, 1969a: 98), restricted to Dongola, Northern Province, Sudan by Koopman (1975): see Gray *et al.* (1999: 2).

1840. *N[ycteris] discolor* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 1: 440. Type locality: South Africa: Ecklon. [Goto Description]. - Comments: Allen (1939a: 68) mentioned the type locality as "Südspitze von Afrika". Kock (1969a: 98), Meester *et al.* (1986: 35) mention "Southern tip of Africa; Knysna, fide Roberts (1951: 69).").

1852. *Nycteris fuliginosa* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 46, pl 10. Publication date: 1852. Type locality: Mozambique: 12 mi (19 km) NW Quellimane: Boror [17 53 S 36 51 E]. [Goto Description]. Syntype: NHMUK 1858.6.18.15: ad ♀. See Turni and Kock (2008: 27). Syntype: NHMUK 1907.1.1.337: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters. See Turni and Kock (2008: 27). Syntype: RMNH MAM.35901: ad ♂, mounted skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1846. The RMNH catalog mentions two numbers: 35901.a (skull + loose bones) and 35901.b (mouned skin). Syntype: ZMB 392: ad ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1846. See Turni and Kock (2008: 27). Syntype: ZMB 3954: ad ♂, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1846. See Turni and Kock (2008: 27). Syntype: ZMB 562: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1846. See Turni and Kock (2008: 27).

1861. *Nycteris labiata* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 5. Publication date: 1861. Type locality: Eritrea: Bogos: Cheren [=Keren] [ca. 15 45 N 38 20 E]. [Goto Description]. Syntype: SMNS 980a: ad ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294). Syntype: SMNS 980b: sad ♂, alcoholic (skull not removed). Collected by: Martin Theodor von Heuglin; collection date: 1861. See: Dieterlen *et al.* (2013: 294). Syntype: ZMB 2794a: ♂. Collected by: Martin Theodor von Heuglin; collection date: 1852. Formerly SMNS, see Turni and Kock (2008). Syntype: ZMB 2794b: ♂. Collected by: Martin Theodor von Heuglin; collection date: 1852. Syntype ex SMNS, see Turni and Kock (2008: 27).

1866. *Plecotus æthiopicus* Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 546. Type locality: Sudan: Bahr el Abiat (White Nile) [ca. 14 00 N 33 00 E]. [Goto Description]. - Comments: Meester *et al.* (1986: 35) mention Fitzinger only as author. Nomen nudum (see Allen, 1939a: 68). Included in *macrotis* by Kock (1969a: 93), but rejected as nomen nudum.

1868. *Nycteris Geoffroyi Var. Senegalensis* Hartmann, Z. Gesel. f. Erdk., 3 (28/29): 44. Type locality: Sudan: Sennaar [15 35 N 33 38 E, 425 m]. [Goto Description].

1871. *Nycteris angolensis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 903 , fig 5 (for 1870). Type locality: Angola: Biballe and Rio Coroca: Caconda [13 42 S 15 05 E, 1 900 m]. [Goto Description]. Syntype: NHMUK 1879.1.21.2. Syntype: ZMB 3633: juv ♂, skull and alcoholic. From Rio Corvea, Angola; ex Lisbon Museum; see Turni and Kock (2008). Syntype: ZMB 3637: ♂, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta. Ex Lisbon Museum; this specimen was collected at Caconda, Biballe (see Turni and Kock (2008)). Peters (1871: 904) mentions Anchieta as collector for the type specimen. - Comments: Type locality restricted by Hill and Carter (1941): see Gray *et al.* (1999: 2). The publication covers a meeting held on 22 December 1870.

1871. *Nycteris damarensis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 905, fig 7 (for 1870). Type locality: Namibia: Damaraland: Otjimbingue [22 15 S 16 10 E]. [Goto Description]. Syntype: NHMUK 1838.2.8.4: ad, skin and skull. Collected by: Captain Alexander; original number: 1079. Syntype: NRM |TS539|. See Turni and Kock (2008: 27). Syntype: ZMB 3298: ♂, skull and alcoholic. Collected by: Missionary Hahn. See Turni and Kock (2008: 27). Syntype: ZMB 3887: ad ♂, skull and alcoholic. Collected by: Higgins. See Turni and Kock (2008: 27) [missing]. - Comments: Part of the original series is in the NRM (see Turni and Kock (2008: 27). The publication covers a meeting held on 22 December 1870. Peters (1871: 905) also mentions that the name *damarensis* was already used in the British Museum and in the Catalogue of Mammalia from 1843.

1881. *Nycteris Revoilii* Robin, Bull. Soc. Philom. Paris, (7) 5: 90. Type locality: Somalia: north of 10 ° N. [Goto Description]. Holotype: MNHN ZM-MO-1881-4: ad ♂, alcoholic (skull not removed). Collected by: Georges Emmanuel Joseph Révoil. Number 174 in Rode (1941: 236). Paratype: MNHN ZM-MO-1881-1: ad ♂, alcoholic (skull not removed). Collected by: Georges Emmanuel Joseph Révoil. Number 174a in Rode (1941: 236). Paratype: MNHN ZM-MO-1881-3: ad ♂, alcoholic (skull not removed). Collected by: Georges Emmanuel Joseph Révoil. Number 174b in Rode (1941: 236). Cotype: MCZ 14929: ♀, alcoholic (skull not removed). Collected by: Georges Emmanuel Joseph Révoil. - Comments: Type locality originally "Somalia", restricted to "Somalia, north of 10 °N" by Moreau *et al.* (1946: 399): see Gray *et al.* (1999: 2). Allen (1931: 235) mentions a "cotype" in MCZ (14929), collected by Revoil in Somaliland in 1880.

1900. *Nycteris thebaica var. angolensis:* Seabra, J. Sci. mat. phys. nat., ser 2, 6 (22): 18. (Name Combination).

1900. *Nycteris thebaica var. damarensis:* Seabra, J. Sci. mat. phys. nat., ser 2, 6 (22): 19. (Name Combination).

1900. *Nycteris thebaica var. Fuliginosa:* Seabra, J. Sci. mat. phys. nat., ser 2, 6 (22): 18. (Name Combination).

1904. *Nycteris thebaica capensis:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, supplement, ???. (Name Combination).

1908. *Petalia capensis:* Thomas and Wroughton, Proc. zool. Soc. Lond., ???.

1909. *Nycteris capensis var. fuluginosa:* Seabra, Ann. Scient. Acad. Politecn. Porto, 4: ???.

1910. *Petalia thebaica:* Thomas, Ann. Mag. nat. Hist., ser 8, 6: ???. (Name Combination).

1911. *Petalia revoili:* G.M. Allen, Bull. Mus. comp. Zool., 54 (9): 322.

1912. *Petalia damarensis brockmani* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 548. Publication date: 1 November 1912. Type locality: Somalia: Upper Sheikh. [Goto Description]. Holotype: NHMUK 1910.3.27.4: ad ♀, skin and skull. Collected by: Dr. Ralph Evelyn Drake-Brockman; collection date: 11 January 1910.

1912. *Petalia damarensis damarensis:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): ???.

1912. *Petalia damarensis media* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): 548. Publication date: 1 November 1912. Type locality: Ethiopia: Harar province: Harer [09 18 N 42 08 E, 2 000 m]. [Goto Description]. Holotype: NHMUK 1912.2.28.1: ad, skin and skull. Collected by: G. Kristensen; collection date: 19 January 1912. Presented/Donated by: Nathanial Charles Rothschild.

1912. *Petalia thebaica thebaica:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 10 (59): ???. (Name Combination).

1918. *Nycteris thebaica thebaica:* Wettstein, Denkschr. k. Akad. Wiss. Wien, Math.-Naturw. Kl., 94: ???. (Name Combination).

1923. *Petalia (Nycteris) thebaica aurantiaca* de Beaux, Atti Soc. ital. Sci. nat., 62: 91. Publication date: July 1923. Type locality: Kenya: Northern Guaso Nyiro: Archer's Post [00 39 N 37 41 E, 2 000 ft]. [Goto Description]. Holotype: MSNM 1432: ad ♀, skull and alcoholic. Collected by: L. Franchetti and L. Tonker; collection date: January 1920. This type specimen was destrioyed during a fire in 1943 (Cagnolaro, 1976: 86).
1933. *Nycteris damarensis damarensis:* G.M. Allen and Loveridge, Bull. Mus. comp. Zool., 75: 49, 66. (Name Combination).
1934. *Nycteris capensis capensis:* Shortridge, Mammals of South West Africa, 55. (Name Combination).
1934. *Nycteris capensis damarensis:* Shortridge, Mammals of South West Africa, 56.
1934. *P[etalia (Nycteris)] theb[aica] adana:* de Beaux, Atti Soc. ital. Sci. nat., 62: 93. (Name Combination).
1936. *Nycteris damarensis brockmani:* G.M. Allen and Lawrence, Bull. Mus. comp. Zool., 79 (3): 35, 49.
1936. *Nycteris thebaica revoili:* G.M. Allen and Lawrence, Bull. Mus. comp. Zool., 79 (3): 35, 49. (Name Combination).
1938. *Nycteris thebaica aurantiaca:* Frechkop, Exploration du Parc national Albert, Fasc 10: ???. (Name Combination).
1939. *Nycteris damarensis media:* G.M. Allen, Bull. Mus. comp. Zool., 83: 69.
1944. *Nycteris thebaica albiventer:* Aharoni, Bull. Zool. Soc. Egypt, 6: 26. (Name Combination).
1956. *Nycteris thebaica brockmani:* Toschi, Atti Soc. ital. Sci. nat., 95: 121. (Name Combination).
1971. *Nycteris thebaica labiata:* Hill and Morris, Bull. Br. Mus. (nat. Hist.) Zool., 21 (2): 34. (Name Combination).
1975. *Nycteris thebiaca:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 379. - Comments: Lapsus (actually Koopman uses this name consequently in this publication). (Lapsus).
1998. *Nyteris angolensis:* Van Cakenberghe and De Vree, Bonn. zool. Beitr., 48 (2): 140. Publication date: October 1998. (Lapsus).
1998. *Nyteris thebaica:* Van Cakenberghe and De Vree, Bonn. zool. Beitr., 48 (2): 123. Publication date: October 1998. (Lapsus).
1999. *Nycteris thabaica labiata:* Van Cakenberghe and De Vree, Bonn. zool. Beitr., 48 (2): 147. (Lapsus).
2018. *Nycteris thebica capensis:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Lapsus).
2019. *Nycteris cf. thebaica 1:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris cf. thebaica 2:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 2023. Publication date: 20 August 2019.
2019. *Nycteris cf. thebaica 3:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1026. Publication date: 20 August 2019.
2019. *Nycteris thebaica 1:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris thebaica 2:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris thebaica 3:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris thebaica 4:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris thebaica 5:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2019. *Nycteris thebaica 6:* Demos, Webala, Kerbis Peterhans, Goodman, Bartonjo and Patterson, J. Zool. Syst. Evol. Res., 57 (4): 1023. Publication date: 20 August 2019.
2021. *Nycteris theibaica:* Austen and Barbosa, Pathogens, 10 (9) 1148: 5. Publication date: 6 September 2021. (Lapsus).
2024. *Petalia thebaica aurantica:* Gippoliti, J. Vertebr. Biol., 73 (23110): 3. Publication date: 5 April 2024. (Lapsus).
? *Nycteris capensis:*
? *Nycteris cf. thebaica 1 TD-2019*
? *Nycteris cf. thebaica 2 TD-2019*
? *Nycteris thebaica angolensis:* (Name Combination).
? *Nycteris thebaica complex sp. 1 TD-2019*
? *Nycteris thebaica complex sp. 2 TD-2019*
? *Nycteris thebaica complex sp. 3 TD-2019*
? *Nycteris thebaica complex sp. 4 TD-2019*
? *Nycteris thebaica complex sp. 5 TD-2019*
? *Nycteris thebaica complex sp. 6 TD-2019*
? *Nycteris thebaica damarensis:* (Name Combination).
? *Nycteris thebaica revoilii:* (Alternate Spelling).

TAXONOMY:



Figure 165. *Nycteris thebaica* (SMG-15760) caught at Marloth Park, Mpumalanga, South Africa.

Meester *et al.* (1986) state that the subspecies classification of *thebaica* is uncertain. Hayman and Hill (1971), while acknowledging that the species may include valid subspecies, do not attempt to recognize any. Kock (1969a), however, lists seven subspecies, and Koopman (1975), while not providing a complete synonymy of the species, appears to come to broadly similar conclusions to Kock concerning those names that he does consider. Simmons (2005: 393) recognises seven subspecies - *adana* K. Andersen, 1912; *angolensis* Peters, 1870; *brockmani* K. Andersen, 1912; *capensis* A. Smith, 1829; *damarensis* Peters, 1870; *labiata* Heuglin, 1861; and *najdiya* Nader and Kock, 1982.

Van Cakenberghe and De Vree (1999a) suggest that the status of *brockmani* and *damarensis* remains unclear as these forms may represent distinct species (Harrison and Bates, 1991; Gray *et al.*, 1999).

thebaica species group (Van Cakenberghe and De Vree, 1999a; Simmons, 2005: 393).

COMMON NAMES:
Afrikaans: Gewone-spleetneusvlermuis, Egiptiese spleetneusvlermuis, Kaapse Langoorvlermuis. Arabian: Khafash Teiba, Khaffash. Castilian (Spain): Rinolofo egipcio. Chinese: 非洲凹脸蝠. Czech: rýhonos egyptský, šerowec tébský, dutonosec, netopýr koptový, nykteris egyptská. Dutch: Thebaanse spleetneusvleermuis. English: Egyptian Slit-faced Bat, Common Slit-faced Bat, Geoffroy's Nycteris, Cape Long-eared Bat, Aden Slit-faced bat. French: Nyctère de la Thébaïde, Nyctère égyptienne. German: Großohrrhohlnase, Ägyptische Schlitznasen-Fledermaus, Stirngrubenfledermaus. Hebrew: לילן, leilan, Leylan. Italian: Nitterìde tebàna, Nicterìde tebàna, Nitterìde di Tèbe, Nicterìde di Tèbe. Malawian: Nanthuthu. Portuguese: Morcego orelhudo do Egipto. Kiluba (DRC): Kasusu. Yao (Malawi): Liputiputi (applied to all small bats).

ETYMOLOGY OF COMMON NAME:
So named because they were first described from tombs in Thebes, Egypt (see Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
N. thebaica was found in upper Pleistocene samples at Border Cave, South Africa (Avery, 1991: 6).

Butler (1984: 185) reported on a distal end of a humerus found at Chamtwara (Kenya).

CONSERVATION STATUS:
Global Justification
This species has a large range and faces no major threats, hence is listed as Least Concern LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bk; IUCN, 2009; Monadjem *et al.*, 2017aw).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017aw). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bk; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ce; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016d). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
Habitat destruction and degradation affect the species. Roost disturbance and degradation are the main threats in the Mediterranean region. These are not considered major threats at present (Mickleburgh *et al.*, 2008bk; IUCN, 2009; Monadjem *et al.*, 2017aw).

In the Limpopo province, South Africa, Toussaint and McKechnie (2012: 1138) indicate that the cool baobab tree cavities appear to be critical for the presence of *N. thebaica* in that area and may buffer this species from future increases in extreme maximum ambient temperatures.

Aerial hawking and water stress are believed to be the major risk factors linked to climatic change (Sherwin *et al.*, 2012: 174).

Collinson *et al.* (2015: 311) report on two roadkills in the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA), South Africa.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bk) [in IUCN (2009)] and Monadjem *et al.* (2017aw) report that it may occur within some protected areas. No specific conservation measures are known. Protection of the roost sites is required and also legal protection of the species should be improved. Further research is required on the population size and trends.

GENERAL DISTRIBUTION:
Nycteris thebaica is broadly distributed across savanna and riparian zones. Mostly found in sub-Saharan Africa; also found in Morocco, Libya, Egypt (primarily down the Nile River valley, but also into Sinai) and the Middle East (Israel, Palestine and Jordan). Recorded form the islands of Unguja [=Zanzibar] and Pemba [see Simmons (2005: 393), although not from the latter by O'Brien (2011: 289)]. Elevation from sea level to 2,000 m.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,704,632 km^2 (covering 27 % of the total surface). In South Africa, its distribution is mainly affected by the minimum temperature of the coldest month (Babiker Salata, 2012: 49).

Corbet (1984: 8) states that the inclusion of Corfu (Greece) in the range could be the result of a vagrant specimen from N Africa (for details see Van Cakenberghe and De Vree, 1999a).

Native: Angola (Crawford-Cabral, 1989; Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 548); Benin (Simmons, 2005: 393); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 548); Burkina Faso (Simmons, 2005: 393; Kangoyé *et al.*, 2015a: 617); Burundi; Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 548); Côte d'Ivoire; Djibouti (Pearch *et al.*, 2001: 397; Simmons, 2005: 393); Egypt (Simmons, 2005: 393); Eritrea; Swaziland (Monadjem, 2001, Monadjem, 2006b; Simmons, 2005: 393; Monadjem *et al.*, 2010d: 549, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 133); Gambia; Ghana (Simmons, 2005: 393); Guinea (Konstantinov *et al.*, 2000: 144; Simmons, 2005: 393; Decher *et al.*, 2016: 264); Guinea-Bissau; Israel (Simmons, 2005: 393); Jordan (Al-Omari *et al.*, 2000: 5); Kenya (Simmons, 2005: 393); Libyan Arab Jamahiriya; Malawi (Ansell and Dowsett, 1988: 31; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 548); Mali (Simmons, 2005: 393); Morocco (Simmons, 2005: 393; Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 358; Dbiba *et al.*, 2025: 6); Mozambique (Smithers and Lobão Tello, 1976; Lopes and Crawford-Cabral, 1992; Monadjem *et al.*, 2010d: 548; Monadjem *et al.*, 2010c: 382); Namibia; Niger (Simmons, 2005: 393; Monadjem *et al.*, 2010d: 548); Nigeria (Simmons, 2005: 393); Palestinian Territory, Occupied; Rwanda; Saudi Arabia; Senegal (Simmons, 2005: 393); Sierra Leone; Somalia (Simmons, 2005: 393); South Africa (Simmons, 2005: 393; Monadjem *et al.*, 2010d: 549); Sudan; Tanzania (Stanley and Goodman, 2011: 43); Togo (Amori *et al.*, 2016: 218); Uganda (Kityo and Kerbis, 1996: 60); Yemen; Zambia (Ansell, 1969; Ansell, 1973; Ansell, 1978; Ansell, 1986; Monadjem *et al.*, 2010d: 549); Zimbabwe (Monadjem *et al.*, 2010d: 550).

Presence uncertain: Lebanon; Lesotho; Liberia; Mauritania.

Bates *et al.* (2013: 338) reject the presence of *N. thebaica* in the Republic of Congo as the locality (Kemo) mentioned by Pousargues (1896: 259) and Van Cakenberghe and De Vree (1999a: 143) is actually located in the Central African Republic.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Schoeman and Jacobs (2002: 157) mention the following wing parameters for 8 specimens from the Algeria Forestry Station (RSA): Fa: 48.2 ± 0.8 mm, Wing area: 155.4 ± 7.4 cm^2, Wing span: 28.7 ± 1.1 cm, Wing loading: 8.3 ± 0.9 N/m^2, and aspect ratio: 5.3 ± 0.3.

Four piebald (all-white fur/skin patches, eyes always normally coloured) specimens were reported from a mine in Tanzania (Howell, 1980a; Lucati and López-Baucells, 2016: Suppl.).

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on both the dorsal and ventral sides of all the wing parts (proximal and distal arm, forearm, plagiopatagium, propatagium).

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 2.49 to 2.97 mm in length, the shaft is slender and parallel-sided, the base is expanded, in lateral profile it is usually angled ventrally, while the tip is simple with a small expansion (Thomas *et al.*, 1994: 22).

Brain

From specimens collected in Bénin, Amrein *et al.* (2007) reported that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus was found to be absent. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. Amrein *et al.* (2007) could not detect any antigen in the antibody against DCX, and no NeuroD was detected in the hippocampal granule cells.

Reproduction system
Carter and Enders (2016: 284) found that *N. thebaica* has an extensive smooth chorioallantois, and its luminal epithelium is incomplete.

Gastro-intestinal tract (GIT)
Aylward *et al.* (2019: 1108) reported for six specimens an average weight of 10.17 ± 1.71 g and a GIT of 0.61 ± 0.14 g (6.02 ± 1.31 %).

FUNCTIONAL MORPHOLOGY:
Zhuang *et al.* (2012: 1) showed that the pit in the noseleaf of *Nycteris thebaica* has an effect on focusing the acoustic near field as well as shaping the radiation patterns and therefore enhancing the directionality.

Toussaint *et al.* (2012) investigated the patterns of heterothermy exhibited by *N. thebaica* during the austral winter in a tropical semi-arid environment. They expected that it would use pronounced heterothermy during the warm, dry winter months, but found this not to be the case. As possible reasons for this, they suggest the relatively high risk of predation, the communal roosting, the species' reproduction cycle (although they find this highly unlikely as the results for both sexes were similar), and the relatively long nightly foraging period.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.3 Pa, aspect ratio 5.5 and tip shape index of 3.62 for a wingspan of 31 cm and a wing area of 171 cm^2 and a body mass of 11 g.

SEXUAL DIMORPHISM:
In Swaziland, Monadjem (2001: 49) found that females were heavier and had longer forearms than males.

ECHOLOCATION:
Schoeman and Waddington (2011: 291) mention a F_{peak}: 90.3 ± 0.7 kHz and a duration of 1.7 ± 0.1 ms for specimens from Durban, South Africa. Davies *et al.* (2013b: Table S8) report a F_{peak}: 88.23 kHz (55.97 - 75.5 kHz). However, also in the Durban area, Naidoo *et al.* (2011: 23) mention a F_{peak}: 65.8 ± 20.1 kHz, and a duration of 1.7 ± 1.0 ms. From the Algeria Forestry Station (RSA), Schoeman and Jacobs (2002: 157) report the type of call to be "Low duty echolocation dominated by frequency modulated calls", with F_{peak}: 77.4 ± 2.7 kHz, and a low intensity. Parker and Bernard (2018: 57) recorded one call at the Mapungubwe National Park (RSA): F_{char}: 62.50 kHz, F_{max}: 83.40 kHz, F_{min}: 62.40 kHz, F_{knee}: 63.10 kHz, duration: 1.68 ms and 11.63 calls/sec.

Although very common in their study area in Swaziland, Monadjem *et al.* (2017c: 181) were unable to detect this species using an Anabat Express Detector due to its whispering (low db) calls. Even at distances of 0.1 m, they could not detect a call.

For Morocco, Disca *et al.* (2014: 226) recorded the following information: call type: FM multi H, F_{start}: 137.0 ± 1.2 kHz, F_{end}: 19.6 ± 0.5 kHz, F_{peak}: 84.5 ± 3.9 kHz, $F_{max\ all\ harmonics}$: 27.9 ± 0.2 kHz, $F_{max\ first\ harmonic}$: 56.1 ± 0.7 kHz, $F_{max\ third\ harmonic}$: 105.4 ± 3.2 kHz, bandwidth: 117.4 ± 1.5 kHz, duration: 2.4 ± 0.3 ms. This information is based on one single sequence they were not able to identify in hand.

Hackett *et al.* (2016: 223) reported the following values for 13 calls from Israel: Pulse duration: 1.35 ± 0.13 ms, F_{start}: 78.45 ± 3.08 kHz, F_{end}: 63.20 ± 1.99 kHz, F_{peak}: 70.18 ± 2.00 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 70.18 kHz, F_{start}: 78.45 kHz, F_{end}: 63.2 kHz, Band width: 15.25 kHz, and duration: 1.35 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 1 *Nycteris thebaica* call from the Kruger Park (RSA): F_{min}: 62.4 kHz, Duration: 1.7 ms, F_{max}: 83.4 kHz, F_{knee}: 63.1 kHz, F_{char}: 42.1 kHz.

Barclay and Jacobs (2022: 139) [referring to Fenton *et al.* (1983)] mention that *N. thebaica* responded more to the sounds of flapping wings of potential prey, than to their echolocation calls.

MOLECULAR BIOLOGY:
Karyotype
Both Peterson and Nagorsen (1975) and Rautenbach *et al.* (1993) reported $2n$ = 42, FN = 78, BA = 38, with a submetacentric X chromosome, and a metacentric Y chromosome.

An Ethiopian female studied by Tolera *et al.* (2021: 126) had 2n = 42 and FN either 78 or 80, depending on whether the X chromosome is either acrocentric or bi-armed. With the

exception of the acrocentric (X?) pair, all others are bi-armed.

HABITAT:
This species has a wide distribution and is found in most habitats throughout its range.

Cooper-Bohannon *et al.* (2016: Table S2) indicate that - in southern Africa - it occurs primarily in Savanna (63 %) areas, followed by SW arid (18 %) and Afromontane (10 %) habitats.

Based on the study of stable isotope ratios of carbon, nitrogen and hydrogen, Voigt *et al.* (2013: 755) suggest that *N. thebaica* might potentially be a migratory bat species, as far as elevational migration along the slopes of Mount Kilimanjaro is concerned. However, they also point out that the very low wing loading and aspect ratio is atypical for a migratory species, and therefore still categorize it as a sedentary species. Foord *et al.* (2018: 5), furthermore, indicate that *N. thebaica* moves less than one km per night between its roost and foraging sides.

HABITS:
In Swaziland male *N. thebaica* exhibit less roost site fidelity than females: there is greater roost movement in males than females (Monadjem, 2006b).

Stanley *et al.* (2007b: 209) report on a specimen in a Victor Rat trap, because it probably chased insects attracted to the bait used in the trap.

Thomas and Jacobs (2013: 125) found that, at De Hoop Nature Reserve (South Africa), *N. thebaica* emerged significantly earlier during mid-summer than during early and late summer. They also reported that bats feeding on Lepidoptera (*N. thebaica* and *Rhinolophus capensis*) emerged earlier than bats feeding on Diptera (*Tadarida aegyptiaca*).

ROOST:
Roosting in caves, mine audits and various other hollow sites (Churchill *et al.*, 1997), road culverts (Monadjem, 1998a; 2001; 2006b), under houses (LaVal and LaVal, 1980; Seamark and Bogdanowicz, 2002). Avery *et al.* (1990: 7) indicate that cool and moist caves or cave-like structures are used as daytime roosts. Howell (1980b: 26) reported that observed 300 *N. thebaica* individuals in short side pasages in the twilight zone of an abandoned kaolin mine in the Pugu Forest (Tanzania), where the humidity was 80 - 85 %. The same mine - but deeper inside - also housed about 500 000 *Hipposideros ruber* and 172 000 *Triaenops afer* bats.

Webala *et al.* (2022: 2) reported on several groups of *N. thebaica* specimens in Kenya using pit latrines as day or (possibly) night roosts and also as maternity roost.

In Swaziland, Monadjem *et al.* (2015: 15) found that roost switching occurs frequently, with more transitions to roosts where large numbers of bats were staying. They also found that moving to another roost was related to the distance of the new roost from the original one.

MIGRATION:
The species is not known to undergo migration (Monadjem, 2006a), and Laycock (1973) and Wingate (1983) suggest that *N. thebaica* does not have any homing ability. Monadjem (2006b) states that bat numbers vary greatly with season, suggesting that some movement is taking place. Monadjem (2006b) also reported that a banded female in Swaziland was discovered 107 km from where it was originally banded.

DIET:
Casual observations in Israel (Makin, 1979), Sudan (McLellan, 1986) and Namibia (Felten, 1956) reported that scorpions formed a stable part of *N. thebaica* diet. Yerbury and Thomas, 1895) examined cull-parts in Arabia, identifying various species of Orthoptera. Whereas Chapman (1958, in Tanzania), Roer (1975, in Namibia), and LaVal and LaVal (1980, in South Africa) found that Orthoptera, Lepidoptera, and Coleoptera were the primary prey orders consumed by *N. thebaica*. LaVal and LaVal (1980) presented results for early autumn (April), mid-winter (July), spring (November), and summer (January to March), listing a monthly breakdown of all prey orders consumed and finding that Orthoptera predominated in the study. In Zimbabwe, Fenton (1975) combined the results of his wet season collection (November 1969 to March 1970), finding only Orthoptera and Lepidoptera wings. Fenton *et al.* (1977a) and Fenton and Thomas (1980) examined the faeces of *N. thebaica* in Zimbabwe, and found that in the wet season (January and February 1976) Lepidoptera, Diptera and Coleoptera formed the bats' diet, while in the dry season (June 1977) he found only Lepidoptera (100 percent volume). In Zambia, Whitaker and Black (1976) examined the stomach contents of 33 *N. thebaica* which they separated into summer (November to March) and winter (May to September) categories. They found similar prey orders in *N. thebaica* diet, but also found many wingless insects.

At Farm Laatstgevonden, South Africa, Taylor *et al.* (2012b: 62) found the following prey groups: Lepidoptera (31.5 %), Coleoptera (24.75 %),

Hemiptera (19.5 %), Orthoptera (12.75 %), and other (11.5 %).

Bowie *et al.* (1999) at Mkuzi Game Reserve, KwaZulu Natal, South Africa, found that the diet consisted mainly of non-volant prey, primarily orthopterans and arachnids.

Feldman *et al.* (2000), in Israel, found they fed on Lepidoptera and Diptera.

Seamark and Bogdanowicz (2002) showed that prey eaten by *N. thebaica* varies significantly by order but not by season, and there was a significant interaction between the prey category and season, suggesting that these two factors are not independent from each other. Coleoptera (49.6 %) in the culled parts, (calculated as percent composition) dominated in spring (September-November), Orthoptera (38.8 %) in summer (December-February), Hemiptera (42.8 %) in autumn (March-May) and Lepidoptera (36.3 %) in winter (June-August). The diet also included a frog and small fish. Sometimes, geckos are taken too, but in general, vertebrate prey is rarely eaten (Happold and Happold, 2023: 111).

From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 51 faecal pellets from 8 bats (in volume percent): Lepidoptera (34.9 ± 27.3), Orthoptera (23.5 ± 19.6), Coleoptera (21.3 ± 17.6), Arachnida (13.5 ± 27.4), Diptera (3.8 ± 10.6), Hymenoptera (1.6 ± 4.6), and Hemiptera (1.5 ± 4.5).

Weier *et al.* (2019c: 6) examined droppings from this species in the Levubu region (Limpopo, RSA) and found DNA sequences of *Cryptophlebia peltastica* (Meyrick, 1921) (Lepidoptera) and *Nezara viridula* (Linnaeus, 1758) (Hemiptera).

Using Next Generation Sequencing (NGS), (Taylor *et al.* (2017b: 243, 252 - 254) reported on the 28 food items found in faecal pellets in the Limpopo province (RSA): Lepidoptera (occurred in 100 % of analysed pellets - *Toxocampinae tathorhynchus* + *Eutelia polychorda* + *Acanthovalva inconspicuaria* + *Isturgia roraria* + *Scopula rufisalsa* + *Hyblaea puera* + *Sena* sp. + *Sena prompta* + *Enmonodia capensis* + *Leucania BioLep10* + *Pandesma robusta* + *Pericyma atrifusa* + *Argyrogrammatini* sp. + *Thysanoplusia indicator* + *Tycomarptes* sp. + *Garella nilotica* + *Maurilia arcuata* + *Phycitinae* sp. + *Arotrura JFL201* + unmatched), Blattodea (50 % - *Pycnoscelus* + unmatched), Orthoptera (33 %), Coleoptera (17 % - *Cybister tripunctatus* + unmatched); Hemiptera (17 % - *Macrorhaphis acuta* + *Nezara viridula*); Orthoptera (Tettigoninae sp.).

PREDATORS:
Perrin (1982: 16) and Avery *et al.* (2005: 1054) found this species in pellets from *Tyto alba* (Scopoli, 1769) in South Africa.

Mikula *et al.* (2016: Supplemental data) and Malan *et al.* (2022: 67) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure
Monadjem (2001: 50) mentions that sex ratio was highly skewed with adult females outnumbering adult males by 2.8:1, even though the sex ratio of juveniles was 1:1. Sex ratios of adults varied seasonally, being highly skewed in July/August, October and December. Monadjem (2001: 50) suggests that this might be due to the females being resident and males joining them in late summer to mate.

Density
Fairly common through most of its range. However, an uncommon species in the Mediterranean region. In Morocco only three small colonies (usually 10 to 30 and occasionally up to 100 individuals) are known (Stéphane Aulagnier *pers. comm.* 2007 in Mickleburgh *et al.*, 2008bk; IUCN, 2009; Monadjem *et al.*, 2017aw).

Trend
2016: Unknown (Monadjem *et al.*, 2017aw).
2008: Unknown (Mickleburgh *et al.*, 2008bk; IUCN, 2009).

LIFESPAN:
In Swaziland, Monadjem (2006b) found that for both males and females, survivorship was low in the first year, but increased thereafter. While 15 % of females and 10 % of males banded as juveniles in 1998 and 1999 survived to three years of age. Monadjem (2006a) reported the age of *N. thebaica* in Swaziland to reach at least 7 to 8 years. Monadjem *et al.* (2015) studied the effect of time, age and sex class and climatic variables on survival from 1450 marked individuals from 16 roosts over a 10-year period. They found that the annual survival rate was highest in adult males and lowest in juvenile females. Climatological factors did not seem to have an influence.

ACTIVITY AND BEHAVIOUR:
Female *N. thebaica* in Eswatini appear to be resident year-round in the culverts, which

suggests that males join females in late summer for the purpose of mating (Monadjem, 2001). Lindeque (1987) describes the inflight behaviour of mating, where the active pursuit of the female by the male bat can be equated to courtship phase, with the butting phase inducing the female bat to hover and allowing the male to copulate, the brief frontal approach and head-neck biting by the male could be relict of some incomplete behaviour sequence.

Korine *et al.* (2015: 5) mention that the activity of *N. thebaica* could be underestimated because of the whispering nature of its echolocation calls.

REPRODUCTION AND ONTOGENY:
Martin and Bernard (2000: 32) mention that the corpus luteum is only present for the first half of pregnancy, and is subsequently completely regressed (Badwaik and Rasweiler, 2000: 276).

Bernard (1982a) [in Krutzsch (2000: 114)] indicated that this species is monoestrous in the subtropical, temperate regions of South Africa with a longer than usual gestation of five months and a three-month anoestrus. Male and female cycles are synchronized; spermatogenesis commences in late summer and the epididymides contain mature sperm from autumn to summer (see Bernard, 1976).

In Malawi, females are in reproductive synchrony, give birth at the end of the dry season and lactate their young for at least 1.5 months (Happold and Happold, 1990b: 566).

A pregnant female was collected on 22 July 1992 in the West Usambara Mountains (Tanzania) (Stanley and Goodman, 2011: 43).

Pregnant females were collected by Pakenham (1984: 29) on 4 November on Zanzibar.

MATING:
Mating system is not known (Monadjem, 2001).

PARASITES:
BACTERIA
Four out of 49 specimens tested at Mlawula (Swaziland) by Dietrich *et al.* (2016b: 3) tested positive for *Bartonella* and one was positive for *Rickettsia*.

Dietrich *et al.* (2016a: 4) found *Leptospira* in the urine of a bat from South Africa, and *Coxiella* in its faeces. For the RSA, these bacteria were further identified as *Leptospira borgpetersenii*, whereas in bats from Swaziland sequences belonging to *L. interrogans* were found.

Federici *et al.* (2022: 5) [referring to Dietrich *et al.* (2016a)] mentions Proteobacteria *Burkholderia, Helicobacter* and *Bartonella*.

FUNGI
Brennan *et al.* (2015: 145) found no antibodies against *Pseudogymnoascus destructans* (White-nose syndrome) in blood samples from bats from Botswana.

PROTOZOA
Schaer *et al.* (2015a: 381) found *Nycteria* sp. parasites in *N. thebaica* from South Sudan. Garnham and Heisch (1953: 357) described *Nycteria medusiformis* from a "*Nycteris capensis*".

24 of the 36 southern African *N. thebaica* specimens reported by Clément *et al.* (2019a: 5) were infected by *Trypanosoma* cf. *livingstonei*_likeA, likeB (5), likeC (5), likeD, likeE, likeF, likeG, likeI, likeJ, likeK (3), likeL, likeM, likeN (2). Based on otder references, Babyesiza *et al.* (2025: 4) reported *T. livingstonei* in bats from Uganda.Austen and Barbosa (2021: 7) also mentions the presence of *Trypanosoma (Megatrypanum) heybergi* from "*Nycteris capensis*" in the DRC.

NEMATODA
Spiruridae
An infection by *Spirura nycterisi* Khalil, 1975 in Tanzania was reported by Peralta-Rodríguez *et al.* (2012: 1006).

DIPTERA
Streblidae
Raymondia alulata Speiser, 1908, for which *N. thebaica* is the typical host, occurs in many parts of southern Africa from the Cape northwards to the Kaokoveld in Namibia and eastwards to Bukawayo in Zimbabwe (Haeselbarth *et al.*, 1966: 102). Shapiro *et al.* (2016: 249) reported it for the first time from Swaziland. *Raymondia hardyi* Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254). *Raymondia planiceps* Jobling, 1930 (Haeselbarth *et al.*, 1966: 102). *Raymondia seminuda* Jobling, 1954 from southern Botswana (Haeselbarth *et al.*, 1966: 103; Shapiro *et al.*, 2016: 255).

Nycteribiidae
Eucampsipoda africana Theodor, 1955 was repoted by Pawęska *et al.* (2021: 5) in the RSA.

Nycteribia scissa rhodesiensis Theodor, 1957 from Zimbabwe and Malawi (Haeselbarth *et al.*, 1966: 108). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114; Verrett *et al.*, 2022: 8).

Dick *et al.* (2023) mentioned the flies have been found on *Nycteris thebaica*: *Cyclopodia greeffi greeffi* Karsch, 1884, *Basilia (Tripselia) blainvillii blainvillii* (Leach, 1817), *Nycteribia schmidlii scotti* Falcoz, 1923, *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) and *Penicillidia (Penicillidia) pachymela* Speiser, 1901. *Phthiridium rhodesiense* (Theodor, 1957) has also been found on *Nycteris thebaica capensis* and *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) on *Nycteris thebaica* clade 4.

HEMIPTERA
Polyctenidae
Eoctenes nycteridis (Horváth, 1910) was reported from the DRC and Egypt by Szentiványi *et al.* (2022: 5) [referring to Anciaux de Faveaux (1965)].

SIPHONAPTERA
Pulicidae
Echidnophaga aethiops Jordan and Rothschild, 1906 described from Klipfontein, Namaqualand, South Africa and also found in Namibia, Botswana, Tanzania, Kenya and Somalia (Haeselbarth *et al.*, 1966: 135).

Ischnopsyllidae
Oxparius isomalus (Waterston, 1915) locality not stated (Haeselbarth *et al.*, 1966: 188).

ARACHNIDA
Argasidae
Sándor *et al.* (2021a: 4) reported the presence of *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) and *Chiropterargas confusus* (Hoogstraal, 1955).

Laelapidae
Metaspinolaelaps aelleni Till ([May] 1958) was described from *Nycteris thebaica capensis* from Zululand. Till (1960: 223) suggests that this possibly might be a synonym of *Bewsiella fledermaus* Domrow, [March] 1958, but this view doesn't seem to be followed (e.g., https://en.wiki2.org/wiki/Metaspinolaelaps).

Macronyssidae
Steatonyssus longipes Radovsky and Yuker, 1953 was described from an Egyptian slit-faced bat (Negm *et al.*, 2018: 728).

Trombiculidae
Vercammen-Grandjean and Fain (1958: 24) mention the presence of *Trombigasta (Trombigastia) mounti* (Radford, 1954) on "*N. capensis damarensis*" in Asmara, Eritrea. Stekolnikov (2018a: 50, 119, 160, 173) reported *Whartonia oweni* Vercammen-Grandjean and Brennan, 1957, *Trombigastia mounti* (Radford, 1954) (from "*N. thebaica damarensis*"), *Microtrombicula minutissima* (Oudemans, 1910) (from "*N. thebaica capensis*"), *Microtrombicula tanzaniae* Goff, 1982.

VIRUSES:
Astroviridae
Four out of 14 Mozambican bats tested by Hoarau *et al.* (2018: 2) were positive for this group of viruses. In Egypt, El Taweel *et al.* (2020: 5) found bats infected by viruses of the genus Mamastrovirus.

Bats carrying viruses of this family were also reported from Mozambique by Hoarau *et al.* (2021: Suppl.).

Dorrestein *et al.* (2024:9) reported that astroviruses found in *Nycteris thebaica* resolved into two very different positions across the virus phylogeny tree: one clustered within the Molossids and another as basal to the Yinpterochiropteran clade.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in six individuals from Limpopo Province, South Africa, none were tested positive (0/6). Hoarau *et al.* (2021: Suppl.) reported on bats from Mozambique testing positive for viruses of this family.

Hantaviridae
In Zambia, Sarii *et al.* (2024: 14) found *Nycteris thebaica* to be seropositive for Robina virus.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that one out of twelve examined South African *N. thebaica* specimens tested positive for *Paramyxovirus* sequences.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Duvenhage Virus
In 1986, Foggin (1988) recovered the Duvenhage (DUVV) virus from a *Nycteris thebaica* in Zimbabwe (see Paweska *et al.*, 2006; Hayman *et al.*, 2011a: 88; van Eeden *et al.*, 2011: 67). Markotter *et al.* (2013: 1000) report on antibodies for DUVV that were recovered from bats from Swaziland. Kuzmin and Rupprecht (2015: 71) [referring to Markotter *et al.* (2013)] indicate that *N. thebaica* might be a regionally important host for DUVV.

Rabies
Oelofsen and Smith (1993) tested 12 individual brains, from three localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Congo (Democratic Republic of the), Djibouti, Egypt, Eritrea, Eswatini, Ethiopia, Ghana, Guinea, Kenya, Malawi, Mali, Morocco, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Uganda, Zambia, Zimbabwe.

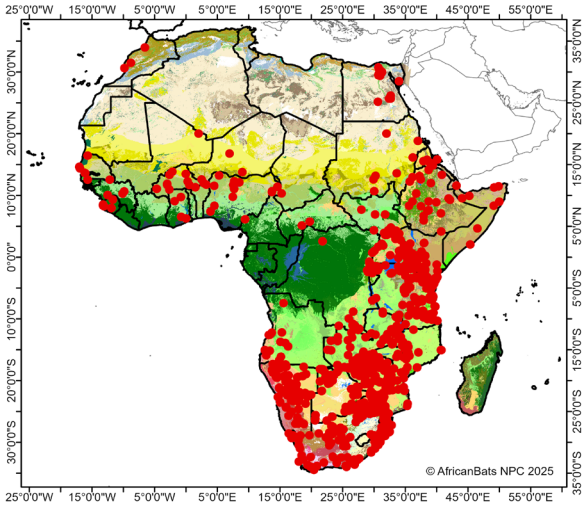

Figure 166. Distribution of *Nycteris thebaica*.

Nycteris woodi K. Andersen, 1914

*1914. *Nycteris woodi* K. Andersen, Ann. Mag. nat. Hist., ser 8, 13 (78): 563. Publication date: 1 June 1914. Type locality: Zambia: Chilanga [15 33 S 28 11 E, 4 100 ft]. [Goto Description]. Holotype: NHMUK 1914.4.22.2: ad, skin and skull. Collected by: Rodney Carrington Wood Esq. Collection date: November 1913. - Etymology: In honour of Rodney C. Wood, a well-known naturalist, who collected the original specimens at Chilanga, near Lusaka, Zambia (see Smithers, 1983: 118; Taylor, 2005). (Current Combination).
1946. *Nycteris woodi sabiensis* Roberts, Ann. Transv. Mus., 20 (4): 304. Type locality: Zimbabwe: Melsetter district: Sabi River: Birchenough Bridge [19 54 S 32 14 E]. [Goto Description]. Holotype: TM 8578: ad ♀, skin and skull. Collected by: A.G. White; collection date: 11 January 1938. (Name Combination).
1946. *Nycteris woodi woodi:* Roberts, Ann. Transv. Mus., 20 (4): 304. (Name Combination).
2018. *Nycteris woodii:* Parker and Bernard, Mammalia, 83 (1): 53. Publication date: 14 April 2018. (Lapsus).

TAXONOMY:
Van Cakenberghe and De Vree (1985) included *parisii* and *benuensis*. Thomas *et al.* (1994) elevated *parisii* to full species rank, followed by Simmons (2005: 393), who included *benuensis* as a subspecies of *parisii*.

Simmons (2005: 394) recognised one subspecies *sabiensis* Roberts, 1946.

COMMON NAMES:
Afrikaans: Wood se spleetneusvlermuis, Wood-spleetneusvlermuis, Woodse Langoorvlermuis. Czech: rýhonos jihoafrický. English: Wood's Slit-faced Bat, Wood's Long-eared Bat. French: Nyctère de Wood. German: Woods Schlitznasen-Fledermaus. Malawian: Liputiputi, Ndemiya, Namzeze.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in some protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ab; IUCN, 2009; Monadjem *et al.*, 2017w).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017w). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008ab; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004ap; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: NT B1ab(ii,iii,iv, v) ver 3.1 (2001) (Schoeman *et al.*, 2016b). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
It is possibly locally threatened in parts of its range by habitat loss (particularly through conversion of land to cotton farming), pesticide use, and disturbance of roosting sites (Mickleburgh *et al.*, 2008ab; IUCN, 2009; Monadjem *et al.*, 2017w).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ab) [in IUCN (2009)] and Monadjem *et al.* (2017w) report that it has been recorded from some protected areas (e.g., Kruger National Park, South Africa). Additional studies are needed into the distribution, natural history and possible threats to this poorly known species.

GENERAL DISTRIBUTION:
Nycteris woodi has been recorded from Zimbabwe, South Africa, to Zambia, north-west Mozambique and Malawi. It may range into southwestern Tanzania, however, it has yet to be recorded in this country. It is generally a lowland species. South of 8° S, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 308,190 km^2.

Native: Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 30; Monadjem *et al.*, 2010d: 550); Mozambique (Simmons, 2005: 394; Monadjem *et al.*, 2010d: 550); South Africa (Simmons, 2005: 394; Monadjem *et al.*, 2010d: 550); Zambia (Ansell, 1967; Ansell, 1986; Simmons, 2005: 394; Monadjem *et al.*, 2010d: 550); Zimbabwe (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 550).

Presence uncertain: Tanzania (Simmons, 2005: 394).

DETAILED MORPHOLOGY:
Baculum
The baculum ranges from 2.49 to 2.73 mm in length, the shaft is straight and parallel-sided, the base is expanded, in lateral profile it is angled ventrally, while the tip is simple and unexpanded, unlike *N. macrotis* and *N. parisii* (Thomas *et al.*, 1994:21).

ECHOLOCATION:
See Taylor (1999b).

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 42, FN = 78, BA = 38, a metacentric X chromosome, and an acrocentric Y chromosome, for a specimen from South Africa.

POPULATION:
Structure and Density
The abundance of this species is not well known. It has been recorded in colonies of a few dozen individuals, otherwise animals have been recorded individually (Mickleburgh *et al.*, 2008ab; IUCN, 2009; Monadjem *et al.*, 2017w).

Trend
2016: Decreasing (Monadjem *et al.*, 2017w).
2008: Decreasing (Mickleburgh *et al.*, 2008ab; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Although data were inconclusive, Happold and Happold (1990b: 566) indicate that young were born early in the wet season in Malawi.

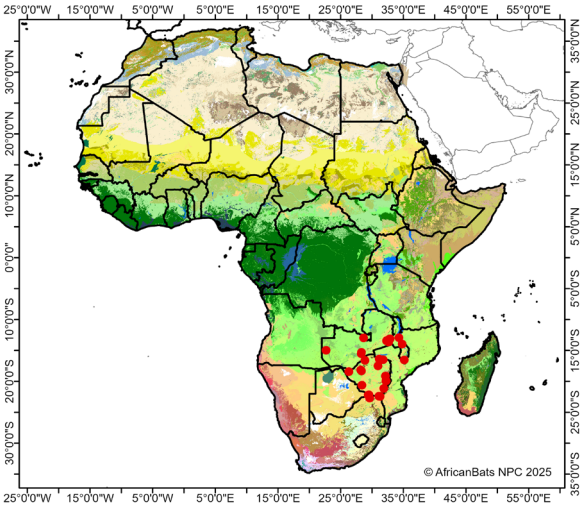

Figure 167. Distribution of *Nycteris woodi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Malawi, Mozambique, South Africa, Tanzania, Zambia, Zimbabwe.

INFRAORDER VESPERTILIONIFORMACEI Van Cakenberghe, Kearney and Seamark, 2007

*2007. *VESPERTILIONIFORMACEI* Van Cakenberghe, Kearney and Seamark, African Chiroptera Report. Publication date: July 2007. - Comments: The name of the Infraorder is based on *Vespertilio* Linnaeus, 1758 (type of VESPERTILIONIDAE Gray, 1821). (Current Combination).
? *Yangochiroptera*

TAXONOMY:
Currently two superfamily is known from within the Infraorder VESPERTILIONIFORMACEI for Africa: **MOLOSSOIDEA** Gervais, 1856; **VESPERTILIONOIDEA** Gray, 1821.

COMMON NAMES:
Czech: netopýrotvaří, netopýři.

Superfamily MOLOSSOIDEA Gervais, 1856

*1856. *Molossoidae* Gervais. (Current Combination).
1998. *Molossoidea:* Simmons, Interfamilian relationships in bats, 11. - Comments: Originally included the families Molossidae Gervais, 1855 and Antrozoidae Simmons, 1998 [= Antrozoinae Miller, 1897]. Considered a synonym of Molossidae by Jackson and Groves (2015: 257).

Family MOLOSSIDAE Gervais, 1856

*1856. *Molossidae* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool, (Sec 7), Vol 1, pt 2 (Mammifères): 53 footnote. Publication date: 23 July 1856. - Comments: Type genus: *Molossus* E. Geoffroy St. Hillaire, 1805. - Etymology: The name of the family is derived from the Greek "*molossus*", a kind of dog used by Greek shepherds, in ancient times (see Taylor, 2005). (Current Combination).
1866. *Molossi* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 258. - Comments: Type genus: *Molossus* E. Geoffroy, 1805. Originally included the genera *Dysopes* Illiger, 1811 [= *Molossus* É. Geoffroy, 1805]; *Molossus* É. Geoffroy, 1805; *Promops* Gervais, 1855; *Mormopterus* Peters, 1865; *Nyctinomus* É. Geoffroy, 1818 [= *Tadarida* Rafinesque, 1814]; and *Chiromeles* [= *Cheiromeles*] Horsfield, 1824 (see Jackson and Groves, 2015: 257).
1866. *Molossina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 93. Publication date: 1 February 1866. - Comments: Type genus: Molossus E. Geoffroy, 1805. Proposed as tribe and originally included the genera *Molossus* É. Geoffroy, 1805; *Promops* Gervais, 1855 and *Nyctinomus* É. Geoffroy, 1818 [= *Tadarida* Rafinesque, 1814] (see Jackson and Groves, 2015: 257).
1869. *Gymnorhinidæ* Fatio, Faune des Vertébrés de la Suisse.
1872. *Molossidae* Gill, Smiths. Misc. Coll., 11 (1): 17. - Comments: Type genus: *Molossus* E. Geoffroy, 1805. Originally included the genus *Molossus* É. Geoffroy, 1805 (see Jackson and Groves, 2015: 257). (Current Combination).
1889. *Gymnuridae* Ameghino, Actas Acad. Nac. Ciencias, Argentine e Cordoba, p 351. - Comments: See Taylor (1934).
1893. *Molossini* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 24. - Comments: Type genus: *Molossus* E. Geoffroy, 1805. Proposed as tribe(?) and originally included the genera *Mystacina* J. Gray, 1843; *Nyctinomus* É. Geoffroy, 1818 [= *Tadarida* Rafinesque, 1814]; *Chiromeles* [= *Cheiromeles*] Horsfield, 1824; and *Molossus* É. Geoffroy, 1805 (see Jackson and Groves, 2015: 257).
1952. *Mollossidae:* Srivastava, Proc. zool. Soc. Bengalen, 5 (2): 121. Publication date: September 1952. (Lapsus).
1961. *Mollosidae:* Siddiqi, Biologia, 7 (1/2): 117. (Lapsus).

TAXONOMY:
Koopman (1993a: 232) mentioned Gervais, 1856, whereas Corbet and Hill (1992: 156) and Peterson *et al.* (1995: 142) mentioned Gill 1872: 17 as author for this family.

Revised by Freeman (1981b). For a very different arrangement see Legendre (1984). See also Lamb *et al.* (2011).

Pavlinov *et al.* (1995: 90) recognise two subfamilies: Cheiromelinae and Tadaridinae.

Most recent authors (Hoofer and Van Den Bussche, 2003: 2; Simmons, 2005; Lamb *et al.*, 2011: 1) accept that the Molossidae consists of two subfamilies: Molossinae and Tomopeatinae. The latter subfamily used to be assigned to the Vespertilionidae, but Hoofer and Van Den Bussche (2003: 2) clearly indicate that this subfamily belongs to the Molossidae. Representatives of this subfamily only occur in South America and are therefore not included here.

Based on 102 morphological characters from the skull, dentition, postcrania, external morphology, tongue, and penis, Gregorin and Cirranello (2015: 2) distinguish two clades within the Molossidae, both of which include taxa from the Old and the New World: One clade is comprised of *Mormopterus, Platymops, Sauromys, Neoplatymops, Molossops, Cynomops, Cheiromeles, Molossus*, and *Promops*, whereas the second includes *Tadarida, Otomops, Nyctinomops, Eumops, Chaerephon*, and *Mops*. The relation of *Myopterus* to these two clades remains unclear. They also found that genera such as *Tadarida, Chaerephon* and *Molossops sensu lato* do not appear to be monophyletic.

Ammerman *et al.* (2012: 12) distinguish 16 - 17 genera, including 110 species worldwide.

Currently (Simmons and Cirranello, 2024b) recognized genera within the family MOLOSSIDAE: *Austronomus* Troughton, 1941; *Cabreramops* Ibãñez, 1980; *Cheiromeles* Horsefield, 1824; *Cynomops* Thomas,1920; *Eumops* Miller, 1906; *Micronomus* Throughton, 1944; *Molossops* Peters, 1866; *Molossus* E.

Geoffroy, 1805; ***Mops*** Lesson, 1842; ***Mormopterus*** Peters, 1865; ***Myopterus*** E. Geoffroy, 1818; *Neoplatymops* Peterson, 1965; *Nyctinomops* Miller, 1902; ***Otomops*** Thomas, 1913; *Ozimops* Reardon, McKenzie and Adams, 2014; ***Platymops*** Thomas, 1906; *Promops* Gervais, 1856; ***Sauromys*** Roberts, 1917; *Setirostris* Reardon, McKenzie and Adams, 2014; ***Tadarida*** Rafinesque, 1814 and *Tomopeas* Miller, 1900..

COMMON NAMES:
Castilian (Spain): Murcielagos cola de raton o de cola libre. Czech: morousovití, netopýři buldočí, tadaridovití. Dutch: Buldogvleermuizen. English: Free-tailed Bats, Wrinkled-lipped Bats, Bulldog Bats, Mastiff Bats, Bonneted Bats, Wolf-dog Bats. Finnish: Doggilepakot. French: Molossidés, Chauves-souris à queue libre, Molosses. German: Bulldoggfledermäuse, Bulldogg-Fledermäuse. Italian: Molòssidi. Norwegian: Buldoggflaggermus, foldeleppede flaggermus. Russian: Свободнохвостые, Бульдоговые. Tanoboase (Ghana): afrifraa, frede frede. Ukrainian: Молоссові [= Molossovi]. Vietnamese: Họ dơi thò đuôi.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Lavocat (1961) found an indetermined Molossid species from the Mio-Pliocene at Beni Mellal. While Butler (1978: 66) found four indetermined species from the early Pleistocene at Olduvai, Avery (1991: 6) found the remains of two different sized molossids in the upper Pleistocene at Border Cave, South Africa.

Shi and Rabosky (2015: 1532) report that the approximate fossil date for the Molossidae is 37.2 million years ago. The family-level stem ages/crown ages are respectively 53.8 and 45.2 mya. Ammerman *et al.* (2012: 12) indicate that the split between the Old and New World Molossid bats took place about 29 Mya.

MOLECULAR BIOLOGY:
Karyotype
Across the family, the 2*n* value varies between 34 and 52 (Sotero-Caio *et al.*, 2017: 5).

HABITS:
Rainho *et al.* (2023: 7) assigned the molossid bats occurring in the Meru county (Kenya) to two high-flying guilds: one containing *Otomops harrisoni* and flying at an approximate altitude of 15 - 550 m and all the others in a guild flying between 5 and 100 of altitude.

ROOST:
López-Baucells *et al.* (2018: 30) investigated roost selection by molossid bats in rural Madagascar and found that they predominantly roosted in modern public buildings (e.g., schools, offices and libraries), built with cement and bricks. Small, traditional housed made from mud and wood were much less used by molossids but housed small colonies of vespertilionids. Very similar results were reported by Lunn *et al.* (2024b: 1) from Kenya, where modern-build styles and triangular roofing were found to be building-level predictors of bat occupancy and the proportion of modern buildings a landscape predictor of bat occupancy.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention unidentified Molossidae to be taken by Grey kestrels (*Falco ardosiaceus* Vieillot, 1823) and Dickinson's kestrel (*Falco dickinsoni* Sclater, 1864), Red-necked falcon (*Falco ruficollis* Daudin, 1800), Eastern chanting goshawk (*Melierax poliopterus* Cabanis, 1868) [the latter three preying on "*Tadarida*" sp, where they also include *Mops* and *Chaerephon*].

PARASITES:
HEMIPTERA
Cimicidae
Crassicimex sexualis Ferris and Usinger, 1957 described from a single female taken 50 miles SE of Torit, Uganda (Haeselbarth *et al.*, 1966: 12, host referenced as a *Tadarida* sp.).

SIPHONAPTERA
Ischnopsyllidae
Araeopsylla scitula (Rothschild, 1909) found in southern Africa Cape Province, Lesotho, Natal, Transvaal and Botswana, where it has been collected from Free-tailed bats which are its true host (Haeselbarth *et al.*, 1966: 189). *Lagaropsylla* Jordan and Rothschild, 1921 almost all records of hosts are from Free-tailed Bats (Haeselbarth *et al.*, 1966: 190). *Lagaropsylla hoogstraali* Smit, 1957 from Sudan host recorded as a molossid (Haeselbarth *et al.*, 1966: 190). *Lagaropsylla idea* Smit, 1957 recorded mainly from free-tailed bats, with distributions in tropical Africa (Haeselbarth *et al.*, 1966: 190). *Lagaropsylla oblique* Smit 1957 known to infest molossid species from Sierra Leone, Cameroon and the Congo (Haeselbarth *et al.*, 1966: 191). *Lagaropsylla tauffliebi* Smit 1962 a series was taken from a free-tailed bat (*Tadarida* sp.) near Bangui, Central African Republic (Haeselbarth *et al.*, 1966: 191; host referenced as a *Tadarida* sp.).

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 40 % of the species

belonging to this family are confirmed viral carriers.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Angola, Cameroon, Congo (Democratic Republic of the), Egypt, Ethiopia, Ghana, Guinea, Guinea-Bissau, Kenya, Madagascar, Mozambique, Namibia, Senegal, South Africa, South Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Subfamily Molossinae Gervais, 1856

*1856. *Molossinae* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool, (Sec 7), Vol 1, pt 2 (Mammifères): 53 footnote. Publication date: 23 July 1856. - Comments: Type genus: *Molossus* E. Geoffroy St. Hilaire, 1805. (Current Combination).

1866. *Molossina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 93. Publication date: 1 February 1866. - Comments: Type genus: Molossus E. Geoffroy, 1805. Proposed as tribe and originally included the genera *Molossus* É. Geoffroy, 1805; *Promops* Gervais, 1855 and *Nyctinomus* É. Geoffroy, 1818 [= *Tadarida* Rafinesque, 1814] (see Jackson and Groves, 2015: 257).

1984. *Cheiromelinae* Legendre, Rev. suisse Zool., 91 (2): 425. Publication date: June 1984. - Comments: Type genus: *Cheiromeles* Horsfield, 1824. Pavlinov *et al.* (1995: 90) recognise this as a subfamily, but see R(3345: 432) and Jackson and Groves (2015: 257).

1984. *Molossinae:* Legendre, Rev. suisse Zool., 91 (2): 399, 425. Publication date: June 1984. - Comments: Type genus: *Molossus* E. Geoffroy, 1805. Originally included the genera *Molossus* É. Geoffroy, 1805; *Eumops* Miller, 1906; *Molossops* Peters, 1865 [including the subgenera *Cynomops* Thomas, 1920 and *Neoplatymops* Peterson 1965]; *Myopterus* É. Geoffroy, 1818 and *Promops* Gervais, 1855 (see Jackson and Groves, 2015: 258).

1984. *Tadaridinae:* Legendre, Arch. Zool. Mus., Moscow State Univ., 91 (2): 399, 426. - Comments: Type genus: *Tadarida* Rafinesque, 1814. Originally included the genera *Tadarida* Rafinesque, 1814; *Mormopterus* Peters, 1865a; *Nyctinomops* Miller, 1902; *Otomops* Thomas, 1913; and *Rhizomops* Legendre, 1984 [= *Tadarida* Rafinesque, 1814 (see Jackson and Groves, 2015: 257). (Lapsus).

1995. *Tadarinae:* Peterson, Eger and Mitchell, Faune de Madagascar, 84: 143. (Lapsus).

TAXONOMY:
Bronner *et al.* (2003) state that the genera *Mops* and *Chaerephon* have often been included as subgenera of *Tadarida* (Ellerman *et al.*, 1953; Hayman and Hill, 1971; Swanepoel *et al.*, 1980; Meester *et al.*, 1986; Corbet and Hill, 1992). Roberts (1951) elevated these taxa to generic rank, an approach followed by Freeman (1981b), Koopman (1982, 1993a) and Simmons (2005). In southern Africa, *Mops* is therefore represented by two species (*M. midas* and *M. condylurus*); *Chaerephon* by five (*C. bivittata, C. ansorgei, C. nigeriae, C. chapini* and *C. pumilus*); and *Tadarida* by four (*T. aegyptiaca, T. lobata, T. ventralis* and *T. fulminans*). Other African genera are *Mormopterus, Myopterus, Otomops, Platymops* and *Sauromys* (Lamb *et al.*, 2011: 2), with *Myopterus, Platymops* and *Sauromys* being endemic to mainland Africa.

Ammerman *et al.* (2012: 23) suggest that this subfamily should be subdivided into four tribes: Molossini containing the New World taxa (*Molossus, Eumops, Molossops, Cynomops, Neoplatymops, Nyctinomops*, and *Promops*), tribe Tadarini containing Old World taxa (*Tadarida, Chaerephon, Mops, Platymops, Sauromys, Myopterus*, and *Otomops*), tribe Cheiromelini, and tribe Mormopterini.

Based on five nuclear sequence markers, Napier (2013) found strong support for the monophyly of the combined genera *Chaerephon* and *Mops* (with the exception of *C. jobimena*). There was no support for monophyly of either of these genera, suggesting that both should be combined in a single genus. Her study also suggests that a new species of *Otomops* should be names from northeast Africa and Arabia.

COMMON NAMES:
Czech: praví morousi. English: Free-tailed Bats, Wrinkled-lipped Bats, Bulldog Bats, Mastiff Bats, Bonneted Bats, Wolf-dog Bats. French: Molosses.

PARASITES:
ACARI
Rosensteiniidae
Fain (1979: 124) reported a "*Tadarida* sp." parasitised by *Nycferiglyphus tadaridae* Fain, 1963.

Genus ***Mops*** Lesson, 1842

*1842. *Mops* Lesson, Nouv. Tabl. Regn. Anim. Mammifères, 18. Publication date: 1842. - Comments: Type species: *Mops indicus* Lesson, 1842 (=*Molossus mops* de Blainville, 1840; Genotype *Mops indicus* Lesson = *Dysopes mops* F. Cuvier; listed in synonymy of *Nyctinomus* by Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 251; but listed as a genus with distinct characters by Thomas, 1913, J. Bombay Nat. Hist. Soc., 22, p. 91). - Etymology: From the masculine German substantive *Mops*, meaning "pug", a small companion dog resembling a bulldog,

corresponding to the French "carlin" and the Italian "carlino"; the name refers to the wrinkled lips characteristic of the genus *Mops* and the family Molossidae. According to one seemingly erroneous interpretation, from the Malaysian substantive *mòps*, meaning "bat" (see Lanza *et al.*, 2015: 293). (Current Combination).

1907. *Chaerephon:* Andersen. (Name Combination).

1951. *Tadarida (Chaerephon):* Ellerman and Morrison-Scott. (Name Combination).

TAXONOMY:

Formerly included in *Tadarida*; for synonyms see Freeman (1981b: 158). See also Legendre (1984). Harrison and Bates (1991: 64), Ansell and Dowsett (1988: 45), Corbet and Hill (1992: 157), Grubb *et al.* (1998: 93) and Horáček *et al.* (2000: 137), who include *Mops* as subgenus in *Tadarida*. A key for the species traditionally assigned to *Mops* is provided by Dunlop (1999: 1, Mammalian Species, 615), whereas a key for the species traditionally assigned to *Chaerephon* is provided by Bouchard (1998: 1, Mammalian Species, 574).

In their molecular phylogeny study, Lamb *et al.* (2010: 204; 2011: 9) found strong support for the monophyly of the *Chaerephon* + *Mops* taxa (about 17.2 Mya old), but not for either of the genera separated. They also found some indications that certain *Mops* species are ancestral and *Chaerephon* species more derived. Their results suggest that *Chaerephon* should not be considered a subgenus of *Tadarida*, nor a genus on itself. They suggest combining *Chaerephon* (except *Chaerephon jobimena*) together with *Mops* into a single genus pending a more complete study.

Ammerman *et al.* (2012: 20) also found support for a *Mops* - *Chaerephon* clade, which resulted in paraphyly of *Chaerephon*, and confirm again that *Chaerephon* is distinct from *Tadarida*. A further morphological study by Gregorin and Cirranello (2015: 10) confirmed the paraphyly of *Chaerephon* but was unable to resolve the relationships within the genus.

The morphological study by Gregorin and Cirranello (2015: 10) was unable to resolve the relations within the genus *Mops*, but it supports the monophyly of the genus.

Simmons and Cirranello (2020) included "*Chaerephon*" in the list of synonyms for *Mops*, but did not assign it to as subgenus, as they do for the species traditionally assigned to the genus *Mops*. For convenience reasons, however, we tentatively retain *Chaerephon* as a subgenus.

Currently, Simmons and Cirranello (2024b) do not recognize subgenera, but these are retained here. They do recognize the following species in the genus *Mops*:

Mops Lesson, 1842: ***condylurus*** (A. Smith, 1833); ***congicus*** J. A. Allen, 1917; ***demonstrator*** (Thomas, 1903); ***leucostigma*** G. M. Allen, 1918; ***midas*** (Sundevall, 1843); *mops* (de Blainville, 1840) – western Malaysia, Sumatra, Borneo perhaps Java (Simmons, 2005: 443); ***niangarae*** J. A. Allen, 1917; ***niveiventer*** Cabrera and Ruxton, 1926; *sarasinorum* (A. Meyer, 1899) – Sulawesi (Indonesia) and adjacent small islands, Philippines (Simmons, 2005: 443); ***trevori*** J. A. Allen, 1917.

Xiphonycteris Dollman, 1911: ***bakarii*** Stanley, 2008; ***brachypterus*** (Peters, 1852); ***nanulus*** J. A. Allen, 1917; ***petersoni*** (El Rayah, 1981); ***spurrelli*** (Dollman, 1911); ***thersites*** (Thomas, 1903).

No subgenus assigned: ***aloysiisabaudiae*** (Festa, 1907); ***ansorgei*** Thomas, 1913; ***atsinanana*** Goodman, Buccas, Naidoo, Ratrimomanarivo, Taylor and Lamb, 2010; ***bemmeleni*** (Jentink, 1879); ***bivittatus*** (Heuglin, 1861); *bregullae* (Felten, 1964) – Vanuatu, Fiji Isls (Simmons, 2005: 433); ***chapini*** J. A. Allen, 1917; ***gallagheri*** (Harrison,1975); *jobensis* (Miller, 1902) – Seram (Moluccas), Yapen Isl (Indonesia), New Guinea, northern and central Australia (Simmons, 2005: 434); ***jobimena*** Goodman and Cardiff, 2004; *johorensis* (Dobson, 1873) – western Malaysia, Sumatra (Indonesia) (Simmons, 2005: 433); ***leucogaster*** A. Grandidier, 1870; ***major*** (Trouessart, 1897); ***nigeriae*** Thomas, 1913; *plicatus* (Buchannan, 1800) – India and Sri Lanka to southern China, Hong Kong, Cambodia and Vietnam, southeast through Malyasia to the Philippines, Borneo and Lesser Sunda Isls, Hainan (China), Cocos Keeling Isl (Indian Ocean) (Simmons, 2005: 434); ***pumilus*** (Cretzschmar, 1830-1831); ***pusillus*** (Miller, 1902); ***russatus*** J. A. Allen, 1917; ***shortridgei*** (Thomas, 1926); *solomonis* (Troughton, 1931) – Solomon Isls (Simmons, 2005: 435); ***tomensis*** (Juste and Ibañez, 1993).

Additionally, there is the extinct African ***†rusingae*** Arroyo-Cabrales, Gregorin, Schlitter and Walker, 2002.

COMMON NAMES:

Czech: velcí morousi. English: Mops Bats, Greater Free-tailed Bats, Mops Free-tailed Bats. French: Tadarides. Italian: Pipistrèllo carlìno.

SEXUAL DIMORPHISM:
El-Rayah (1980: 163) confirmed the sexual dimorphism in the premolar size reported earlier: in males the first lower premolar is larger at the base than the second lower premolar, whereas in females this is the opposite.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burundi, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Ghana, Kenya, Madagascar, Malawi, Namibia, South Africa, South Sudan, Tanzania, The Gambia, Uganda, Zambia, Zimbabwe.

Subgenus *Mops (Chaerephon)* Dobson, 1874

1874. *Chœrephon:* Dobson, J. Asiatic Soc. Bengal, 431. - Comments: "Incorrect subsequent spelling", see Jackson and Groves (2015: 259), who indicated that "this spelling does not appear to have [been] subsequently used", although Bræstrup (1935b: 94) and Roberts (1932a: 17; 1935: 245) a.o. used *Choerephon*. Most authors (including Jackson and Groves, 2015: 259) assign this spelling to another publication by Dobson (Dobson, 1878), but this was actually the original spelling. - Phonetics: keer'-ef-on.

*1874. *Nyctinomus (Chaerephon)* Dobson, J. Asiatic Soc. Bengal, 43 (2): 144. Publication date: 17 October 1874. - Comments: Type species: *Molossus (Nyctinomus) johorensis* Dobson, 1873. Not *Chaerephon* Godman in Godman and Salvin, 1900 (Insecta, Lepidoptera, Hesperiidae) (see Jackson and Groves, 2015: 258). - Etymology: From the Greek "*chaerephon*" meaning joyful-sounding. Flannery (1990: 370; 1995a: 404) refers to it as "a proper name, significance unknown". Dobson (1874) in Bouchard (1998: 4) and Lanza *et al.* (2015: 268) indicate that it refers to the friend of Socrates who is depicted as "*Χαιρεφῶν*" ("Chaerephon the bat") in Aristophanes' comedy, *Aves*, maybe alluding to his nocturnal habits or bony appearance or as suggested by Plato in Apology, to his sudden, excitable nature.

1914. *Nyctinommus:* Alluaud and Jeannel, in: Jeannel and Racovitza, Arch. Zool. exp. gen., 53: 373. Publication date: 7 March 1914. (Lapsus).

1917. *Chærephon (Lophomops)* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 460, text-fig 9 - 11. Publication date: 29 September 1917 [Goto Description]. - Comments: Type species: *Chærephon (Lophomops) chapini* J.A. Allen, 1917, by original designation (see Jackson and Groves, 2015: 259).

1938. *Lephomops:* Frechkop, Exploration du Parc National Albert, 48. - Comments: Reported as subgenus of *Chaerephon* by Frechkop (1938: 48), but clearly a lapsus, as furtheron (p. 53) the correct *Lophomops* is used. (Lapsus).

1962. *Tadarida (Chaerophoron):* Taufflieb, Bull. Inst. Rech. Sci. Congo, 1: 112. (Lapsus).

1965. *Nyctinimus:* Koopman, Am. Mus. Novit., 2219: 21. Publication date: 22 June1965. (Lapsus).

2004. *Chaeraphon:* Okafor, Igbinosa and Ezenwaji, Anim. Res. Int., 1 (1): 64. Publication date: April 2004. (Lapsus).

2017. *Chaereophon:* Weiss, Dabrowski, Kurth, Leendertz and Leendertz, Virology J., 14 (181): 1. Publication date: 18 September 2017. (Lapsus).

2021. *Cherephon:* Tolera, Woldegebriel and Woldegebriel, Am. J. Biosci. Bioeng., 9 (4):125. Publication date: 26 August 2021. (Lapsus).

2024. *Nyctinomys:* Gippoliti, J. Vertebr. Biol., 73 (23110):. Publication date: 5 April 2024. (Lapsus).

? *Chaerephon sp. DMR-2017*

? *Chaerephon sp. IVK-2011*

? *Chaerephon sp.:*

? *Chaerophon:* (Lapsus).

? *Mops (Chaerephon):* (Current Combination).

TAXONOMY:
Formerly included in *Tadarida*; see Freeman (1981b: 60, 133, 150); see also Legendre (1984). Harrison and Bates (1991: 62) and Ansell and Dowsett (1988: 45), Corbet and Hill (1992: 157), Grubb *et al.* (1998: 93) and Horáček *et al.* (2000: 137) include *Chaerephon* in *Tadarida*. A key is provided by Bouchard (1998: 1, Mammalian Species, 574).

Nyctinomus is considered a valid genus by McFarland (1998: 34), but included in *Tadarida* by Koopman (1993a: 240), Grubb *et al.* (1998: 93), or included in *Chaerephon* by Simmons (2005), or in *Mormopterus* by Jacobs and Fenton (2002, Mammalian Species, 703: 1). Grubb *et al.* (1998: 93) also indicate that Mahoney and Walton (1988a: 148 - 149) considered that *Nyctinomus* was dated from 1813 and was therefore the prior name for the genus *Tadarida* Rafinesque, 1814. Their case is unconvincing, and Grubb *et al.* (1998) do not think it desirable to change the long established usage of *Tadarida*. However, since *Chaerephon* Dobson, 1874 is clearly more recent it might be that *Nyctinomus* should be used instead of *Chaerephon*.

Simmons and Cirranello (2020) include "*Chaerophon*" Dobson, 1874 in the list of synonyms of "*Mops*" Lesson, 1842, but they do not mention any of the *Chaerephon* species in their listing.

In their molecular phylogeny study, Lamb *et al.* (2010: 204; 2011: 9) found strong support for the monophyly of the *Chaerephon* + *Mops* taxa (about 17.2 Mya old), but not for either of the genera separated. They also found some indications that certain *Mops* species are ancestral and *Chaerephon* species more derived. Their results suggest that *Chaerephon* should not be considered a subgenus of *Tadarida*, nor a

genus on itself. They suggest combining *Chaerephon* (except *Chaerephon jobimena*) together with *Mops* into a single genus pending a more complete study.

Ammerman *et al.* (2012: 20) also found support for a *Mops* - *Chaerephon* clade, which resulted in paraphyly of *Chaerephon*, and confirm again that *Chaerephon* is distinct from *Tadarida*. A further morphological study by Gregorin and Cirranello (2015: 10) confirmed the paraphyly of *Chaerephon* but was unable to resolve the relationships within the genus.

Simmons and Cirranello (2020) include all the "*Chaerephon*" species in the genus *Mops*.

Benda *et al.* (2025: 81) tentatively follow the traditional view and consider *Chaerephon* a valid genus until this phylogenetic question is resolved.

Currently recognized species of the subgenus *Chaerephon*: ***aloysiisabaudiae*** (Festa, 1907); ***ansorgei*** Thomas, 1913; ***atsinanana*** Goodman, Buccas, Naidoo, Ratrimomanarivo, Taylor and Lamb, 2010; ***bemmeleni*** (Jentink, 1879); ***bivittatus*** (Heuglin, 1861); *bregullae* (Felten, 1964) – Vanuatu, Fiji Isls (Simmons, 2005: 433); ***chapini*** J. A. Allen, 1917; *jobensis* (Miller, 1902) – Seram (Moluccas), Yapen Isl (Indonesia), New Guinea, northern and central Australia (Simmons, 2005: 434); ***jobimena*** Goodman and Cardiff, 2004; *johorensis* (Dobson, 1873) – western Malaysia, Sumatra (Indonesia) (Simmons, 2005: 433); ***leucogaster*** A. Grandidier, 1870; ***major*** (Trouessart, 1897); ***nigeriae*** Thomas, 1913; *plicatus* (Buchannan, 1800) – India and Sri Lanka to southern China, Hong Kong, Cambodia and Vietnam, southeast through Malyasia to the Philippines, Borneo and Lesser Sunda Isls, Hainan (China), Cocos Keeling Isl (Indian Ocean) (Simmons, 2005: 434); ***pumilus*** (Cretzschmar, 1830-1831); *pusillus* (Miller, 1902); ***russatus*** J. A. Allen, 1917; *solomonis* (Troughton, 1931) – Solomon Isls (Simmons, 2005: 435).

For convenience reasons, however, we tentatively retain *Chaerephon* as a subgenus.

COMMON NAMES:
Czech: malí morousi, příšerecové. English: Wrinkle-lipped Bats, Lesser Free-tailed Bats, Lesser Mastiff Bats. French: Tadarides. Italian: Cherefónti.

BIOGEOGRAPHY:
Taylor *et al.* (2009) investigated patterns in mitochondrial DNA (cytochrome *b* and D-loop) variation in *Chaerephon* spp. specimens from southern Africa and Madagascar, including individuals from Madagascar with distinct phenotypic characters and identified as *C. leucogaster* and *C. pumilus*. Taylor *et al.* (2009) found southern African populations of *C. pumilus* to be paraphyletic, Malagasy *C. leucogaster* to be nested within *C. pumilus* sensu lato, and Malagasy *C. pumilus* forming a sister group to a complex of African *C. pumilus* and Malagasy *C. leucogaster* clades. Goodman *et al.* (2010a) including *C. pusillus* samples from the Comoros (all four islands) and Aladabra, found that on Mayotte and Madagascar individuals that can phenotypically be assigned to *C. leucogaster* and *C. pumilus* sensu lato, are known to occupy the same day roost sites. Morphological and molecular genetics data indicate they act as a good biological species. The individuals from the Comoros and Aldabra formed a monophyletic group, which shows morphological similarity. Comorian individuals, classically assigned to *C. pumilus*, are best considered distinct from African and Madagascan populations, and represent the same taxon occurring in the western Seychelles under the name *C. pusillus*.

PARASITES:
BACTERIA
Di Cataldo *et al.* (2020: 2) examined 11 Nigerian *Chaerephon* sp. bats and found 4 (36 %) to be infected by hemoplasma bacteria.

NEMATODA
Durette-Desset and Chabaud (1975: 317) described *Molinostrongylus bauchoti* from a Madagascan bat belonging to this genus.

ACARI
Trombiculidae
Stekolnikov (2018a: 154) mentioned *Microtrombicula intranasalis* Vercammen-Grandjean, 1965 from *Chaerephon* sp.

VIRUSES:
Of the 13 *Chaerephon* sp. specimens from Kisumu, Kenya, one tested positive for *Adenovirus*, one for *Rhabdovirus* and five for *Polyoma virus* (Conrardy *et al.*, 2014: 259). Of the 16 specimens from Moi University, one tested positive for *Adenovirus*, one for *Paramyxovirus* and two for *Polyomavirus*.

Adenoviridae
Conrardy *et al.* (2014) detected an adenovirus in two individuals out of 35 sampled in Kenya. This virus groups within the *Mastadenovirus* genus.

Coronaviridae - Coronaviruses
SARS-CoV
During February 2008 in Ghana, six fecal samples were tested negative for coronavirus

(CoV) RNA by Pfefferle *et al.* (2009) [as *Chaerephon spp.*]. Tong *et al.* (2009) tested several bats collected in Kenya in 2006 positive for the presence of coronavirus RNA in fecal samples (genus *Betacoronavirus*, subgenus *Sarbecovirus*; see Markotter *et al.*, 2020: 5).

Hu *et al.* (2015: 5) indicate that in Ghana, Kenya and Nigeria novel betacoronaviruses related to SARS-CoV have been detected.

12 of the 113 Kenyan specimens tested by Tao *et al.* (2017: Suppl.) were positive for CoV (10.6 %).

Flaviviridae
Pegivirus (BPgV)
1 out of 3 Kenyan *Chaerephon* sp specimens was infected by clade K type *Pegivirus* (Quan *et al.*, 2013: Table S5).

Raulino *et al.* (2022: 256) found antibodies against Dengue virus.

Paramyxoviridae
Conrardy *et al.* (2014) detected a paramyxovirus in one out of 35 individuals sampled in Kenya. This virus groups with Morbillivirus-related viruses.

Polyomaviridae
Orthopolyomavirus (BPyV)
DNA of two novel polyomaviruses were detected from fecal/oral swabs from *Chaerephon* sp specimens from Kenya (Tao *et al.*, 2012).

Rhabdoviridae
Conrardy *et al.* (2014) detected a rhabdovirus in one out of 35 individuals sampled in Kenya. This virus groups with the *Tupavirus* genus, with a near identical sequence detected in *Miniopterus africanus*.

Togavirida
Raulino *et al.* (2022: 256) found antibodies against Chikungunya virus and O'nyong nyong virus.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Congo (Democratic Republic of the), Kenya, Madagascar, Mayotte, Sierra Leone, South Sudan, Tanzania, Uganda.

Mops (Chaerephon) aloysiisabaudiae (Festa, 1907)

*1907.	*Nyctinomus aloysii-sabaudiae* Festa, Boll. Mus. Zool. Anat. Comp. Univ. Torino, 22 (546): 1. Publication date: 21 January 1907. Type locality: Uganda: Western province: Toro distrirct: East of Ruwenzori: "Toro district" [ca. 00 30 N 30 00 E]. [Goto Description]. - Comments: Coordinates mentioned as 01 00 N 30 22 E by Thorn *et al.* (2009: 71). Allen (1939a: 107) mentioned the type locality as "Ruwenzoni". Grubb *et al.* (1998: 84) mention "East of Ruwenzori, Toro district".
1917.	*Nyctinomus aloysii-sabaudiæ:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 460. (Name Combination).
1922.	*Chaerephon angolensis sabaudiae:* de Beaux, Ann. Mus. civ. Stor. nat. Genova, ser 3, (OS 49) 9: 371. Publication date: 28 August 1922. (Lapsus).
1966.	*Tadarida (Chaerephon) cyclotis* Brosset, Biol. gabon., 2 (1): 80. Type locality: Gabon: Bélinga [01 13 N 13 10 E]. [Goto Description]. Holotype: MNHN ZM-MO-1981-1360: ad ♂, skull and alcoholic. Collected by: André Brosset; collection date: January 1963.
1989.	*Chaerophon aloysiisabaudiae:* Fenton, Can. J. Zool., 67 (8): 2034. Publication date: 1 August 1989. (Lapsus).
2020.	*Mops aloysiisabaudiae:* Simmons and Cirranello, BatNames.org. (Current Combination).
2024.	*Nyctinomys aloysii-sabaudiae:* Gippoliti, J. Vertebr. Biol., 73 (23110): 2. Publication date: 5 April 2024. (Lapsus).
?	*Chaerephon aloysiisabaudiae:* (Name Combination).
?	*Mops (Chaerephon) aloysiisabaudiae:* (Current Combination).
?	*Tadarida aloysiisabaudiae:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous vévodský. English: Duke of Abruzzi's Wrinkle-lipped Bat, Abruzzi's Wrinkle-lipped Bat, Duke of Abruzzi's Free-tailed Bat. French: Tadaride du Duc des Abruzzes, Molosse du Duc des Abruzzes. German: Fürst von Abruzzen Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bn; IUCN, 2009; Monadjem *et al.*, 2017ax).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon aloysiisabaudiae*] (Monadjem *et al.*, 2017ax). 2008: LC ver 3.1 (2001) assessed as *Tadarida aloysiisabaudiae* (Mickleburgh *et al.*, 2008bn; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bi; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is threatened by deforestation of its habitat by logging activities (Mickleburgh *et al.*, 2008bn; IUCN, 2009; Monadjem *et al.*, 2017ax).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bn) [in IUCN (2009)] and Monadjem *et al.* (2017ax) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further studies are needed into the distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:
Mops aloysiisabaudiae has been patchily recorded in West and Central Africa. It ranges from Côte d'Ivoire and Ghana in the west, through Cameroon and northern Central Africa, to southern Sudan and western Uganda. It is known from around 50 localities (mostly single specimens).

Native: Cameroon; Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire (Beaucournu and Fahr, 2003: 175); Gabon; Ghana; Guinea (Mamba *et al.*, 2020: 134), Nigeria (Tanshi *et al.*, 2019: 14788); Sudan; Uganda.
Presence uncertain: Ethiopia (Simmons, 2005).

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) reported 2*n* = 48, FN = 66, BA = 20, a submetacentric X chromosome and an acrocentric Y chromosome.

POPULATION:
Structure and Density
This high-flying species is rarely captured. It is found in relatively small groups (Mickleburgh *et al.*, 2008bn; IUCN, 2009; Monadjem *et al.*, 2017ax).

Trend
2016: Decreasing (Monadjem *et al.*, 2017ax).
2008: Decreasing (Mickleburgh *et al.*, 2008bn; IUCN, 2009).

VIRUSES:
Reoviridae
Weiss *et al.* (2017: 1) isolated a new virus belonging to the subfamily Spinareovirinae: Taï Forest reovirus (TFRV) (tentatively assigned to the genus *Coltivirus*) from a bat in Côte d'Ivoire. This was the first bat-borne reovirus in Africa (Weiß, 2013: 65).

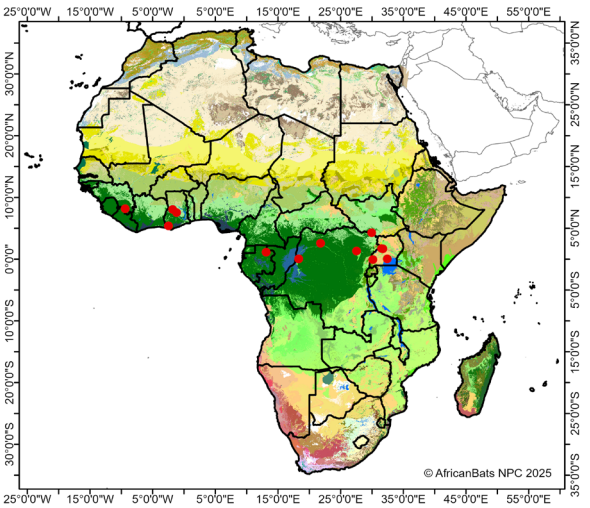

Figure 168. Distribution of *Mops (Chaerephon) aloysiisabaudiae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Ghana, Guinea, Uganda.

Mops (Chaerephon) ansorgei (Thomas, 1913)

*1913. *Nyctinomus ansorgei* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 318. Publication date: 1 March 1913. Type locality: Angola: Malange [=Malanje] [09 32 S 16 20 E, 1 150 m]. [Goto Description]. Holotype: NHMUK 1910.4.8.4: ad ♂. Collected by: Dr. William John Ansorge; collection date: 17 February 1909; original number: 5. - Etymology: In honour of Dr. William John Ansorge (1850 - 1913), a collector of zoological specimens, who collected the type specimen of this species in Malange, northern Angola (see Taylor, 2005; Lanza *et al.*, 2015: 271).
1946. *Nyctinomus rhodesiae* Roberts, Ann. Transv. Mus., 20 (4): 307. Type locality: Zimbabwe: Bindura district: Masembura Native Reserve: Chikupo caves [17 24 S 31 20 E]. [Goto Description]. Holotype: TM 9977: ad ♂, skin and skull. Collected by: H.B. Masterson; collection date: 10 July 1945.
1967. *Tadarida bivittata:* Ansell, Arnoldia Rhod., 2 (38): 25. - Comments: Not of Heuglin, 1861.
1989. *Chaerophon ansorgei:* Fenton, Can. J. Zool., 67 (8): 2034. Publication date: 1 August 1989. (Lapsus).
2020. *Mops ansorgei:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon ansorgei:* (Name Combination).
? *Mops (Chaerephon) ansorgei:* (Current Combination).
? *Tadarida (Chaerephon) ansorgei:* (Name Combination).
? *Tadarida ansorgei:* (Name Combination).

TAXONOMY:
Distinct from *bivittata*; see Eger and Peterson (1979: 1889), who revised it.

COMMON NAMES:
Afrikaans: Ansorge se losstertvlermuis, Ansorge-losstertvlermuis. Chinese: 安氏犬吻蝠. Czech: morous Ansorgeův. English: Ansorge's Wrinkle-lipped Bat, Ansorge's Free-tailed Bat. French: Tadaride d'Ansorge, Molosse d'Ansorge, Molosse d'Afrique du Sud. German: Ansorges Bulldoggfledermaus. Italian: Cherefónte di Ansòrge. Portuguese: Morcego de cauda livre de Ansorge.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Hildebrand *et al.* (2010: 281) recorded this species from the Koka site in southern Ethiopia.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it is likely to occur in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017v).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon ansorgei* (Monadjem *et al.*, 2017v). 2008: LC ver 3.1 (2001) [assessed as *Tadarida ansorgei*] (Mickleburgh *et al.*, 2008ac; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004al; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016aa). 2008: LC ver 3.1 (2001) (Friedmann and Daly, 2004). 1986 - Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species. In parts of West Africa, some populations may be threatened by overharvesting for subsistence food (Mickleburgh *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017v).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ac) [in IUCN (2009)] and Monadjem *et al.* (2017v) report that in view of the species wide range it is presumably present in many protected areas (including Comoe National Park, Côte d'Ivoire). No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Mops ansorgei is widely distributed over much of sub-Saharan Africa. It ranges from northeastern Côte d'Ivoire in the west, through much of the northern part of West and Central Africa (north of the Congo basin), to Ethiopia and East Africa, from here southwards as far as northeastern South Africa. It has been recorded between 400 and 2,000 m asl.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 673,792 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 541; Taylor *et al.*, 2018b: 62); Cameroon (Eisentraut, 1968: 171 - 1st record from West Africa); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 541); Côte d'Ivoire; Ethiopia; Mozambique (Monadjem *et al.*, 2010d: 541: Monadjem *et al.*, 2010c: 382); Nigeria (Tanshi *et al.*, 2022a: 314); South Africa (Monadjem *et al.*, 2010d: 541); Sudan; Uganda (Kityo and Kerbis, 1996: 63); Zambia (Ansell, 1978: Monadjem *et al.*, 2010d: 541); Zimbabwe (Cotterill, 2004a: 261: Monadjem *et al.*, 2010d: 541).

Presence uncertain: Namibia.

ECHOLOCATION:
Jacobs (1996) and Fenton and Bell (1981) reported a F_{max}: 28 kHz for individuals at Sengwa in Zimbabwe.

Taylor (2000: 67) reported call details as: long duration (15 ms), multi-harmonic (up to two), narrow bandwidth (16 - 28 kHz) shallow-FM calls, with low dominant frequency of 18 kHz, in a field guide to bats of Southern Africa.

For "*Chaerephon ansorgei*" from Mozambique, Taylor *et al.* (2013b: 18) reported the following parameters for 3 calls: F_{max}: 23.1 ± 3.5 (20.1 - 27.0) kHz, F_{min}: 186. ± 1.5 (16.9 - 19.8) kHz, F_{knee}: 21.5 ± 1.4 (19.9 - 22.6) kHz, F_{char}: 19.8 ± 1.1 (18.5 - 20.5) kHz, duration: 10.6 ± 1.2 (9.4 - 11.9) ms. And for 12 calls from Waterberg, South Africa: F_{max}: 22.1 ± 1.53 (19.5 - 243) kHz, F_{min}: 18.5 ± 0.92 (17.5 - 20.0) kHz, F_{knee}: 20.1 ± 1.05 (18.9 - 21.8) kHz, F_{char}: 19.0 ± 0.94 (17.8 - 20.5) kHz, duration: 6.4 ± 1.51 (4.5 - 9.3) ms.

At Farm Welgevonden (RSA), Taylor *et al.* (2013a: 556) report a F_{knee} value of 20 (19 - 22) kHz.

In the Soutpansberg area (RSA), Linden *et al.* (2014: 40) mentioned the following characteristics for *C.* cf. *ansorgei*: F_{min}: 17 - 20 kHz, F_{char}: 18 - 21 kHz, F_{knee}: 19 - 23, slope: 24 - 212 OPS, duration: 4 - 12 ms.

20 calls from the Mapungubwe National Park (RSA) were recorded by Parker and Bernard (2018: 57): F_{char}: 18.21 ± 1.01 kHz, F_{max}: 20.92 ± 3.39 kHz, F_{min}: 17.59 ± 1.03 kHz, F_{knee}: 19.38 ± 1.49 kHz, duration: 10.07 ± 3.03 ms with 2.47 ± 1.43 calls/sec.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 18.21 ± 1.01 kHz, F_{max}: 20.92 ± 3.39 kHz, F_{min}: 17.59 ± 1.03 kHz.

Weier *et al.* (2020: Suppl.) reported on 12 calls from the Okavango River Basin with the following characteristics: F_{max}: 19.68 ± 0.53 kHz, F_{min}: 18.35 ± 3.33 kHz, F_{knee}: 19.49 ± 0.45 kHz, F_{char}: 19.19 ± 0.26 kHz, slope: 6.26 ± 9.90 OPS, duration: 5.99 ± 3.52 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 10 bats: F_{max}: 22.28 ± 1.52 kHz, F_{min}: 20.28 ± 3.04 kHz, F_{knee}: 21.79 ± 1.19 kHz, F_{char}: 20.9 ± 0.99 kHz, slope: -226.44 ± 1751.57 OPS, duration: 7.8 ± 3.63 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 15 *Chaerephon ansorgei* calls from the Kruger Park (RSA): F_{min}: 18.8 ± 1 (17.6 - 20.4) kHz, duration: 6.7 ± 2.3 (3.8 - 10.9) ms, F_{max}: 22.4 ± 1.8 (19.5 - 26.3) kHz, F_{knee}: 19.8 ± 1.1 (18.5 - 21.6) kHz, F_{char}: 19.4 ± 1.0 (18.2 - 21.0) kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

58 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 17 - 20 kHz, F_{max}: 19 - 27 kHz, F_{char}: 17 - 21 kHz, F_{knee}): 18 - 22 kHz and duration 4 - 12 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 18.21 ± 1.01 kHz, F_{max}: 20.92 ± 3.39 kHz and F_{min}: 17.59 ± 1.03 kHz.

Molecular Biology:

Karyotype

Smith *et al.* (1986) and Rautenbach *et al.* (1993) agreed on $2n = 48$, and the Y chromosome being acrocentric. However, Smith *et al.* (1986) reported FN = 66, BA = 20, and a subtelocentric X chromosome, whereas Rautenbach *et al.* (1993) reported for specimens from South African, FN = 68, BA = 22, and a submetacentric X chromosome.

Roost:

Happold and Happold (2023: 118) mention that - in NE DRC - these bats roost in groups of up to 40 individuals with about equal numbers of males and females, whereas in Zimbabwe the groups can add up to several hundreds, with males generally outnumbering the females.

Predators:

Mikula *et al.* (2016: Supplemental data) mention the Southern yellow-billed hornbill (*Tockus leucomelas* Lichtenstein, 1842) as diurnal avian predator.

Population:

Structure and Density

It appears to be generally uncommon, although colonies may contain hundreds of bats (Mickleburgh *et al.*, 2008ac; IUCN, 2009; Monadjem *et al.*, 2017v).

Trend

2016: Stable (Monadjem *et al.*, 2017v). 2008: Stable (Mickleburgh *et al.*, 2008ac; IUCN, 2009).

Reproduction and Ontogeny:

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned lactating females in November-January and April.

Parasites:

SIPHONAPTERA

Ischnopsyllidae

Lagaropsylla anciauxi Smit, 1957 from Katanga, Congo (Haeselbarth *et al.*, 1966: 190).

Distribution based on voucher specimens:

Angola, Cameroon, Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Mozambique, Nigeria, Rwanda, South Africa, South Sudan, Uganda, Zimbabwe.

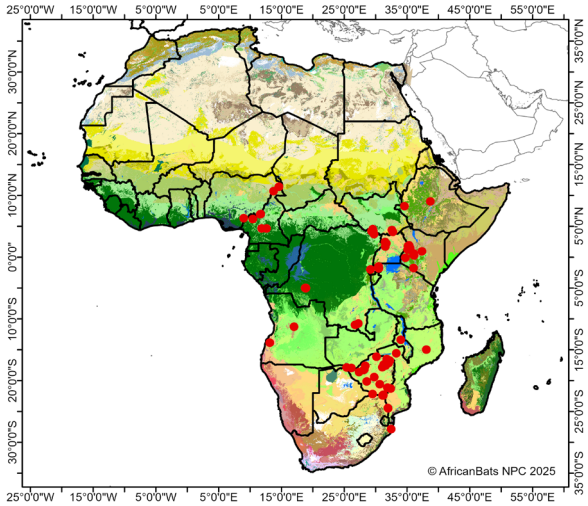

Figure 169. Distribution of *Mops (Chaerephon) ansorgei*.

Mops (Chaerephon) atsinanana (Goodman, Buccas, Naidoo, Ratrimomanarivo, Taylor and Lamb, 2010)

*2010. *Chaerephon atsinanana* Goodman, Buccas, Naidoo, Ratrimomanarivo, Taylor and Lamb, Zootaxa, 2551: 21, figs 34, 6A, 7. Publication date: 28 July 2010. Type locality: Madagascar: Fianarantsoa: Farafangana: Collèges d'Enseignement Général (CEG) Fenoarivo [22 49.275 S 47 49.860 E, 10 m]. Holotype: FMNH 185259: ad ♀, skull and alcoholic. Collected by: Fania H. Ratrimomanarivo; collection date: 26 April 2005. Paratype: FMNH 185260. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185261. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185262. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185263. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185264. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185265. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185266. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185267. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). Paratype: FMNH 185268. Same locality as the type specimen (see Goodman *et al.*, 2010a: 21). - Etymology: The name *atsinanana* is derived from the Malagasy word meaning "from the east" (see Goodman *et al.*, 2010a: 23).
2020. *Mops atsinanana:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon pumilus:*
? *Mops (Chaerephon) atsinanana:* (Current Combination).

TAXONOMY:
Based on mitochondrial markers, Goodman *et al.* (2022: 1904) state that *C. atsinanana* is poorly differentiated from *C. leucogaster*.

COMMON NAMES:
English: Malagasy eastern Free-tailed Bat, Madagascar Free-tailed Bat. French: Molosse de l'est malgache

CONSERVATION STATUS:
Global Justification
This species is known from numerous sites in the eastern portion of the island, particularly in synanthropic settings, where it can be very common (Goodman *et al.*, 2010a; Goodman and Ramasindrazana, 2013).

Assessment History
Global
2016: LC ver. 3.1 (2001) [assessed as *Chaerephon atsinanana*] (Goodman, 2017e).

Regional
None known.

MAJOR THREATS:
Goodman (2017e) report that none are known.

CONSERVATION ACTIONS:
On Madagascar, it has not been recorded from any protected areas, but it has been recorded from houses close to protected areas as "*Chaerephon pumilus*" (Mickleburgh *et al.* (2008dr) [in IUCN (2009)]). While Goodman (2017e) make no suggestions for conservation action.

GENERAL DISTRIBUTION:
Mops atsinanana is known from numerous localities across the eastern half of Madagascar from near sea level to over 1,100 m (see Goodman *et al.*, 2010a: 26).

In Madagascar, the species is restricted to the humid areas of the island (in the north and east)

and can be found up to 1,300 m asl. Its southernmost range in Madagascar is not well understood and it has not been recorded south of Moramanga (Goodman and Cardiff, 2004).

Garbutt (2022: 95) mention the range in eastern Madagascar approximately from Farafangana to Toamasina and Makira, Anjanaharibe-Sud and Marojejy.

Native: Madagascar (Goodman *et al.*, 2010a: 26).

BIOGEOGRAPHY:
Mops atsinanana is common in the mesic eastern portion of Madagascar, across an elevational range from near sea level to 1,100 m a.s.l. (Lamb *et al.*, 2012: 19).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 60) found that the triangular shaped baculum of this species could be subdivided into three morphotypes: morphotype A is more rounded than the flattened morphotype B, and morphotype C is similar to B, but with an indentation in the proximal base. The shaft curvature is more pronounced in types B and C as compared to type A. In all morphotypes, the distal portions are similar, gradually tapering from the midshaft towards a blunt tip. Length: 0.90 ± 0.066 (0.78 - 1.00) mm, width: 0.34 ± 0.056 (0.26 - 0.46) mm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Taylor *et al.* (2012a)] mention a wing loading value of 10.3 Pa and an aspect ratio of 8.4.

MOLECULAR BIOLOGY:
Genetics
See Goodman *et al.* (2010a).

Napier (2013) hypothesized that this species should show relatively low levels of intraspecific genetic structure as bats are strong fliers and are able to traverse the riverine and mountain barriers. However, she needed to reject this hypothesis as genetic distances of up to 8.14 % were found. She furthermore suggests that these differences are consistent with the existence of female philopatry.

HABITAT:
Goodman *et al.* (2010a: 26) report that all of the sites where this species is found, are in urban or at least rural areas and outside of natural forest. They were also unable to find a natural day-roost of this species. A further analysis by Lamb *et al.* (2012: 29) indicated that the predicted distribution pattern was rather patchy and limited to the Madagascar Lowland Forests ecoregion and furthermore strongly associated with human population centres and transport routes.

ROOST:
Wilkinson *et al.* (2012: 160) and Garbutt (2022: 95) indicate that synanthropic structures (including houses and churches) are the typical roosts for this species on Madagascar.

DIET:
The faeces of five specimens examined by Rasoanoro *et al.* (2015: 64) contained the following volume percentages of prey: Coleoptera: 44.0 ± 5.08, Diptera: 8.3 ± 4.15, Hemiptera: 3.1 ± 1.36, Homoptera: 19.0 ± 4.42, Hymenoptera: 0.3 ± 0.31, and Lepidoptera: 25.4 ± 1.86.

Goodman *et al.* (2023b: 238) [referring to Falimiarintsoa (2022)] mention fecal pellets of 21 bats to contain: Odonata (24.6 %), Hemiptera (19.0 %), Coleoptera (18.4 %), Lepidoptera (15.3 %), Diptera (10.7 %), Hymenoptera (9.3 %), and Ephemeroptera (2.7 %). They point out that the high percentage of Odonata is exceptional

Kemp *et al.* (2018: Suppl.) used DNA metabarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Coleoptera, Ephemeroptera, Lepidoptera (*Meyrickiella homosema* (Meyrick, 1887), *Leguminivora* sp., *Mythimna* sp., *Cydia choleropa* (Meyrick, 1913)), Diptera (*Simulium lineatum* (Meigen, 1804), *Culex* MBI-27, *Anopheles squamosus* Theobald, 1901, *Culex annulioris* Theobald, 1901), Orthoptera, Trichoptera, Blattodea, Hemiptera, Sarcoptiformes, Trombidiformes, Odonata, Siphonaptera, Hymenoptera.

POPULATION:
Structure and Density
There are no estimates of its population in Madagascar, but it is thought to be locally common in the eastern zone (Mickleburgh *et al.*, 2008dr; IUCN, 2009, as *C. pumilus*). Not estimated but can be common as a synanthropic species in villages and towns of eastern Madagascar (Goodman, 2017e). Based on inference from genetic data, this species has witnessed a recent population expansion (Lamb *et al.*, 2012).

Trend
2016: Increasing (Goodman, 2017e).

REPRODUCTION AND ONTOGENY:
Goodman *et al.* (2023b: 238) report on 14 females collected at Sarahandrano between 30

April and 2 May 2021. Eleven of these did not show any signs of recent breeding activity, whereas three had large nipples. Of the eleven males, nine had abdominal testes and two had slightly descended testes.

PARASITES:
SIPHONAPTERA
Ischnopsyllidae
Duchemin *et al.* (2022: 1077) mentioned the presence of *Lagaropsylla consularis* Smit, 1957.

VIRUSES:
Wilkinson *et al.* (2012: 160) tested 20 individuals from the Madagascar using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

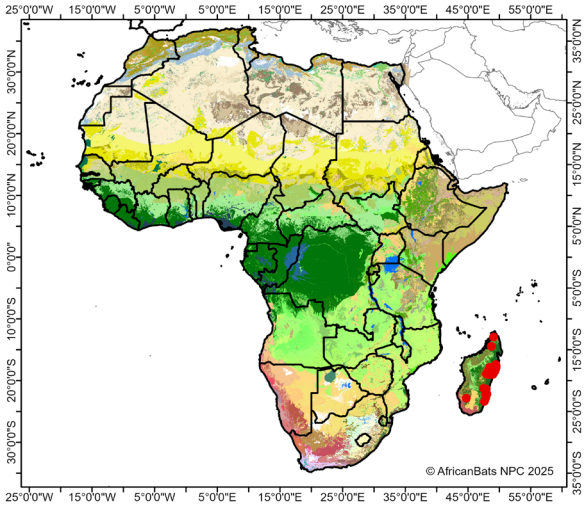

Figure 170. Distribution of *Mops (Chaerephon) atsinanana*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Mops (Chaerephon) bemmeleni (Jentink, 1879)

*1879.	*Nyctinomus Bemmeleni* Jentink, Notes Leyden Mus., 1 (1): 125. Publication date: April 1879. Type locality: "Africa": "Liberia ??". [Goto Description]. Holotype: RMNH MAM.21649: ad ♀, skull and alcoholic. Collection date: 1875. The RMNH catalog mentions two numbers: 21649.a (skull + loose bones) and 21649.b (wet specimen). - Comments: The type locality was originally mentioned as "Liberia", but see Kuhn (1965: 327), who doubts this, since the type specimen had come from a zoo. - Etymology: In honour of Mr. A.A. van Bemmelen, director of the Zoological Gardens at Rotterdam, who presented the type specimen to the museum (see Jentink, 1879b: 127).
1897.	*[Nyctinomus (Nyctinomus)] Vemmeleni:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, nov ed 1, pt 1: 146. Publication date: 1897. (Lapsus).
1903.	*Nyctinomus cisturus* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (71): 502. Publication date: 1 November 1903. Type locality: South Sudan: Equatoria province: 25 mi (37.5 km) N Gondokoro: Mangala (=Mongalla) [05 10 57 N 31 45 00 E, 466 m]. [Goto Description]. Holotype: NHMUK 1902.7.4.4: ad ♂. Collected by: W.L.S. Loat Esq. Original number: 2805. Presented/Donated by: W.L.S. Loat Esq.
1989.	*Chaerophon bemmeleni:* Fenton, Can. J. Zool., 67 (8): 2034. Publication date: 1 August 1989. (Lapsus).
2020.	*Mops bemmeleni* Simmons and Cirranello, BatNames.org. (Current Combination).
?	*Chaerephon bemmeleni:* (Name Combination).
?	*Mops (Chaerephon) bemmeleni:* (Current Combination).
?	*Tadarida bemmeleni cistura:* (Name Combination).
?	*Tadarida bemmeleni:* (Name Combination).

TAXONOMY:
Includes *cisturus*; see Koopman (1975: 425).

The data used by Herkt *et al.* (2017: Appendix S9) support the idea that *bemmeleni* includes more than one species. However, genetic tests to confirm this are not yet available, but material from the small overlapping area can clearly be allocated to the ssp. *cisturus*, rendering a large geographic gap between occurrence records of either population: one in West and western Central Africa (*bemmeleni*) and one in East Africa (*cisturus*).

COMMON NAMES:
Chinese: 腺尾犬吻蝠. Czech: morous liberijský. English: Gland-tailed Wrinkle-lipped Bat, Van Bemmelen's Wrinkle-lipped Bat, Gland-tailed Free-tailed Bat. French: Tadaride à glande caudale, Molosse à glandes caudales. German: Schwanzdrüsen-Bulldoggfledermaus, Bemmelens Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008am; IUCN, 2009; Monadjem *et al.*, 2017ai).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon bemmeleni* (Monadjem *et al.*, 2017ai). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida bemmeleni*"] (Mickleburgh *et al.*, 2008am; IUCN, 2009). 2004: LC ver 3.1 (2001)

(Mickleburgh *et al.*, 2004ba; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is threatened by habitat loss, largely through logging activities and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008am; IUCN, 2009; Monadjem *et al.*, 2017ai).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008am) [in IUCN (2009)] and Monadjem *et al.* (2017ai) report that it is present in Meru National Park, Kenya, and is presumably present in several more protected areas. Further studies are needed into the taxonomy, natural history, threats and distribution of this species.

GENERAL DISTRIBUTION:
Mops bemmeleni is widely distributed in Africa from Sierra Leone in the west, then patchily through West and Central Africa to southern Sudan, Uganda, Kenya and Tanzania in the east. It has been recorded up to 1,700 m asl on Mount Nimba along the border of Côte d'Ivoire and Guinea (J. Fahr, *pers. comm.*, 2004 in Mickleburgh *et al.*, 2008am in IUCN, 2009).

Native: Cameroon; Congo (The Democratic Republic of the); Côte d'Ivoire; Guinea; Kenya (Start, 1969; as "*Tadarida cistura*"); Liberia; Rwanda; Sierra Leone; Sudan; Tanzania; Uganda.

Presence uncertain: Burkina Faso; Central African Republic; Chad; Ethiopia; Guinea-Bissau; Mali; Nigeria; Senegal.

MOLECULAR BIOLOGY:
Karyotype
Nagorsen *et al.* (1976: 10) reported 2*n* = 48, FN = 54, BA = 8, a submetacentric X chromosome and an acrocentric Y chromosome.

POPULATION:
Structure and Density
The abundance of *Mops bemmeleni* is unclear, in parts of the range it seems to be a rare species that is found in small colonies consisting of a few individuals. In East Africa this species exhibits a clumped distribution, yet is relatively abundant locally (Webala *et al.*, 2004).

Trend
2016: Unknown (Monadjem *et al.*, 2017ai). 2008: Unknown (Mickleburgh *et al.*, 2008am; IUCN, 2009).

PARASITES:
Lainson and Naiff (2000: 128) and Duszynski (2002: 21) indicate that *M. bemmeleni* is the type host for *Eimeria levinei* Bray, 1958 (Apicomplexa).

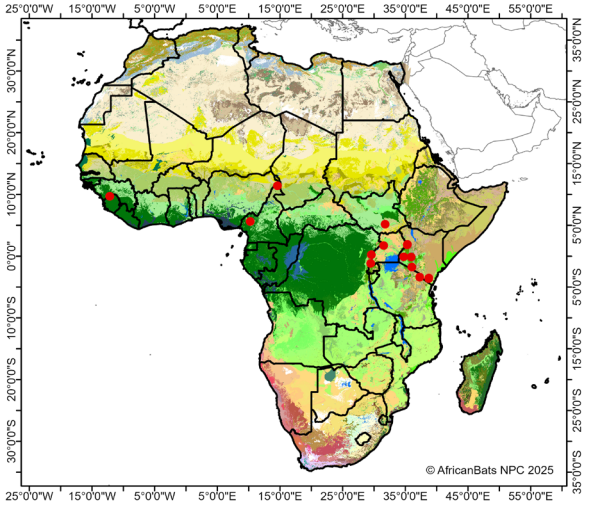

Figure 171. Distribution of *Mops (Chaerephon) bemmeleni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Congo (Democratic Republic of the), Kenya, Liberia, Sierra Leone, South Sudan, Tanzania, Uganda.

Mops (Chaerephon) bivittatus (Heuglin, 1861)

*1861. *Nyctinomus bivittatus* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 13. Publication date: 1861. Type locality: Eritrea: Kérén [ca. 15 45 N 38 20 E]. [Goto Description]. Syntype: RMNH MAM.35876.a: ad. Collected by: Martin Theodor von Heuglin; collection date: 1861. Syntype: RMNH MAM.35876.b: ad ♀. Collected by: Martin Theodor von Heuglin; collection date: 1861. Syntype: ZMB 2792a: skull and alcoholic. Collected by: Theodor Von Heuglin. Formerly SMNS, from "Abyssinia, Bogos[land]". See Turni and Kock (2008: 72). Syntype: ZMB 2792b: skull and alcoholic. Collected by: Theodor Von Heuglin. Formerly SMNS, from "Abyssinia, Bogos[land]". See Turni and Kock (2008: 72). Lectotype: SMNS 981: ad ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. Dieterlen *et al.* (2013: 294) indicated this specimen to be the lectotype, referring to ICZN article 74.6, which would indicate that this status was established by Dobson (1878), who called specimen this "'type". However, Dobson (1878: 426) presents the measurements of an adult male, which he called the "type", but since there are two adult males (981 and 981b), it is not clear which of these two specimens was referred to by Dobson (1878). Paralectotype: SMNS 981a: ad ♀, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294). Paralectotype: SMNS 981b: ad ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294), but see also note above. -

Etymology: From the masculine scientific Latin adjective *bivittàtus*, meaning "bivittate", as the species is provided with two narrow longitudinal stripes on and behind the head (see Lanza *et al.*, 2015: 273).

1967. *Tadarida bivittata:* Ansell, Arnoldia Rhod., 2 (38): 29. (Name Combination).
1999. *Chaerephon bivitattus:* Taylor, Acta Chiropt., 1 (2): 199. (Lapsus).
2002. *Chaerephon bivittata:* Arroyo-Cabrales, Gregorin, Schlitter and Walker, 22 (2): 386.
2016. *Chaerophon bivittattus:* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 43. Publication date: 9 May 2016. (Lapsus).
2020. *Mops bivittatus:* Simmons and Cirranello, BatNames.org. (Current Combination).
2025. *Chaerephon bibittatus:* King, Loeffler, Rosenberger, Wagner, Chhaya, DeLeon, Curtis, Eiting, Santana and Smith, Anat. Rec., xxx (x): 4. Publication date: 6 October 2025. (Lapsus).
? *Chaerephon bivittatus:* (Name Combination).
? *Mops (Chaerephon) bivittatus:* (Current Combination).
? *Tadarida bivittata bivittata:* (Name Combination).

Taxonomy:
Revised by Eger and Peterson (1979).

Common Names:
Afrikaans: Gevlekte losstertvlermuis. Chinese: 斑犬吻蝠. Czech: morous skvrnitý. English: Spotted Wrinkle-lipped Bat, Spotted Free-tailed Bat, Spotted Gland-tailed Bat. French: Tadaride tachetée, Molosse tacheté. German: Gefleckte Bulldoggfledermaus, zweistreifige Doggengrämler. Italian: Cherefónte bivittàto. Portuguese: Morcego de cauda livre malhado.

Etymology of common name:
So named because of the tiny white, and sometimes barely discernible, flecks on the upper parts of the body (see Taylor, 2005).

Conservation status:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ad; IUCN, 2009; Monadjem *et al.*, 2017x).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon bivittatus*] (Monadjem *et al.*, 2017x). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida bivittata*"] (Mickleburgh *et al.*, 2008ad; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as "*Chaerephon bivittata*"] (Mickleburgh *et al.*, 2004an; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

Major threats:
There appear to be no major threats to this species as a whole (Mickleburgh *et al.*, 2008ad; IUCN, 2009; Monadjem *et al.*, 2017x).

Conservation actions:
Mickleburgh *et al.* (2008ad) [in IUCN (2009)] and Monadjem *et al.* (2017x) report that there appear to be no direct conservation measures in place. It is presumably present in some East African protected areas. Further studies are needed into the abundance, distribution and natural history of this bat.

General distribution:
Mops bivittatus is an East African species ranging from Eritrea and Ethiopia in the north, through southern Sudan, Uganda, Kenya and eastern Tanzania, to Zambia, Zimbabwe and Mozambique in the south.

Native: Eritrea; Ethiopia; Kenya; Malawi (Monadjem *et al.*, 2010d: 541); Mozambique (Crawford-Cabral, 1989; Simmons, 2005); Sudan; Tanzania; Uganda; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 541); Zimbabwe (Ansell, 1986; Monadjem *et al.*, 2010d: 541).

Functional morphology:
King *et al.* (2025) investigated the olfactory system of this species.

Molecular Biology:
Karyotype
Peterson and Nagorsen (1975) reported 2*n* = 48, FN = 54, BA = 8, a metacentric X chromosome, and an acrocentric Y chromosome for specimens from Kenya and Zimbabwe.

Population:
Structure and Density
Although there is little information on the abundance of this species, it is common in collections suggesting that it is easily found (Mickleburgh *et al.*, 2008ad; IUCN, 2009; Monadjem *et al.*, 2017x).

Trend
2016: Stable (Monadjem *et al.*, 2017x). 2008: Stable (Mickleburgh *et al.*, 2008ad; IUCN, 2009).

PARASITES:
Beaucournu and Kock (1996) mentioned the first record for the flea *Lagaropsylla anciauxi* Smit, 1957 on this bat.
Hastriter (2016: 15) described the flea *Araeopsylla smiti* from a *M. bivittatus* collected at Maji Moto, Kenya.

Copeland *et al.* (2011: 363) reported the rediscovery of the "terrible hairy fly" (*Mormotomyia hirsuta* (after 62 years) in guano produced by "*Chaerephon* cf. *bivittatus*" and *Tadarida aegyptiaca* at Ukasi Hill, Kenya.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Eritrea, Ethiopia, Kenya, Malawi, Mozambique, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

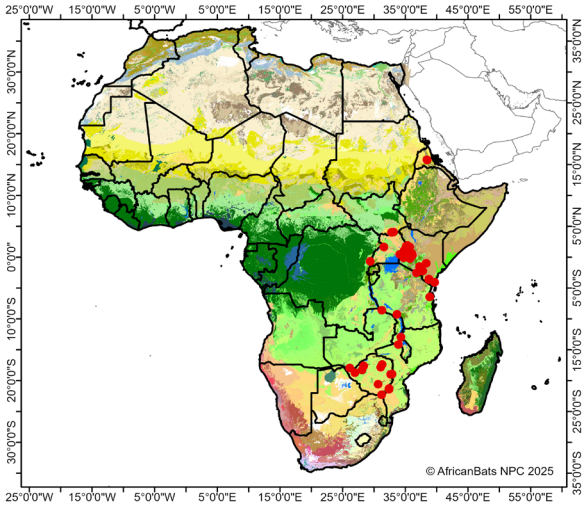

Figure 172. Distribution of *Mops (Chaerephon) bivittatus*.

Mops (Chaerephon) chapini (J.A. Allen, 1917)

*1917. *Chærephon (Lophomops) chapini* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 460, 461, text-fig 9. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 48841: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 11 November 1912; original number: 1971.
1938. *Chærephon lancasteri* Hayman, Ann. Mag. nat. Hist., ser 11, 1 (4): 383. Publication date: 1 April 1938. Type locality: Zambia: Loangwa Valley: Lundazi district: Lunzi River [ca. 11 S 33 E]. [Goto Description]. Holotype: NHMUK 1937.12.8.25: ad ♂, skin and skull. Collected by: D. Gordon Lancaster; collection date: August 1936; original number: 724. Notes: caught in hole in tree. - Comments: Kock (1969a: 140) situates the Lunzi river in Zambia, rather than in Zimbabwe.
1989. *Chaerophon chapini:* Fenton. Publication date: 1 August 1989. (Lapsus).
2009. *Choerephon (Lopomops) langi:* ACR. - Comments: *nomen nudum*.
2016. *C[haerephon] langi:* Naidoo, Goodman, Schoeman, Taylor and Lamb, Mammalia, 80 (6): 627. Publication date: 6 January 2016. (Name Combination).
2020. *Mops chapini:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon chapini chapini:* (Name Combination).
? *Chaerephon chapini lancasteri:* (Name Combination).
? *Chaerephon chapini:* (Name Combination).
? *Mops (Chaerephon) chapini:* (Current Combination).
? *Tadarida chapini lancasteri:* (Name Combination).
? *Tadarida chapini:* (Name Combination).

TAXONOMY:
Included in *pumilus* by Kock (1969a: 139). See Fenton and Eger (2002).

COMMON NAMES:
Afrikaans: Bleek losstertvlermuis. Chinese: 查平犬吻蝠. Czech: morous chocholatý. English: Long-crested Free-tailed Bat, Chapin's Wrinkle-lipped Bat, Long-crested Wrinkle-lipped Bat, Crested Wrinkle-lipped Bat, Chapin's Free-tailed Bat, Pale Free-tailed Bat, Long-crested Gland-tailed Bat, Crested Free-tail Bat. French: Tadaride de Chapin, Molosse à crinière, Molosse pâle. German: Chapins Bulldoggfledermaus.

ETYMOLOGY OF COMMON NAME:
Named after Mr. James P. Chapin, co-organiser of the American Museum expedition to the former Belgian Congo that resulted in the discovery of the species (Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
No fossils are known (Fenton and Eger, 2002).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ae; IUCN, 2009; Monadjem *et al.*, 2017y).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon chapini*] (Monadjem *et al.*, 2017y). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida chapini*"] (Mickleburgh *et al.*, 2008ae; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004ag; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this widespread species as a whole. It may be threatened in parts of its range through habitat loss and degradation (e.g., in northern Zimbabwe and parts of Zambia) (Mickleburgh *et al.*, 2008ae; IUCN, 2009; Monadjem *et al.*, 2017y).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ae) [in IUCN (2009)] report that it has been recorded from Kruger National Park in South Africa, and from Mole National Park in Ghana and Comoe. Monadjem *et al.* (2017y) makes no recommendations for conservation actions.

GENERAL DISTRIBUTION:
Mops chapini has been widely recorded over much of sub-Saharan Africa. It has been collected from Côte d'Ivoire and Ghana in West Africa, southern Sudan, northeastern Democratic Republic of the Congo, Ethiopia, Uganda and Kenya, ranging south into southern Democratic Republic of the Congo and Congo, Angola, Zimbabwe, Zambia, Botswana and Namibia.

Native: Angola (Monard, 1935; Crawford-Cabral, 1989; Hill and Carter, 1941; Monadjem *et al.*, 2010d: 541); Botswana (Monadjem *et al.*, 2010d: 541); Cameroon (Bol A Anong *et al.*, 2011: 46; Bakwo Fils *et al.*, 2014: 3); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Fenton and Eger, 2002: 2; Monadjem *et al.*, 2010d: 541); Ethiopia; Ghana; Kenya (Fenton and Eger, 2002: 2); Namibia (Monadjem *et al.*, 2010d: 541); Sudan (Fenton and Eger, 2002: 2); Uganda; Zambia (Ansell, 1969; Monadjem *et al.*, 2010d: 541); Zimbabwe (Monadjem *et al.*, 2010d: 541).

Bates *et al.* (2013: 338) reject the occurrence of *M. chapini* in the Republic of Congo as the "Marine Park Nature Reserve" was erroneously located in that country in ACR (2012) rather than in the DRC. The record from Cameroon is probably doubtful (Jakob Fahr, pers. comm.).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Fenton and Eger (2002).

DENTAL FORMULA:
Esquivel *et al.* (2021: Suppl.) examined three skulls, of which one had extra teeth (polyodontia).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Fenton and Eger (2002).

DETAILED MORPHOLOGY:
Other
For a description of the crania, teeth, ears and tragus see Fenton and Eger (2002).

SEXUAL DIMORPHISM:
Sexual dimorphism in the structure of interaural crest, with females having a small crest (3 - 5 mm) and males a long, bicolored one (12 - 15 mm) (Fenton and Eger, 2002). Krutzsch (2000: 128) pointed out that this crest is also odoriferous in the breeding male.

ECHOLOCATION:
Jacobs (1996) and Fenton and Bell (1981) reported a F_{max}: 27 kHz for individuals at Sengwa in Zimbabwe.

In Benin, Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 48, FN = 64, BA = 18, a subtelocentric X chromosome, and an acrocentric Y chromosome, for specimens from Namibia and Zimbabwe.

HABITAT:
See Fenton and Eger (2002).

HABITS:
See Fenton and Eger, 2002).

Fenton and Griffin (1997: 248) recorded echolocation calls from "*Tadarida chapini*" at altitudes between 0 and 450 m above a *Brachystegia* woodland in Zimbabwe.

ROOST:
See Fenton and Eger (2002).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
In general there is little information on the abundance of this species over its range (Mickleburgh *et al.*, 2008ae; IUCN, 2009; Monadjem *et al.*, 2017y). It can be common in northwestern Zimbabwe, but it is not regularly recorded. The species is found in small colonies, with a single observation of a small group of breeding females.

Trend
2016: Unknown (Monadjem *et al.*, 2017y). 2008: Unknown (Mickleburgh *et al.*, 2008ae; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
See Fenton and Eger, 2002).

REPRODUCTION AND ONTOGENY:
See Fenton and Eger (2002).

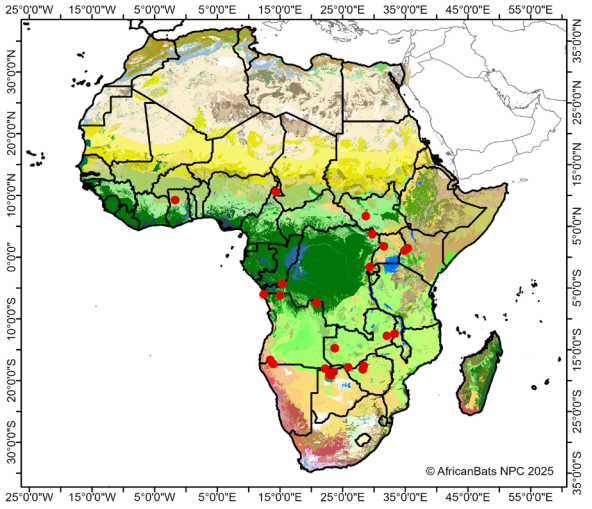

Figure 173. Distribution of *Mops (Chaerephon) chapini*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Cameroon, Congo (Democratic Republic of the), Ethiopia, Ghana, Kenya, Namibia, Rwanda, South Sudan, Uganda, Zambia, Zimbabwe.

Mops (Chaerephon) jobimena (Goodman and Cardiff, 2004)

*2004. *Chaerephon jobimena* Goodman and Cardiff, Acta Chiropt., 6 (2): 230, fig 2, 3, 4. Type locality: Madagascar: Antsiranana province: Ankarana special reserve, 2.6 km E Andrafiabe: Andrafiaba cave, in forest near [12 55.9 S 49 03.4 E, ca. 50 m]. [Goto Description]. Holotype: FMNH 169716: ad ♂, skin and skeleton and skull and tissue. Collected by: Steven M. Goodman; collection date: 23 January 2001; original number: SMG 11932. See Goodman and Cardiff (2004: 230). - Etymology: From the northern dialects of Malagasy, with "*joby*" meaning dark or black and "*mena*" red. The combination refers to the two color morphs of this species (see Goodman and Cardiff, 2004: 230).
2020. *Mops jobimena:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Mops (Chaerephon) jobimena:* (Current Combination).

TAXONOMY:
Lamb *et al.* (2011: 9) and Goodman *et al.* (2022: 1904) indicate that, although morphologically similar to other "*Chaerephon*" taxa, *jobimena* is genetically more similar to *Tadarida aegyptiaca*, and probably should be assigned to the latter genus.

COMMON NAMES:
Czech: morous malgašský. English: Malagasy western Free-tailed bat, Black and Red Free-tailed Bat, Bicoloured free-tailed bat. French: Tadaride rouge ou noir, Molosse de l'ouest malgache. German: Variable Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) because although it appears to be rather rare in the few areas where it is known to occur, it is widespread and its population status may not be related to the amount or state of native forest. Additional information are needed on its propensity for roosting in large colonies in synanthropic settings as this will be crucial to a better understanding of its conservation status (Andriafidison *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017bz).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon jobimena*] (Monadjem *et al.*, 2017bz). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida jobimena*"] (Andriafidison *et al.*, 2008l; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The threats to this species are not well known, but it is probably hunted in the south of Madagascar for food (Andriafidison *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017bz).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008l) [in IUCN (2009)] and Monadjem *et al.* (2017bz) report that this species

is known from in or near to four protected areas, but is never as common or as abundant as other sympatric molossid species (Goodman and Cardiff, 2004; Goodman *et al.*, 2005a) and its conservation status should be reviewed in the future when new data are available. In particular, information on its propensity to dwell in buildings is needed.

GENERAL DISTRIBUTION:
Mops jobimena is endemic to Madagascar where it is found from the north-west to the south-west of the island. It is known to occur in areas with dry deciduous or spiny forest from 50 to 870 m above sea level (Goodman and Cardiff, 2004; Goodman *et al.*, 2005a). Although further surveys may reveal that this species is more widespread than currently known, it has yet to be recorded from some sites with extensive limestone caves, from where it would be expected based on habitat preference and distribution (Goodman and Cardiff, 2004; Goodman *et al.*, 2005a; Cardiff, 2006).

Native: Madagascar (Goodman and Cardiff, 2004; Goodman *et al.*, 2005a; Cardiff, 2006).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 61) report the following shape for the baculum of this species: the proximal portion is notably expanded. Its size decreases slightly in the mid-shaft portion, then more notably distally. The distal tip tapers to a rounded point. Length: 1.16 mm, width: 0.37 mm.

HABITAT:
Dammhahn and Goodman (2013: 108) indicate that this species' foraging habitat consists of open areas and the area above the forest canopy.

ROOST:
M. jobimena roosts in caves and hollow baobab trees, as well as in synanthropic sites. Colonies can count up to 1,200 bats in caves and 40 in buildings (Garbutt, 2022: 95).

POPULATION:
Structure and Density
The population and local abundance of this species are not known, but at Ankarana the recorded roost is 1,200 individuals (S. G. Cardiff *pers. obs.*, in Andriafidison *et al.*, 2008l [in IUCN, 2009]; Monadjem *et al.*, 2017bz). Forty individuals were recorded from a house roughly 10 km from Parc National de Namoroka (A. F. Kofoky *pers. obs.*, in Andriafidison *et al.*, 2008l [in IUCN, 2009]; Monadjem *et al.*, 2017bz).

Trend
2016: Unknown (Monadjem *et al.*, 2017bz).
2008: Unknown (Andriafidison *et al.*, 2008l; IUCN, 2009).

PARASITES:
Hastriter (2016: 9) described the flea *Araeopsylla goodmani* from a male *M. jobimena* collected at Isalo, 3.8 km NW Ranohira, along Namaza River, Madagascar.

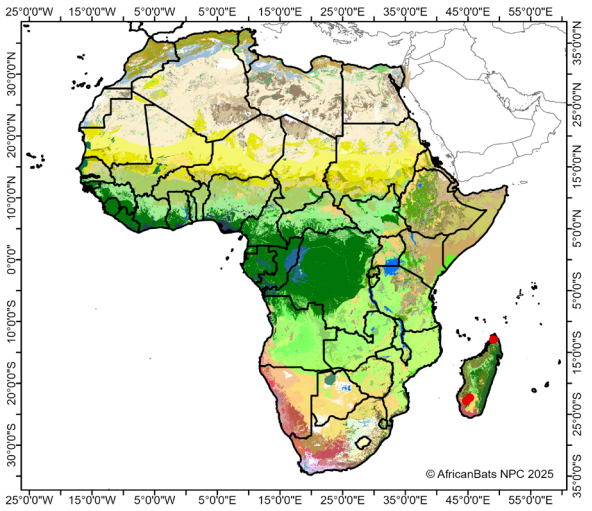

Figure 174. Distribution of *Mops (Chaerephon) jobimena*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Mops (Chaerephon) leucogaster (A. Grandidier, 1869)

*1869. *Nyctinomus leucogaster* A. Grandidier, Rev. Mag. Zool., ser 2, 21: 337. Publication date: September 1869. Type locality: Madagascar: Mahab (?Mahabo) and Ménabé (E of Morondava) [20 23 S 44 40 E, 50 m]. [Goto Description]. Neotype: FMNH 176137: ad ♂, skull and alcoholic. Collected by: H. Vola Razakarivony; collection date: 11 November 2002. - Comments: Ratrimomanarivo *et al.* (2009a: 28) mention "The only specimen possibly fitting the details of the Grandidier type is MCZ 45094, which is in poor condition and the original specimen label bears the following information: 'Cote Ouest' [= west coast], '*Nyctinomus pumelus* [sic]', 'collection Grandidier', and '1901'. Based on numerous characters, including aspects of external, cranial, and dental measurements as well as pelage and soft part coloration, this animal is referable to *C. leucogaster*. However, the collection details are too ambiguous to clearly conclude that this specimen can be considered the type of *C. leucogaster* described by Grandidier (1869) and, further, the skull is considerably damaged." They also select a neotype (FMNH 176137): "collected in the Menabe Region of western coastal Madagascar, specifically at Belo sur Mer (20°44.139'S, 44°00.266'E) at 10 m above sea level on 11 November 2002 by Vola Razakarivony. This site is approximately 80 km southwest of Mahabo. The animal is an adult male, the body was preserved in formalin and subsequently transferred to 70% ethanol, the skull has been extracted, cleaned,

and is in excellent condition.". - Etymology: From the Greek "*leugos*" and "*gaster*" meaning white-bellied (see Kozhurina, 2002: 16).

1908. *Chœrephon websteri* Dollman, Ann. Mag. nat. Hist., ser 8, 2 (12): 546. Publication date: 1 December 1908. Type locality: Nigeria: N Nigeria, on Bénoué river: Yola [09 12 N 12 29 E]. Holotype: NHMUK 1908.10.6.8: ad ♀, skin and skull. Collected by: G.W. Webster; collection date: 27 July 1908; original number: 11.

1917. *Chærephon (Lophomops) cristatus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 463, text-fig 10 A, B. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Kinshasa province: near mouth of Congo River: Boma [05 50 S 13 03 E]. [Goto Description]. Holotype: AMNH 48844: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 26 January 1915; original number: 2628.

1917. *Chærephon frater* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 456. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Kinshasa province: near Boma: Malela [05 57 S 12 38 E, 30 m]. [Goto Description]. Holotype: AMNH 49275: ad ♀, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 8 July 1915; original number: 2613. Topotype: MCZ 17219: ♀, alcoholic (skull not removed). Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 8 July 1915. Topotype: MCZ 17221: ♀, alcoholic (skull not removed). Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 8 July 1915.

1928. *Chærophon (Lophomops) nigri* Hatt, Bull. Soc. zool. France, 53: 374, text-fig B. Publication date: 10 December 1928. Type locality: Mali: Timbuctu district: on Niger River: Bourem [16 59 N 00 20 W]. [Goto Description]. Holotype: MNHN ZM-MO-1956-577a: ad ♂, alcoholic (skull not removed). Collected by: Théodore Monod; collection date: 6 January 1928. Paratype: AMNH 90390: ad ♂, skin and skull. Collected by: Théodore Monod; collection date: 6 January 1928; original number: M.S.A.D. 736b. See AMNH website. Paratype: MNHN ZM-MO-1956-577b: ♀, skull and alcoholic. Collected by: Théodore Monod; collection date: 6 January 1928.

1956. *Chaerephon nigri:* Aellen, Mém. IFAN, 48A: 32. (Name Combination).

2020. *Mops leucogaster:* Simmons and Cirranello, BatNames.org. (Current Combination).

2021. *Chaerephon leucogaste:* Tolera, Woldegebriel and Woldegebriel, Am. J. Biosci. Bioeng., 9 (4): 125. Publication date: 26 August 2021. (Lapsus).

2021. *Cherephon leucogaster:* Tolera, Woldegebriel and Woldegebriel, Am. J. Biosci. Bioeng., 9 (4): 125. Publication date: 26 August 2021. (Lapsus).

? *Chaerephon frater:* (Alternate Spelling).

? *Chaerephon leucogaster:* (Name Combination).

? *Chaerephon pumila cristata:* (Name Combination).

? *Chaerephon pumila websteri:* (Name Combination).

? *Chaerephon websteri:* (Alternate Spelling).

? *Mops (Chaerephon) leucogaster:* (Current Combination).

? *Tadarida frater:* (Name Combination).

? *Tadarida leucogaster leucogaster:* (Name Combination).

? *Tadarida leucogaster websteri:* (Name Combination).

? *Tadarida leucogaster:* (Name Combination).

? *Tadarida pumila frater:*

? *Tadarida websteri:* (Name Combination).

Taxonomy:

Included in *pumilus* by Koopman (1993a: 233), Bouchard (1998: 1).

Considered a valid species in the genus *Tadarida (Chaerephon)* by Peterson *et al.* (1995: 152) and Russ *et al.* (2001). Considered a valid species in the genus *Chaerephon* by Hutson *et al.* (2001: 33), Goodman and Cardiff (2004: 227), Lavrenchenko *et al.* (2004b: 141), and Simmons (2005).

Russ *et al.* (2001) distinguish it from *M. pumilus* on smaller size and different echolocation calls. Ammerman *et al.* (2012: 23) indicate that the separation between *leucogaster* and *pumilus* took place less than 2 million years ago.

Based on mitochondrial markers, Goodman *et al.* (2022: 1904) state that *leucogaster* is poorly differentiated from *C. atsinanana*.

Common Names:

Czech: morous bělobřichý. English: Grandidier's lesser Free-tailed bat, Grandidier's Free-tailed Bat, Madagascan white-bellied Free-tailed Bat. French: Tadaride de Madagascar à ventre blanc, Tadaride à ventre blanc, Petite tadaride de Madagascar, Molosse de Grandidier. German: Grandidiers Bulldoggfledermaus.

Conservation Status:

Global Justification

Assessed by Mickleburgh *et al.* (2014b) as part of *Chaerephon pumilus*.

Assessment History

Global

2014: LC ver. 3.1 (2001) as a synonym of *Chaerephon pumilus* (Mickleburgh *et al.*, 2014b). DD ver 2.3 (1994).

Regional

None known.

General Distribution:

Ethiopia to Ghana, Nigeria, Cameroon (Bol A Anong *et al.*, 2011: 46; Bakwo Fils *et al.*, 2014: 4; Waghiiwimbom *et al.*, 2019b: 6 [as "*Chaerephon nigri*"]), Congo (Bates *et al.*, 2013: 336), Congo

(Democratic Republic of the Congo?), Mali, Madagascar (Russ *et al.*, 2001), Nosy Be and Nosy Komba (Rakotonandrasana and Goodman, 2007: 6).

O'Brien (2011: 288) reports it further from the Comoros, and the Tanzanian islands of Pemba, Unguja [=Zanzibar], and Mafia.

BIOGEOGRAPHY:
Mops leucogaster is found across an elevational range of 0 - 920 m a.s.l., and is confined almost exclusively to the more extensive and drier western portion of Madagascar (Lamb *et al.*, 2012: 19).

GEOGRAPHIC VARIATION:
Tidière *et al.* (2022: 11) found some mitochondrial discordance in the animals from Mayotte. Some specimens showed ambiguous morphological traits. They were found to have $_{mt}$DNA haplotypes, but grouped with the *pusillus* microsatellite-cluster, suggesting that hybridization between the two species has occurred.

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 61) describe the baculum of *M. leucogaster* as "Eiffel tower shaped", with a bifurcated proximal tip that tapers abruptly to a distal point; length: 0.78 ± 0.072 (0.65 - 0.89) mm, width: 0.47 ± 0.055 (0.37 - 0.58) mm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Ramasindrazana and Goodman (2011) and Taylor *et al.* (2012a)] mention a wing loading value of 9.6 Pa, aspect ratio 8.1 for a wingspan of 27 cm and a wing area of 87 cm^2 and a body mass of 9 g.

MOLECULAR BIOLOGY:
Karyotype
From Ethiopia, Tolera *et al.* (2021: 125) reported *2n* = 48 and FN = 54. The autosomal chromosomes include four pairs of metacentrics and 19 pairs of acrocentrics; the X chromosome is metacentric and the Y chromosome is acrocentric.

HABITAT:
Lamb *et al.* (2012: 29) indicate that the highly suitable habitat for this species was associated with low annual rainfall, high mean annual temperature, and high human influence. Dammhahn and Goodman (2013: 108) indicate that this species' foraging habitat consists of open areas and the area above the forest canopy.

ROOST:
Ravelomanantsoa *et al.* (2019: 111) indicated that *Mops leucogaster* uses human constructions for roosting. Occasionally found in natural roosts under bark of dead trees (Garbutt, 2022: 96).

DIET:
Rocha *et al.* (2019: 188) found the paddy swarming armyworm (*Spodoptera mauritia*, Lepidoptera) in faecal samples of *Mops leucogaster*.

Tomita (2025: Suppl.) reported the sugarcone cicada (*Yanga guttulata* (Signoret, 1860)) as a prey item.

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of four individuals in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar. Razakaratrimo *et al.* (2019: 117) indicate that these bats are much more taken as prey during the wet season than during the dry season.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

Montade *et al.* (2024: 7) [referring to Lamb *et al.* (2012)] indicated that this species encountered a reduction in population size during the late Holocene.

REPRODUCTION AND ONTOGENY:
Nine females collected in December (?) at Ankajely (Madagascar) were all pregnant with embryos (crown-rump length 15 - 23 mm) (Goodman *et al.*, 2025: 214). Two males had large scrotal testes and well developed epididymides.

PARASITES:
BACTERIA
Gomard *et al.* (2016: 5) found 1 out of 94 tested bats to be positive for *Leptospira*.

SIPHONAPTERA
Ischnopsyllidae
Lagaropsylla consularis Smit, 1957 from Ethiopia, Kenya, Uganda, Congo and Congo (Democratic Republic of), Angola, Zimbabwe and

Mozambique (Haeselbarth *et al.*, 1966: 190, host referred to as "*Tadarida frater*").
Duchemin *et al.* (2022: 1077) reported the presence of *Lagaropsylla idae* Smit, 1957.

VIRUSES:
Astroviridae
Hoarau *et al.* (2021: Suppl.) reported these viruses from swab samples.

Paramyxoviridae
Specimens from this species tested by Wilkinson *et al.* (2014: 8270) were found to be positive for paramyxoviruses. Mélade *et al.* (2016b: 4) tested 94 Madagascan specimens, of which 6 were found positive for paramyxoviruses.

Rhabdoviridae
Mélade *et al.* (2016a: 6) tested 28 bats for *Duvenhage lyssavirus* and found seroreactivlty in nine of them.

UTILISATION:
See Goodman *et al.* (2008d).

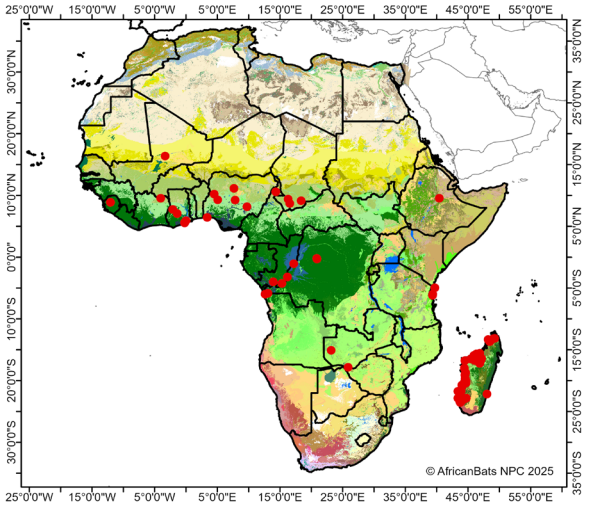

Figure 175. Distribution of *Mops (Chaerephon) leucogaster*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Ghana, Madagascar, Mali, Nigeria, Sierra Leone, Tanzania, Zambia.

Mops (Chaerephon) major (Trouessart, 1897)

*1897. *[Nyctinomus (Nyctinomus) pumilus] Var. Major* Trouessart, Catalogus Mammalium tam viventium quam fossilium, nov ed 1, pt 1: 146. Publication date: 1897. Type locality: Sudan: N Sudan: 5th Cataract of the Nile [18 32 N 33 41 E]. [Goto Description]. Holotype: NHMUK 1849.2.8.36: Collected by: Sir Francis Galton. - Comments: Kock (1969a: 148) mentions "Nilus super = 5. Nil-Katarakt, nördlich Berber, Sudan" as original type locality. He also states that de Winton (1901a: 40) changed the type locality in "erster Kakarakt der Nil".). - Etymology: From the Latin "*maior*" (see Kozhurina, 2002: 16).
1901. *Nyctinomus Emini* de Winton, Ann. Mag. nat. Hist., ser 7, 7 (37): 40. Publication date: 1 January 1901. Type locality: Tanzania: "Mosambiro" [=Usambiro] [03 00 S 32 34 E]. [Goto Description]. Holotype: NHMUK 1890.6.8.15: ad ♂, skin and skull. Collection date: 9 September 1889. Notes: Local name - 'Katunke'. - Comments: See Thorn *et al.* (2009: 72).
1917. *Chærephon (Lophomops) abæ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 464, text-fig 11. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 48887: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 17 December 1911; original number: 1823.
1967. *Tadarida (Chaerephon) pumila:* Happold, Sudan Notes & Records, 48: 122. - Comments: Preoccupied by *pumilus* Cretzschmar, 1830 (see Simmons, 2005). Attribution to *major* seems strange.
1989. *Chaerophon major:* Fenton, Can. J. Zool., 67 (8): 2035. Publication date: 1 August 1989. (Lapsus).
2020. *Mops major:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon abae:* (Alternate Spelling).
? *Chaerephon major:* (Name Combination).
? *Mops (Chaerephon) major:* (Current Combination).
? *Tadarida (Chaerephon) major:* (Name Combination).
? *Tadarida abae:* (Name Combination).
? *Tadarida major:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Chinese: 垂耳犬吻蝠. Czech: morous nubijský. English: Large Wrinkle-lipped Bat, Lappet-eared Wrinkle-lipped Bat, Lappet-eared Free-tailed Bat, Giant gland-tailed bat. French: Tadaride à oreillettes, Grand molosse à glandes caudales. German: Stirnlappen-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017z).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Chaerephon major*] (Monadjem *et al.*, 2017z). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida major*"] (Mickleburgh *et al.*, 2008ah; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004am; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There are no major threats to this species. Some populations are threatened by general habitat loss and disturbance of old buildings (Mickleburgh *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017z).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ah) [in IUCN (2009)] and Monadjem *et al.* (2017z) report that the species has a wide range, and likely occurs in some protected areas, although this needs to be confirmed. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Mops major is a lowland species is found throughout much of West Africa (including Senegal, Liberia, Côte d'Ivoire, Mali, Burkina, Ghana, Togo, Benin, Niger, and Nigeria), as well as a narrow distribution following the Nile from northern Sudan to Uganda. A second population is known from the east of Lake Victoria in eastern Uganda, western Kenya, and north-western Tanzania. A third, apparently disjunct, population is present in southeastern Kenya and northeastern Tanzania.

The records from Liberia should be re-examined as they may represent a different species, while the record from Malawi is doubtful (J. Fahr *pers. comm.* 2004 in Mickleburgh *et al.*, 2008ah in IUCN, 2009).

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2015a: 617); Cameroon (Bakwo Fils *et al.*, 2014: 4); Congo (The Democratic Republic of the); Côte d'Ivoire; Ghana; Guinea; Kenya; Liberia; Mali; Niger; Nigeria; Senegal; Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 63); Zambia (Monadjem *et al.*, 2010d: 541).

ECHOLOCATION:
From Maroua, Cameroon, Manga Mongombe (2012: 79) and Bakwo Fils *et al.* (2018: 4) reported for 16 calls a call type of FM and the following parameters: F_{max}: 39.3 ± 6.9 (31.9 - 53.1) kHz, F_{min}: 37.4 ± 6.7 (25.9 - 49.0) kHz, F_{mean}: 36.4 ± 6.7 (28.7 - 51.0) kHz, F_{knee}: 38.2 ± 7.3 (29.9 - 53.1) kHZ, F_{char}: 33.7 ± 7.3 (26.2 - 49.0) kHz, and duration: 1.66 ± 0.40 (0.85 - 2.73) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

POPULATION:
Structure and Density
This is a relatively common species, found in fairly small colonies (Mickleburgh *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017z).

Trend
2016: Stable (Monadjem *et al.*, 2017z). 2008: Stable (Mickleburgh *et al.*, 2008ah; IUCN, 2009).

PARASITES:
ARACHNIDA
Macronyssidae
Budinski and López-Baucells (2023: 154) mentioned this species as host for *Chelanyssus aethiopicus* (Hirst, 1921).

SIPHONAPTERA
Beaucournu and Kock (1996) reported the first record for the flea *Lagaropsylla anciauxi* Smit, 1957 on "*Tadarida major*" from Burkina Faso.

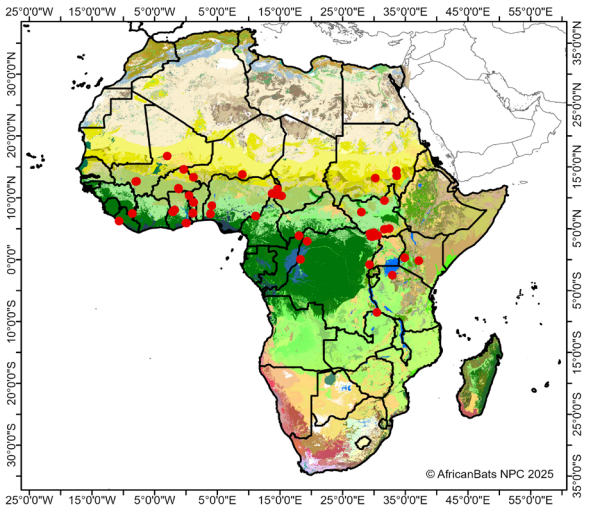

Figure 176. Distribution of *Mops (Chaerephon) major*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burkina Faso, Cameroon, Central African Republic, Congo (Democratic Republic of the), Ghana, Kenya, Liberia, Mali, Niger, Nigeria, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Mops (Chaerephon) nigeriae (Thomas, 1913)

*1913. *Chærephon nigeriæ* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 319. Publication date: 1 March 1913. Type locality: Nigeria: Northern region: Zaria province [ca. 11 01 N 07 44 E]. [Goto Description]. Holotype: NHMUK 1911.3.22.1: ad ♀. Collected by: A.C. Francis Esq. Presented/Donated by: A.C. Francis Esq. - Etymology: From the genitive scientific Latin feminine substantive *nigèriae*, meaning "from Nigeria", as the species was described from a Nigerian specimen (see Lanza *et al.*, 2015: 277).
1957. *Tadarida (Chearephon) spillmani:* Ansell, Ann. Mag. nat. Hist., ser 12 (10): 539. (Lapsus).
1988. *Tadarida chaeraphon nigeriae:* Okafor, Misc. Zool., 12: 11. (Lapsus).
1989. *Chaerophon nigeriae:* Fenton, Can. J. Zool., 67 (8): 2035. Publication date: 1 August 1989. (Lapsus).
2004. *Tadarida (Chaeraphon) nigeriae:* Okafor, Igbinosa and Ezenwaji, Anim. Res. Int., 1 (1): 64. Publication date: April 2004. (Name Combination, Lapsus).
2020. *Mops nigeriae:* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon nigerae:* (Lapsus).
? *Chaerephon nigeriae:* (Current Spelling).
? *Mops (Chaerephon) nigeriae:* (Name Combination).
? *Tadarida (Chaerephon) nigeriae nigeriae:* (Name Combination).
? *Tadarida nigeriae nigeriae:* (Name Combination).
? *Tadarida nigeriae:* (Name Combination).

TAXONOMY:



Figure 177. *Mops (Chaerephon) nigeriae* (ECJS-77/2009) caught in the Okavango, Botswana.

See Willis *et al.* (2002, Mammalian Species, 710).

This may be a complex of two distinct species, with *Mops nigeriae* in the north of the known distribution and *M. spillmanni* in the south. We follow Simmons (2005) in currently recognizing *spillmanni* Monard, 1933 as a subspecies of *M. nigeriae*.

Herkt *et al.* (2017: Appendix S9) found that the localities in the southern part of the distribution area suggest rather different ecological niches than those for the northern part, which would suggest that more than one species might be included.

COMMON NAMES:

Afrikaans: Nigeriese losstertvlermuis. Azande (DRC): Fulo. Czech: morous nigerijský. English: Nigerian Free-tailed Bat, Nigerian Wrinkle-lipped Bat. French: Tadaride du Nigeria, Molosse du Nigéria. German: Nigeria-Bulldoggfledermaus. Italian: Cherefónte nigeriàno.

ETYMOLOGY OF COMMON NAME:

The species was originally described from a specimen from Nigeria (see Taylor, 2005).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017d).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Chaerephon nigeriae*] (Monadjem *et al.*, 2017d). 2008: LC ver 3.1 (2001) [assessed as "*Tadarida nigeriae*"] (Mickleburgh *et al.*, 2008ai; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004af; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2004: considered a vagrant not assessed, not recorded in SA (Friedmann and Daly, 2004).

MAJOR THREATS:

There appear to be no major threats to this species (Mickleburgh *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017d). The ability of the species to exploit buildings as roosts, and its association with cleared rainforest in Nigeria, suggests that it is relatively resistant to anthropogenic impacts (Willis *et al.*, 2002).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008ai) [in IUCN (2009)] and Monadjem *et al.* (2017d) report that in view of the species wide range, it is presumably present in some protected areas. No direct conservation

measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Mops nigeriae is widely distributed over much of sub-Saharan Africa. It ranges from Sierra Leone in the west to Ethiopia in the east, being recorded as far south as Angola, Botswana and Zimbabwe. There are some additional records from the Arabian Peninsula in Yemen and western Saudi Arabia. The species has been found at elevations of up to 1,000 m asl, and possibly occur higher.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,133,308 km^2.

Native: Angola (Crawford-Cabral, 1989; Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 541; Taylor *et al.*, 2018b: 60); Botswana (Archer, 1977; Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 541); Burkina Faso (Kangoyé *et al.*, 2012: 6024; 2015a: 618); Burundi; Cameroon; Central African Republic (Al-Jumaily, 2002: 55); Chad (Al-Jumaily, 2002: 55); Congo; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 541); Côte d'Ivoire (Beaucournu and Fahr, 2003: 157; but see Al-Jumaily, 2002); Ethiopia (Al-Jumaily, 2002: 55); Ghana (Al-Jumaily, 2002: 55); Guinea (Al-Jumaily, 2002: 55; Ziegler *et al.*, 2002: 78); Malawi (Happold and Happold, 1997b: 823; Al-Jumaily, 2002: 55); Mali (Al-Jumaily, 2002: 55); Mozambique; Namibia (Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 541); Niger (Al-Jumaily, 2002: 55); Nigeria (Al-Jumaily, 2002: 55); Saudi Arabia (Nader and Kock, 1980); Sierra Leone (Al-Jumaily, 2002: 55); Sudan; Tanzania (Al-Jumaily, 2002: 55); Uganda (Al-Jumaily, 2002: 55); Yemen (Al-Jumaily, 2002: 55; Benda *et al.*, 2011b: 46); Zambia (Ansell, 1957; Ansell and Ansell, 1973; Cotterill, 2004a: 261; Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 541); Zimbabwe (Al-Jumaily, 2002: 55; Monadjem *et al.*, 2010d: 542).

Presence uncertain: Togo (Al-Jumaily, 2002: 55).

ECHOLOCATION:
Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 17 kHz and duration: 10 ms.

Eight calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 16.51 ± 0.57 kHz, F_{min}: 14.11 ± 4.77 kHz, F_{knee}: 16.29 ± 0.54 kHz, F_{char}: 16.12 ± 0.43 kHz, slope: 2.99 ± 9.56 OPS, duration: 6.83 ± 4.45 ms.

In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 9 calls: Interpulse interval: 136.0 ± 128.2 (37.5 - 465.0) ms; F_{max}: 24.6 ± 3.6 (20.7 - 30.3) kHz; Start slope: -4.0 ± 1.8 (-1.7 - -6.5) kHz/ms; End slope: -2.7 ± 1.9 (0.0 - -5.7) kHz/ms; Ledge duration: 0.4 ± 0.0 (0.4 - 0.5) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

See also Taylor (1999b).

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 48, FN = 62, BA = 16, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from Namibia and Zimbabwe

ROOST:
In Zimbabwe, a group of six individuals was noticed leaving a roost under bark, whereas in Botswana a similar roost contained at least 25 animals, and in Zambia, colonies of 30 to 100 individuals were reported (Happold and Happold, 2023: 126).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
This species is typically found in small groups of 10 to 15 animals, with maternity roosts being formed of up to 25 bats (Mickleburgh *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017d).

Trend
2016: Unknown (Monadjem *et al.*, 2017d). 2008: Unknown (Mickleburgh *et al.*, 2008ai; IUCN, 2009).

PARASITES:
BACTERIA
Bartonellae
Kamani *et al.* (2014: 628) tested 16 Nigerian *C. nigeriae* animals, and found 2 of them testing positive for *Bartonella* DNA. Of the two Nigerian bats examined by Di Cataldo *et al.* (2020: 2), one was infected by hemoplasma bacteria.

HELMINTHS
Okafor *et al.* (2004: 64) investigated the helminth parasite load of 857 *M. nigeriae* specimens from Nigeria and found 658 (76.78 %) of them to be infected by 9 species: Nematodes: *Rictularia*

chaerephoni, Histostrongylus coronatus, Capillaria annulosa Dujardin, 1845, *Cheiropteronema globocephala* Sandground, 1929, *Litosoma pujoli* Bain, 1966; Trematodes: *Posthodendrium panouterus, Castroia nyctali* Gvosdev, 1954; Cestodes: *Hymenolepis kerivoulae* (Prudhoe and Manger, 1969), *Oochoristica agamae* Bayliss, 1919.

ARACHNIDA
Macronyssidae
Orlova *et al.* (2024: 154) mentioned this species as host for *Chelanyssus aethiopicus* (Hirst, 1921).

DIPTERA
Nycteribiidae
16 Nigerian bats examined by Stuckey *et al.* (2017: 22) were parasitized by *Cyclopodia greefi* Karsch, 1884 bat flies.

VIRUSES:
Paramyxoviridae
Ayolabi *et al.* (2021) reported on the presence of Paramyxoviruses (PmV) in these bats from Lagox (Nigeria).

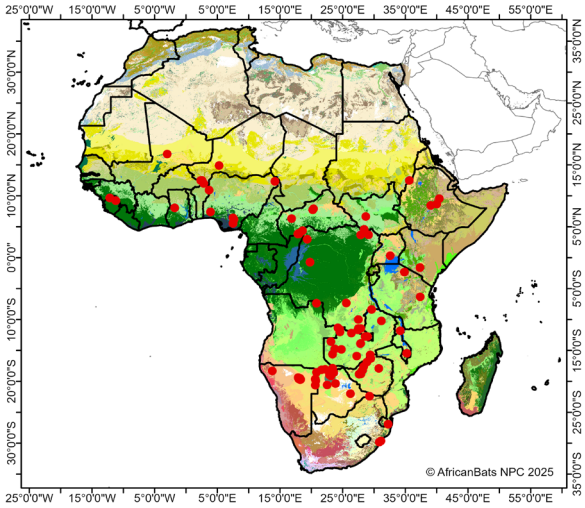

Figure 178. Distribution of *Mops (Chaerephon) nigeriae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

Mops (Chaerephon) nigeriae nigeriae (Thomas, 1913)

*1913. *Chærephon nigeriæ* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 319. Publication date: 1 March 1913. Type locality: Nigeria: Northern region: Zaria province [ca. 11 01 N 07 44 E]. [Goto Description]. - Etymology: From the genitive scientific Latin feminine substantive *nigèriae*, meaning "from Nigeria", as the species was described from a Nigerian specimen (see Lanza *et al.*, 2015: 277).
? *Chaerephon nigeriae nigeriae:* (Name Combination).
? *Mops (Chaerephon) nigeriae nigeriae:* (Current Combination).
? *Tadarida (Chaerephon) nigeriae nigeriae:* (Name Combination).
? *Tadarida nigeriae nigeriae:* (Name Combination).

GENERAL DISTRIBUTION:
E Côte d'Ivoire, Ghana, Benin, Togo, Nigeria, Cameroon, Central African Republic to NE Democratic Republic of the Congo; Niger; Chad; Ethiopia; Saudi Arabia (Harrison and Bates, 1991: 64).

Subsaharan Africa to NE Zaire: see Horáček *et al.* (2000: 137). E Côte d'Ivoire, Ghana, Benin, Togo, Nigeria, Cameroon, Central African Republic, N Zaire, Niger, Chad, Ethiopia: see Willis *et al.* (2002: 2).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Ghana, Mali, Niger, Nigeria, Sierra Leone, South Sudan.

Mops (Chaerephon) nigeriae spillmanni (Monard, 1933)

*1933. *Nyctinomus spillmanni* Monard, Bull. Soc. Neuchât. Sci. nat., 57: 51 (for 1932?). Publication date: 1933. Type locality: Angola: South-Central Angola: Vila da Ponte [14 25 S 16 15 E]. [Goto Description]. - Etymology: In honour of Mr. C.-R. Spillman from la Chaux-de-Fonds (Monard, 1933: 51).
1963. *Tadarida (Chaerephon) spillmanni:* Hayman. (Name Combination, Current Spelling).
1965. *Nyctinimus spillmani:* Koopman, Am. Mus. Novit., 2219: 21. Publication date: 22 June 1965. (Lapsus).
1967. *Tadarida nigeriae spillmanni:* Ansell, Arnoldia Rhod., 2 (38): 25. (Name Combination).
? *Chaerephon nigeriae spillmani:* (Lapsus).
? *Chaerephon nigeriae spillmanni:* (Name Combination).
? *Mops (Chaerephon) nigeriae spillmanni:* (Current Combination).
? *Tadarida (Chærephon) spillmani:* (Name Combination, Alternate Spelling).

COMMON NAMES:
Tshokwe (Angola): Kanga.

GENERAL DISTRIBUTION:
Southern Africa (Angola (Horáček *et al.*, 2000: 137), Namibia (Willis *et al.*, 2002: 2), Botswana (Willis *et al.*, 2002: 2), Zimbabwe (Wilson and La Val, 1974: 2), Zambia (Willis *et al.*, 2002: 2), S Democratic Republic of the Congo (Willis *et al.*, 2002: 2), Tanzania (Horáček *et al.*, 2000: 137).

PARASITES:
SIPHONAPTERA
Ischnopsyllidae
Lagaropsylla lipsi Smit,1957 known only from the vicinity of Elisabethville, Katanga, Congo (Haeselbarth *et al.*, 1966: 191).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Congo (Democratic Republic of the), Kenya, Malawi, Namibia, South Africa, Tanzania, Uganda, Zambia, Zimbabwe.

Mops (Chaerephon) pumilus (Cretzschmar, 1826)

*1826. *Dysopes pumilus* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 69, pl 27a. Type locality: Eritrea: Massawa [15 37 N 39 26 E]. [Goto Description]. Lectotype: SMF 4311: ♀, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1825. Old catalog II.K.3.a: see Mertens (1925: 20). Paralectotype: RMNH MAM.27334: ad, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell. - Comments: The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831". - Etymology: From the masculine Latin adjective *pùmilus*, meaning "of short stature, dwarf or pygmy" as the species is a particularly small African molossid (see Lanza *et al.*, 2015: 282).

1838. *Nyctinomus pusilus:* Lesson, Compléments de Buffon, ed 2, Paris, 1: 328. Publication date: 1838. (Lapsus).

1852. *Dysopes dubius* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 60, pl 15, fig 2. Publication date: 1852. Type locality: Mozambique: South bank of Zambezi River: Sena [17 28 S 35 01 E]. [Goto Description]. Holotype: ZMB 85539: juv, skull only. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. Pullus specimen; see Turni and Kock (2008: 72). - Comments: Preoccupied by *dubius* A. Smith, 1833 (see Simmons, 2005). Allen (1939a: 111) also mentioned *Nyctinomus dubius* A. Smith, 1833 as a separate species. Turni and Kock (2008: 72) state that no other African molossid collected was ever identified with *D. dubius* until Ellerman *et al.* (1953: 68) synonymized it without any comment. Peters´ species description on the *pullus* specimen ZMB 85539 is very questionable, so they conclude that *dubius* is a *nomen dubium*.

1852. *Dysopes limbatus* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 56, pl 14. Publication date: 1852. Type locality: Mozambique: Mozambique Island [15 03 S 40 46 E]. [Goto Description]. Syntype: NHMUK 1907.1.1.704. Syntype: ZMB 537/85520: ad ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008) [skin: ZMB 537 / skull: ZMB 85520]. Syntype: ZMB 538/85519: ad ♀, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008) [skin: ZMB 538 + skull: ZMB 85519]. Syntype: ZMB 539: juv, skin only. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). - Comments: Peters (1852: 56) mentions "Africa orientalis, Insula Mozambique, Sena at 15° ad 17° Let. Aust.", and Roberts (1951: 98) "Mozambique Island and Sena"). Possibly valid as a subspecies. Considered a valid species by Peterson *et al.* (1995: 159).

1877. *Nyctinomus [(Nyctinomus)] limbatus:* Dobson, Proc. zool. Soc. Lond., 1876, IV: 724. Publication date: April 1877. (Name Combination).

1877. *Nyctinomus [(Nyctinomus)] pumilus:* Dobson, Proc. zool. Soc. Lond., 1876, IV: 723. Publication date: April 1877. (Name Combination).

1878. *Nyctinomus limbatus:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 428. Publication date: 15 June 1878. - Comments: . (Name Combination).

1901. *Nyctinomus gambianus* de Winton, Ann. Mag. nat. Hist., ser 7, 7 (37): 39. Publication date: 1 January 1901. Type locality: The Gambia: "Gambia". [Goto Description]. Holotype: NHMUK 1889.10.7.3.

1904. *Nyctinomus hindei* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (75): 210. Publication date: 1 March 1904. Type locality: Kenya: Fort Hall [=Muranga] [00 43 S 37 09 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1903.3.2.4: ad ♂. Collected by: Mrs. Hildegarde Beatrice Hinde; collection date: 1 January 1903; original number: 134. Presented/Donated by: Mrs. Hildegarde Beatrice Hinde. - Comments: Possibly valid as a subspecies. Considered a valid species by Peterson *et al.* (1995: 159). Thomas (1904a: 210) mentions 2 specimens.

1914. *Chaerephon pumilus:* G.M. Allen, Bull. Mus. comp. Zool., 58 (7): 353. Publication date: July 1914. (Name Combination).

1916. *Chaerephon pumilus naivashæ* Hollister, Smiths. Misc. Coll., 66 (1) (2406): 4. Publication date: 10 February 1916. Type locality: Kenya: Naivasha Station [00 43 S 36 26 E]. [Goto Description]. Holotype: USNM 166658: ad ♂, skull and alcoholic. Collected by: John Alden Loring; collection date: 7 August 1909; original number: 6955. Topotype: ROM 36466: ad ♂, skin and skull. Collected by: John George Williams; collection date: 10 July 1965. Topotype: ROM 36467: ad ♀, skin and skull. Collected by: John George Williams; collection date: 17 July 1965. Topotype: ROM 36468: ad ♀, skin and skull. Collected by: John George Williams; collection date: 17 July 1965. Topotype: ROM 36469: ad ♀, skin and skull. Collected by: John George Williams; collection date: 17 July 1965. Topotype: ROM 36470: ad ♂, skin and skull. Collected by: John George Williams; collection date: 17 July 1965. Topotype: ROM 36471: ad ♀, skin and skull. Collected by: John George Williams; collection date: 10 August 1965. Topotype: ROM 36472: ad ♀, skin and skull. Collected by: John George Williams; collection date: 10 August 1965. Topotype: ROM 41842: juv ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41843: juv ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41844:

juv ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41845: juv ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41846: juv ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41847: juv ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41848: juv ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41849: juv ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41850: ad ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41851: ad ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41852: ad ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41853: ad ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41854: ad ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41855: ad ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41856: ad ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41857: ad ♂, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41858: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41859: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41860: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41861: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41862: juv ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41863: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41864: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41865: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41866: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41867: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41868: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41869: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41870: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41871: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41872: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41873: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41874: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41875: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41876: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41877: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41878: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41879: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41880: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41881: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41882: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41883: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41884: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41885: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41889: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41890: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41891: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41892: ad ♂, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41893: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41894: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41895: ad ♀, skull and alcoholic. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41896: ad ♂, alcoholic (skull not removed). Collected by:

Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41897: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41898: ad ♀, alcoholic (skull not removed). Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41899: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41900: ad ♂, complete skeleton. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41901: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41902: ad ♀, complete skeleton. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41903: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41904: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41905: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41906: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41907: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 41908: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 9 August 1967. Topotype: ROM 47000: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47001: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47002: ad ♂, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47003: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47004: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47005: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47006: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47007: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47008: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47009: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47010: ad ♂, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47011: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47012: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47013: ad ♂, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47014: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47015: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47016: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47017: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47018: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47019: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47020: ad ♂, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. Topotype: ROM 47021: ad ♀, skin and skull. Collected by: John George Williams; collection date: 30 June 1968. - Comments: Considered a valid species by Peterson *et al.* (1995: 157).

1926. *Chaerophon pumilus elphicki* Roberts, Ann. Transv. Mus., 11: 245. Publication date: 14 September 1926. Type locality: South Africa: SE Transvaal province: Barberton district: Malelane Estate [25 29 S 31 31 E]. [Goto Description]. Holotype: TM 2488: ad ♂, skin and skull. Collected by: Captain G.J. Elphick; collection date: 30 March 1920.

1932. *Choerephon (Lophomops) langi* Roberts, Ann. Transv. Mus., 15 (1): 17. Publication date: 1 October 1932. Type locality: Botswana: N Bechuanaland, Ngamiland,: Tsotsoroga Pan [18 40 S 24 25 E]. [Goto Description]. Holotype: TM 6554: ad ♂, skin and skull. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 29 June 1930; original number: 870. - Comments: Possibly valid as a subspecies.

1951. *Tadarida (Chaerephon) faini* Hayman, Rev. Zool. Bot. afr., 45 (1-2): 82. Publication date: 22 December 1951. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Upper Congo, between Blukwa and Lake Albert: Wago Forest [ca. 01 44 N 30 39 E]. [Goto Description]. Holotype: RMCA 20509: ad ♂, skin and skull. Collected by: Dr. Alexandre Fain; collection date: 1 June 1951; original number: 1. Paratype: NHMUK 1951.629: ad ♀, skin and skull. Collected by: Dr. Alexandre Fain; original number: 2. - Comments: Possibly valid as a subspecies.

1975. *Chaerophon limbatus:* Durette-Desset and Chabaud, Ann. Parasit., 50 (3): 315. (Lapsus).

1989. *Chaerophon naivashii:* Fenton, Can. J. Zool., 67 (8): 2035. Publication date: 1 August 1989. (Lapsus).

1989. *Chaerophon pumila:* Fenton, Can. J. Zool., 67 (8): 2035. Publication date: 1 August 1989. (Lapsus).

1999. *Chaerephon pumilla:* Dumont, Etzel and Hempel, Mammalia, 63 (2): 159. (Lapsus).

2016. *C[haerephon] elphicki:* Naidoo, Goodman, Schoeman, Taylor and Lamb, Mammalia, 80 (6): 627. Publication date: 6 January 2016. (Name Combination).

2016. *C[haerephon] naivashae:* Naidoo, Goodman, Schoeman, Taylor and Lamb, Mammalia, 80 (6): 627. Publication date: 6 January 2016. (Name Combination).

2017. *Chaerophon pumiluss:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 5. Publication date: 6 April 2017. (Lapsus).

2019. *Chaerephon pumilas:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

2020. *Mops pumilus:* Simmons and Cirranello, BatNames.org. (Current Combination).

2021. *Cherephon pumila:* Tolera, Woldegebriel and Woldegebriel, Am. J. Biosci. Bioeng., 9 (4): 125. Publication date: 26 August 2021. (Lapsus).

? *Chaerephon cf. pumilus DMR-2017*

? *Chaerephon cf. pumilus:*

? *Chaerephon limbatus:* (Name Combination).

? *Chaerephon pumila hindei:* (Name Combination).

? *Chaerephon pumila langi:* (Name Combination).
? *Chaerephon pumila limbata:* (Alternate Spelling).
? *Chaerephon pumila limbatus:* (Name Combination).
? *Chaerephon pumilus elphicki:* (Name Combination).
? *Chaerephon pumilus hindei:* (Name Combination).
? *Chaerephon pumilus langi:* (Name Combination).
? *Chaerephon pumilus limbatus:* (Name Combination).
? *Chaerephon pumilus naivashae:* (Alternate Spelling).
? *Chaerephon pumilus pumilus:* (Name Combination).
? *Chaerephon pumilus sensu lato:*
? *Chaerephon pusillus:*
? *Chaerophon pumilus:* (Name Combination).
? *Mops (Chaerephon) pumilus:* (Current Combination).
? *Mops pumilus elphicki:*
? *Mops pumilus langi:* (Name Combination).
? *Mops pumilus limbata:* (Alternate Spelling).
? *Mops pumilus naivashae:* (Name Combination).
? *Nyctinomus pumilus:* (Name Combination).
? *Tadarida (Chaerephon) pumila frater:* (Name Combination).
? *Tadarida (Chaerephon) pumila:* (Name Combination).
? *Tadarida faini:* (Name Combination).
? *Tadarida limbata:* (Name Combination).
? *Tadarida naivashae:* (Name Combination).
? *Tadarida pumila elphicki:*
? *Tadarida pumila faini:* (Name Combination).
? *Tadarida pumila frater:* (Name Combination).
? *Tadarida pumila hindei:* (Name Combination).
? *Tadarida pumila langi:* (Name Combination).
? *Tadarida pumila limbata:* (Name Combination).
? *Tadarida pumila naivashae:* (Name Combination).
? *Tadarida pumila pumila:* (Name Combination).
? *Tadarida pumila pumila-limbata:*
? *Tadarida pumila pumila-naivashae:*
? *Tadarida pumila websteri:* (Name Combination).
? *Tadarida pumila:* (Name Combination).

TAXONOMY:

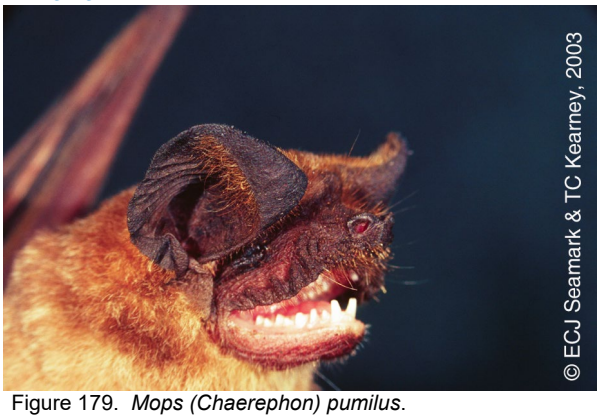

Figure 179. *Mops (Chaerephon) pumilus*.

See Bouchard (1998, Mammalian Species, 574). Formerly included *pusillus*; see Hayman and Hill (1971: 64), but see Goodman and Ratrimomanarivo (2007: 391). The description date is sometimes mentioned as "1830 or 1831" (see Happold and Happold (1997b: 823). Peterson *et al.* (1995: 162) consider *pumilus* not to include most of the forms occurring on Madagascar. Horáček *et al.* (2000: 136) include *pumilus* in the genus *Tadarida*, subgenus *Chaerephon*. Taylor (1999b), Aspetsberger *et al.* (2003: 250; 252) indicate that cryptic species might exist within the genus *Chaerephon* (more specifically in *pumilus*), but find it premature to identify them already. Jacobs *et al.* (2004ar: 17) identified five haplotypes, but indicate they represent only one species.

Naidoo *et al.* (2013c: 134) indicate that southeast African *M. pumilus s.l.* contains several well-supported sympatric genetic lineages (they identified three clades), which exhibit paraphyly with the Malagasy *M. leucogaster*. They were not able to to distinguish these clades based on echolocation characteristics (p. 137) but suggest that these stable sympatric lineages might be the result of female philopatry or roost faithfulness.

Naidoo *et al.* (2016) used cyt *b*, control region, and Rag2 data on a large number of representatives from the *Mops pumilus* species complex from islands in the western Indian Ocean, and eastern and southeastern Africa. They found that *Mops pumilus* s.s. (Eritrea and Yemen) is specifically distinct from the following taxa/samples: *M. pumilus* from southeastern Africa, the syntype of *limbatus*, the holotypes of *elphicki* and *langi*, and the topotype of *naivashae*. They suggest (p. 642) that additional evidence from more variable nuclear markers is necessary to resolve the issue of the number of species present in this complex. The genetic differentiation is probably the result of habitat fragmentation during glacial maxima when the ancestral population was separated over isolated

subtropical forests (Schoeman and Monadjem, 2018: 4).

Benda *et al.* (2023a: 44; 2025: 81) indicate that bats traditionally assigned to "*Chaerephon pumilus*" are currently believed to belong to a complex of several species, which still needs to be resolved. Most sub-Saharan populations would not belong to *Chaerephon pumilus* s.s.

COMMON NAMES:
Afrikaans: Klein losstertvlermuis. Chinese: 小犬吻蝠. Czech: morous malý, tadarida malá. English: Little Free-tailed Bat, Lesser Free-tailed Bat, Little Wrinkle-lipped Bat, White-bellied Free-tailed Bat. French: Petite tadaride, Petit molosse à glandes caudales, Tadaride bornée. German: Kleine Bulldoggfledermaus, Zwerg-Doggengrämler, Sena-Doggengrämler, Gesäumte Doggengrämler. Italian: Cherefónte pigmèo. Kiluba (DRC): Kasusu. Malawian: Liputiputi, Ndemiya, Namzeze. Nyungwe (Malawi): Kalemawalema (not specific). Portuguese: Morcego pequeno de cauda livre.

ETYMOLOGY OF COMMON NAME:
From the Latin "*pumilus*" meaning dwarf, because it is the smallest of the molossids occurring in the (southern African sub)region (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a broad range of habitats, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dr; IUCN, 2009; Mickleburgh *et al.*, 2014b; Mickleburgh *et al.*, 2019m).

Assessment History
Global
2018: LC ver 3.1 (2001) assessed as *Chaerephon pumilus* (Mickleburgh *et al.*, 2019m). 2014: LC ver 3.1 (2001) assessed as "*Chaerephon pumilus*" (Mickleburgh *et al.*, 2014b). 2008: LC ver 3.1 (2001) assessed as "*Tadarida pumila*" (Mickleburgh *et al.*, 2008dr; IUCN, 2009). 2004: LC ver 3.1 (2001) assessed as "*Chaerephon pumila*" (Mickleburgh *et al.*, 2004ah; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016a). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There are no major threats to the species. In some parts of its range, it is threatened from persecution as a pest, especially since it roosts in buildings (Mickleburgh *et al.*, 2008dr; IUCN, 2009; Mickleburgh *et al.*, 2014b; Mickleburgh *et al.*, 2019m).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2014b) and Mickleburgh *et al.* (2019m) reported that due to its wide range it seems probable that this species is present in some protected areas. On Madagascar, it has not been recorded from any protected areas, but it has been recorded from houses close to protected areas. The status of the population on Aldabra need to be clarified with complementary research needed into the conservation status of this population.

GENERAL DISTRIBUTION:
This widespread species is found from Senegal in the west of its range, eastwards to Yemen and southwestern Saudi Arabia, and as far south as South Africa, where Babiker Salata (2012: 49) found that its distribution is strongly associated with the mean temperature of the coldest quarter. It has been recorded from the island of Bioko and the Annobon Islands (Equatorial Guinea), Pemba and Zanzibar (Tanzania).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 809,867 km^2.

Records from Western Cape Province are rejected by Jacobs and Fenton (2001), since these represent *Sauromys petrophilus*.

Records from the Seychelles [Aldabra] (Hutson, 2004a) and the Comoros (Louette, 2004; Goodman, 2007; ACR, 2006, 2007, 2008, 2009, 2010) are rejected by Goodman *et al.* (2010a) since these represent *Mops pusillus*.

Records from Madagascar (Bouchard, 1998; Russ *et al.*, 2001; Goodman and Cardiff, 2004; ACR, 2006, 2007, 2008, 2009,2010) are now assigned to *Mops atsinanana* (Goodman *et al.*, 2010a).

Native:
Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 542; Taylor *et al.*, 2018b: 62); Benin (Capo-Chichi *et al.*, 2004: 164); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 542); Burkina Faso (Kangoyé *et al.*, 2015a: 618); Burundi; Cameroon (Bakwo Fils *et al.*, 2014: 4): Chad; Congo (Bates *et al.*, 2013: 336); Congo (The Democratic Republic of the) (Allen, 1917;

Schouteden, 1944; Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 542); Côte d'Ivoire; Equatorial Guinea [Annobón, Bioko]; Eritrea; Eswatini (Monadjem *et al.*, 2010d: 543, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 132; Benda *et al.*, 2020: 2586); Gambia (Emms and Barnett, 2005: 50); Ghana; Guinea; Guinea-Bissau (Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 73); Kenya; Liberia (Fahr, 2007a: 104); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 46; Monadjem *et al.*, 2010d: 542); Mali (Meinig, 2000: 105); Mozambique (Smithers and Lobão Tello, 1976; Lopes and Crawford-Cabral, 1992; Monadjem *et al.*, 2010d: 542; Monadjem *et al.*, 2010c: 382); Namibia (Monadjem *et al.*, 2010d: 542); Niger; Nigeria; Rwanda; São Tomé and Príncipe [São Tomé] (Juste and Ibáñez, 1993c: 906; Rainho *et al.*, 2010a: 37); Saudi Arabia; Senegal; Sierra Leone; Somalia; South Africa (De Graaf, 1960; Monadjem *et al.*, 2010d: 542); Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62); Yemen (Benda *et al.*, 2011b: 47); Zambia (Ansell, 1969; Ansell, 1973; Ansell, 1978; Monadjem *et al.*, 2010d: 543); Zimbabwe (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 543).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data: Fa: 38.95 mm, mass: 10.5 g, wing loading: 12.4 N/m^2, aspect ratio: 7.3.

DETAILED MORPHOLOGY:
Brain
Tambusso and Fariña (2015: Suppl.) mention a brain mass of 0.29 g for an average body mass of 13.3 g.

Amrein *et al.* (2007) from specimens collected from Bénin reported moderate proliferating cell activity, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus, with doublecortin (DCX) they detected young migrating neuron in the subgrannular layer of the hippocampus. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. No NeuroD was detected in the hippocampal granule cells (Amrein *et al.*, 2007). Kruger *et al.* (2010a) describe, based on three brains from Kenya, using immunohistochemical methods, the nuclear organization of the cholinergic, catecholaminergic and serotonergic systems. Kruger *et al.* (2010b) describes, based on three brains from Kenya, the distribution of Orexin-A immunoreactive cell bodies and terminal networks.

Gastro-intestinal tract (GIT)
Aylward *et al.* (2019: 1108) reported for six specimens an average weight of 9.17 ± 0.85 g, and a GIT of 0.44 ± 0.05 g (4.85 ± 0.40 %).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 11.8 Pa, aspect ratio 8.6 and tip shape index of 1.66 for a wingspan of 27 cm and a wing area of 87 cm^2 and a body mass of 11 g.

In their study on rewarming along an altitudinal gradient in the RSA, Marsden *et al.* (2022: 5) found that the body mass of these bats decreases with increasing altitude. Their mass-specific rewarming rate was positively correlated with altitude.

SEXUAL DIMORPHISM:
Chaverri *et al.* (2018: 1944) [referring to Bouchard, 2001b] indicates that the sexes can be distinguished by scent produced from the interaural and muzzle glandular areas.

ECHOLOCATION:
Frequency modulated call. In Kenya, Taylor *et al.* (2005) reported a peak frequency of 25.6 ± 1.7 kHz from Kivoko. In Tanzania, Aspetsberger *et al.* (2003) reported a F_{max}: 22.7 ± 3.3 kHz from Amani Nature Reserve. In Swaziland, Taylor (1999b) reported a F_{max}: 32.9 ± 4.5 kHz from Mlawula, and maximum frequencies at three different localities around Durban in South Africa of 43.0 ± 1.0 kHz, 28.7 ± 1.8 kHz and 28.7 ± 2.5 kHz. Fenton *et al.* (2004) reported a F_{max}: 29 ± 4.6 kHz for a locality in Durban, South Africa. Rainho *et al.* (2010a: 21) reports the calls [as *Tadarida pumila*] of 32 individuals from Sao Tomé. Bohmann *et al.* (2011: 1) [referring to Monadjem *et al.* (2010d)] mention F_{peak}: 25 - 40 kHz. Schoeman and Waddington (2011: 291) mention a F_{peak} 28.2 ± 1.5 kHz and a duration: 10.8 ± 0.2 ms for specimens from Durban, South Africa. From the Durban area, Naidoo *et al.* (2011: 23) report F_{peak} = 24.7 ± 1.0 kHz and a duration: 12.4 ± 0.9 ms.

Taylor *et al.* (2013b: 18) recorded the following parameters for 8 calls from specimens from Swaziland: F_{max}: 27.7 ± 4.40 (23.0 - 32.8) kHz, F_{min}: 23.3 ± 2.38 (20.9 - 27.4) kHz, F_{knee}: 26.2 ± 3.34 (22.6 - 30.8) kHz, F_{char}: 24.3 ± 2.91 (21.5 - 28.1) kHz, duration: 8.3 ± 2.10 (5.3 - 11.9) ms, and for 6 calls from KwaZulu-Natal, South Africa: F_{max}: 31.6 ± 4.05 (24.6 - 36.7) kHz, F_{min}: 24.5 ± 1.55 (21.7 - 26.5) kHz, F_{knee}: 28.9 ± 2.51 (24.4 - 31.3) kHz, F_{char}: 25.6 ± 1.57 (22.7 - 27.3) kHz, duration: 8.4 ± 1.71 (6.6 - 11.0) ms. From

Swaziland also, Monadjem *et al.* (2017c: 179) reported the following values: F_{min}: 23.3 ± 1.41 (20.8 - 26.5) kHz, F_{knee}: 26.1 ± 2.09 (22.5 - 29.6) kHz, F_c: 24.0 ± 1.53 (21.3 - 27.2) kHz and duration: 9.0 ± 2.10 (3.9 - 12.6) ms. They were able to detect these calls up to a distance of 15 m.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 29 (24 - 31) kHz.

Linden *et al.* (2014: 40) mentioned the following parameters for the Soutpansberg area (RSA): F_{min}: 21 - 27 kHz, F_{char}: 22 - 28 kHz, F_{knee}: 23 - 31 kHz, slope: 13 - 124 OPS, duration: 5 - 12 ms.

20 calls from Mapungubwe National Park (RSA) were recorded by Parker and Bernard (2018: 57) with the following characteristics: F_{char}: 26.65 ± 2.53 kHz, F_{max}: 34.87 ± 5.75 kHz, F_{min}: 24.67 ± 2.68 kHz, F_{knee}: 29.72 ± 3.05 kHz, duration: 8.80 ± 2.65 ms, with 4.24 ± 1.89 calls/sec.

Monadjem *et al.* (2011: 32) reported values for two calls from a "*Chaerephon* cf. *pumilus*" from western Uganda: F_{min}: 24.95 kHz, F_{max}: 27.78 kHz, F_{char}: 25.22 kHz, F_{knee}: 75.61 kHz, and duration: 8.4 ms.

Two calls from specimens from the Aberdares Range in Kenya were reported by Eisenring *et al.* (2016: SI 2) with F_{peak}: 26.3 ± 2.8 (24.4 - 28.3) kHz, F_{max}: 32.6 ± 1.2 (31.8 - 33.5) kHz, F_{min}: 20.9 ± 0.4 (20.6 - 21.1) kHz, duration: 11.8 ± 1.5 (10.7 - 12.9) ms.

From Maroua, Cameroon, Manga Mongombe (2012: 79) reported for 3 calls a call type of FM and the following parameters: F_{max}: 44.2 ± 3.4 (40.4 - 47.0) kHz, F_{min}: 38.2 ± 2.6 (35.3 - 40.4) kHz, F_{mean}: 41.2 ± 3.0 (37.9 - 43.7) kHz, F_{knee}: 44.1 ± 3.4 (40.4 - 47.0) kHz, F_{char}: 39.1 ± 2.4 (36.5 - 41.2) kHz, and duration: 1.32 ± 0.11 (1.26 - 1.45) ms.

Two calls by bats from the Kalahari Desert had the following characteristics: F_{char}: 22.9 ± 0.3 kHz, F_{max}: 25.0 ± 0.1 kHz, Fmin: 22.4 ± 0.4 kHz and duration: 5.6 ± 1.5 ms (Adams and Kwiecinski, 2018: 4).

Weier *et al.* (2020: Suppl.) reported on 11 calls from the Okavango River Basin with the following characteristics: F_{max}: 29.69 ± 4.89 kHz, F_{min}: 22.96 ± 1.91 kHz, F_{knee}: 25.46 ± 1.84 kHz, F_{char}: 23.65 ± 1.71 kHz, slope: 35.10 ± 33.29 OPS, duration: 8.54 ± 4.71 ms.

Luo *et al.* (2019a: Supp.) reported the following data (bats leaving their roost): F_{peak}: 23.9 kHz, F_{start}: NA kHz, F_{end}: NA kHz, Band width: NA kHz, and duration: 13.6 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 6 bats: F_{max}: 39.45 ± 8.59 kHz, F_{min}: 26 ± 5.24 kHz, F_{knee}: 30.63 ± 2.69 kHz, F_{char}: 27.92 ± 2.46 kHz, slope: -357.75 ± 2923 OPS, duration: 7.42 ± 4.04 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 14 *Chaerephon pumilus* calls from the Kruger Park (RSA): F_{min}: 22 ± 1.4 (20.1 25.4) kHz, duration: 7.6 ± 2.0 (3.2 10.9) ms, F_{max}: 26.2 ± 4.8 (21.9 36.9) kHz, F_{knee}: 23.7 ± 3.2 (21.3 33.8) kHz, F_{char}: 22.9 ± 2.2 (20.9 29.4) kHz.

Rainho *et al.* (2022: 605) reported on 32 calls froù Sáo Tomé: F_{min}: 24.9 ± 2.7 (19.8 - 29.4) kHz, F_{max}: 36.0 ± 8.7 (24.7 - 51.5) kHz, F_{maxE}: 28.4 ± 2.3 (23.4 - 31.5) kHz, duration: 13.6 ± 3.0 (8.1 - 18.6) ms and interpulse interval: 258.4 ± 156.5 (62.8 - 472.0) ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 26.65 ± 2.53 kHz, F_{max}: 34.87 ± 5.75 kHz and F_{min}: 24.67 ± 2.68 kHz.

For Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 6 calls: Interpulse interval: 118.9 ± 27.4 (87.9 - 160.0) ms; F_{max}: 25.7 ± 4.0 (23.0 - 33.6) kHz; Start slope: -3.1 ± 1.3 (-2.1 - -5.5) kHz/ms; End slope: -3.8 ± 1.3 (-2.1 - -5.3) kHz/ms; Ledge duration: 0.4 ± 0.1 (0.3 - 0.5) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

Molecular Biology:

Karyotype

Đulić and Mutere (1973a), Smith *et al.* (1986), Rautenbach *et al.* (1993) and Sreepada *et al.* (2008) all reported 2*n* = 48, and an acrocentric Y chromosome. However, while Đulić and Mutere (1973a) and Smith *et al.* (1986) reported FN = 58, BA = 12, Rautenbach *et al.* (1993) reported FN = 66, BA = 20. And, while Đulić and Mutere (1973a) and Rautenbach *et al.* (1993) reported a metacentric X chromosome, Smith *et al.* (1986) reported a submetacentric X chromosome. The work of Rautenbach *et al.* (1993) included specimens from the Western Cape that have subsequently been reidentified as *Sauromys petrophilus* (Jacobs and Fenton, 2001: 134), hence these karyotypic variations should be viewed with caution.

For an Ethiopian female, Tolera *et al.* (2021: 125) reported *2n* = 48 and FN = 54. Five pairs were metacentric, 11 pairs acrocentric-subacrocentric and eight pairs acrocentric. The X chromosomes are most likely medium sized metacentrics.

Genetics
See Hoofer and Van Den Bussche (2003).

Reddy (2008: ii) used the cytochrome *b* (845 nucleotides) and D-loop (314 nucleotides) regions of the mitochondrial DNA to assess the phylogenetic relationships within *M. pumilus* (southern Africa) and in relation to "*Chaerephon*" species from Madagascar (*Mops pumilus, M. leucogaster*). The result indicates the possibility of cryptic species in southern African *M. pumilus*, which are closer related to the Malagasy *M. leucogaster* than to the Malagasy *M. pumilus*.

In South Africa, Naidoo *et al.* (2015b) were able to retrieve a strong mitochondrial structure, but only little nuclear genetic structure, which suggests a single interbreeding population. They found these data to be consistent with female philopatry, secondary contact between diverged genetic lineages and introgression.

HABITAT:
Noer *et al.* (2012: 1) found that *M. pumilus* preferred to forage over sugarcane fields rather than over savanna, riparian forest and urban areas. To reach their foraging grounds, they travelled up to 4.2 km from their roost, and their mean activity area encompasses 976 to 1319 ha.

On São Tomé, Castro-Fernandes *et al.* (2024: 2) reported this species to be an open-space forager.

Uusitalo *et al.* (2024: 1, 5) found that the strongest drivers for current environmental suitability fo this species were close proximilty to rivers, higher precipitation during the driest months, sparse vegetation (which is generally linked to urban areas) and a restricted yearly temperature variation. These conditions are currently present in the area south of the central and southern Taita Hills (Kenya). Areas below 750 m or above 1 500 m appeared less suitable for *Mops pumilus*, although this species was found at altitudes higher than 1 500 m.

HABITS:
Bouchard (2001b: 109) found that, in scent-choice-experiments, only males were able to distinguish the gender of conspecifics as well as the difference between roost mates and strangers. Females did not show any preference during these experiments.

Happold and Happold (2023: 127) indicate that these bats can not hover, nor take off from the ground. They must dive at least 1.5 m to have sufficient speed to be able to fly, and they must swoop upward to reduce their speed before landing.

ROOST:
Taylor *et al.* (1999: 67) found these bats to be roosting in a variety of roofs in the Durban area: from corrugated iron to tiles, between the tiles and the plastic lining underneath, or in any convenient crevices between rafters and brickwork. These roofs were located at a height of 3 to 12 m.

In the Mount Nimba area, Monadjem *et al.* (2016y: 367) found a roost in the roof of a school at 540 m.

In Taita-Taveta county (Kenya), Jackson *et al.* (2023: 5) reported 65 roosts in buildings, of which 21 were shared with six other species.

DIET:
Based on DNA analysis of 59 faecal pellets collected between April and May (austral summer) in the Simunye region of Swaziland, Bohmann *et al.* (2011) reported insects from 24 families (belonging to seven orders) being taken as prey. The highest frequency of occurrence was for Lepidoptera (52.5 %), Diptera (40.7 %), and Hemiptera (18.6 %). Within the Lepidoptera, Noctuidae (Owlet moths - 25.4 %), Nymphalidae (Brush-footed butterflies 30.5 %) and Crambidae (Grass moths - 10.2 %) were found the most. Within the Diptera, it were representatives of the Culicidae (Mosquitoes - 27.1 %), which occurred most frequently, followed by the Tephritidae (Fruit flies and kin - 10.2 %). In the Hemiptera, both Lygaeidae (Chinch bugs and seed bugs) and Pentatomidae (Stink bugs) were found in 10.2 % of the faecal pellets.

Naidoo *et al.* (2011: 26) reported the following volume percentages in the bat's diet at Umbilo River (KwaZulu Natal, RSA): in summer: Lepidoptera (9.9 ± 9.5), Coleoptera (47.7 ± 30.5), Hemiptera (32.8 ± 6.9), Diptera (5.4 ± 8.3), and Trichoptera (4.2 ± 7.2); in winter: Lepidoptera (30.3 ± 16.0), Coleoptera (19.5 ± 16.5), Hemiptera (8.0 ± 7.4), Diptera (24 ± 7.7), Trichoptera (6.5 ± 10.4), and Hymenoptera (11.8 ± 11.1).

In the Limpopo province (RSA), Taylor *et al.* (2017b: 246, 252 - 254) found the diet to contain

21 prey items, covering five insect orders: Coleoptera (unmatched), Hemiptera (*Macrorhaphis acuta* + *Nezara viridula* + unmatched), Lepidoptera (*Toxocampinae tathorhynchus* + *Isturgia roraria* + *Sena* sp. + *Sena prompta* + *Cortyta canescens* + *Enmonodia capensis* + *Leucania imperfecta* + *Pericyma atrifusa* + *Rhesala moestalis* + *Spodoptera exigua* + *Maurilia arcuata* + *Stenoptilia* sp. + unmatched), Orthoptera (Tettigoniinae + unmatched) and Blattodea (unmatched). They also remarked that the diet of *C. pumilus* varies geographically.

From Maroua (Cameroon), and based on faecal analyses, Bol A Anong (2013: 31) reported the diet to include Hemiptera (35.60%), Coleoptera (34.81%), Lepidoptera (17.00%), Diptera (10.22%), Hymenoptera (1.55%) and Orthoptera (0.02%).

PREDATORS:
At the Kruger Park, Rautenbach *et al.* (1990: 17) reported that "*Tadarida pumila*" was regularly taken as prey by a pair of African goshawks (*Accipiter tachiro* (Daudin, 1800)). On some occasions, 1 to 5 bats were taken per evening (see Kemp and Rautenbach, 1987).

Mikula *et al.* (2016: Supplemental data) mention the following avian predators for "*Tadarida pumila*": African goshawk (*Accipiter tachiro* (Daudin, 1800)), Fox kestrel (*Falco alopex* (Heuglin, 1861)), Lanner falcon (*Falco biarmicus* Temminck, 1825), Eurasian hobby (*Falco subbuteo* Linnaeus, 1758), Common kestrel (*Falco tinnunculus* Linnaeus, 1758), Wahlberg's eagle (*Hieraaetus wahlbergi* (Sundevall, 1850)), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850), Black kite (*Milvus migrans* (Boddaert, 1783)).

POPULATION:
Structure and Density
The colonies of this species range from a few animals (between 5 and 20) to hundreds of individuals (Mickleburgh *et al.*, 2008dr; IUCN, 2009; Mickleburgh *et al.*, 2014b; Mickleburgh *et al.*, 2019m). There are no estimates of its population in Madagascar, but it is thought to be locally common in the eastern zone. On Aldabra, the population might be fewer than 250 animals.

In Kenya, Lunn *et al.* (2024a: 9) found a relatively balanced male-to-female population composition of 1:1.84.

Trend
2018: Unknown (Mickleburgh *et al.*, 2019m).
2014: Unknown (Mickleburgh *et al.*, 2014b).
2008: Unknown (Mickleburgh *et al.*, 2008dr; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
van der Merwe *et al.* (1986: 355) indicate that in Transvaal *M. pumilus* has an extended breeding of 8 months. They found females to be polyoestrous and could have up to three pregnancies (one young) per breeding season. Implantation only occurs in the right uttering horn and the gestation period was about 60 days. The young are weaned before 21 days of age and females become sexually mature at the age of 5 to 12 months.

Happold and Happold (1989b: 133) found that in Malawi, *Mops pumila* can have up to 5 births per year, all followed by a post-partum oestrus. Happold and Happold (1990b: 568) mention two to four consecutive litters, with births at the end of November, January, March, and May. Females giving birth in November, all had a second litter in January, and 44 % had a third litter in March.

Krutzsch (2000: 95) refers to Marshall and Corbet (1959), who pointed out that in Uganda spermatogenesis was not continuous in all males (as "*Tadarida (Chaerephon) hindei*"). They also indicated that it is one of the best known virtually continuous breeding molossids.

le Grange *et al.* (2011: 173 - 174) indicate that *M. pumilus* is a seasonal polyoestrous bat, which reduces the number of reproductive cycles per season with increasing latitude.

In Ethiopia, Kruskop *et al.* (2016: 61) found a maternity colony with both pregnant and lactating females (one even in both stages) on 9 November 2012.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births in early November, late January and April.

Lunn *et al.* (2024a: 2) report that gestation takes place after 67 to 72 days and the lactation period spans 21 to 28 days.

MATING:
Webber *et al.* (2017: Suppl.) indicate that this species' mating system is polygyny.

McWilliam (1988a) and McCracken and Wilkinson (2000: 331) showed that there is a correlation between the male body size and the harem size, where larger males have larger harems, consisting of up to 21 females). McWilliam (1988a) also suggests that the harem might be kin groups.

PARASITES:

BACTERIUM

Gram-negative bacterium

Cassel-Béraud and Richard (1988), Cassel-Beraud *et al.* (1989: 234), and Sara (2002: 41) reported *Alkalescens dispar*, *Aeromonas hydrophila*, *Citrobacter freundii*, *Enterbacter aerogens*, *Enterobacter agglomerans*, *Enterobacter cloacae*, *Enterobacter intermedius*, *Enterobacter* sp., *Escherichia coli*, *Hafnia alvei*, *Klebsiella oxytoca*, *Klebsiella pneumoniae*, *Kluyvera* sp., *Koserella trabulsii*, *Proteus mirabilis*, *Proteus morganii*, *Proteus rettgeri*, *Proteus vulgaris*, *Providencia* sp., *Pseudomonas* spp., *Salmonella enterica* subsp. *enterica*, *Salmonella enteritidis*, and *Serratia marcescens*.

Kamani *et al.* (2021: 5) reported *Leptospira borgpetersenii* from eight out pf nine Nigerian *Chaerephon pumilus* specimens examined.

APICOMPLEXA

Lainson and Naiff (2000: 128) and Duszynski (2002: 20) indicate that "*Nyctinomus limbatus / C. pumila*" is the type host of *Eimeria dukei* Lavier, 1927.

PROTOZOA

In northern Nigeria, Kamani *et al.* (2022a: Suppl.) found three out of eight examined *Mops* cf. *pumilus* to be infected by *Trypanosoma* cf. *erneyi*.

ARACHNIDA

Laelapidae

Taufflieb (1962: 112) reported *Chelanyssus aethiopious* Hirst, 1921 from "*Tadarida limbata*" from Brazzaville, Congo.

Macronyssidae

Orlova *et al.* (2024: 154) mentioned this species as host for *Chelanyssus aethiopicus* (Hirst, 1921).

Sarcoptidae

Fain (1959e: 149) described *Notoedres (Notoedres) tadaridae* from "*Tadarida (Chaerephon) faini*" from Mount Wago, near Blukwa, Haut-Ituri, DRC.

Trombiculidae

Stekolnikov (2018a: 163) reported *Microtrombicula nyctinomi* (Taufflieb, 1960) from a bat from Brazzaville, Congo.

HEMIPTERA

Cimicidae

Haeselbarth *et al.* (1966: 9) found a great number of *Loxaspis barbara* (Roubaud, 1913) in a roost, near Mopti, Former French Sudan (Haute Senegal-Niger). *Loxaspis miranda* Rothschild, 1912 recorded in Uganda (Haeselbarth *et al.*, 1966: 10, host referred to as "*Tadarida limbata*").

Polyctenidae

Hypoctenes clarus Jordan, 1922, from Congo (Haeselbarth *et al.*, 1966: 18, host referred to as "*Tadarida limbata*"; Szentiványi *et al.*, 2022: 6).

Hypoctenes faini Benoit, 1958 from Kenya (Szentiványi *et al.*, 2022: 6).

DIPTERA

Streblidae

Raymondia seminuda Jobling, 1954 in Nairobi, Kenya (Haeselbarth *et al.*, 1966: 103, host referred to as "*Tadarida faini*").

Nycteribiidae

Basilia ansifera Theodor, 1956 mainly a West African species, reaching Lake Victoria in the east and Lake Nyasa in the south, nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110). *Dipseliopoda biannulate* (Oldroyd, 1953) distributed over the tropical parts of Africa and recorded from localities in Nigeria, Cameroon, the Congo and the Sudan and Kenya (Haeselbarth *et al.*, 1966: 116, host referred to as "*Tadarida faini*"). However, Dick *et al.* (2023: 72) indicate that host-parasite association between "*T. faini*" and *Dipseliopoda biannulata* (Oldroyd, 1953) is most probably erroneous.

SIPHONAPTERA

Ischnopsyllidae

Lagaropsylla consularis Smit, 1957 from Ethiopia, Kenya, Uganda, Congo and Congo (Democratic Republic of), Angola, Zimbabwe and Mozambique (Haeselbarth *et al.*, 1966: 1990, host referred to as "*Tadarida limbata*"), Malawi (Beaucournu and Kock, 1996), Madagascar (Hastriter, 2016: 16). *Lagaropsylla idae* Smit ,1957 widespread in tropical Africa (Haeselbarth *et al.*, 1966: 190, host referred to both "*Chaerephon pumilus*" as well as "*Tadarida limbata*"). *Lagaropsylla oblique* Smit, 1957 from Sierra Leone, Cameroon and the Congo (Haeselbarth *et al.*, 1966: 191, host referred to as "*Tadarida limbata*").

NEMATODA

Durette-Desset and Chabaud (1975: 315) described *Molinostrongylus benexae* from a "*Chaerophon limbatus*" from Périnet, Madagascar.

TREMATODA

Prosthodendrium (Prosthodendrium) chilostomum madagascariense was described by Richard (1966: 423) from a "*Chaerophon limbatus*" from Périnet, Madagascar.

VIRUSES:
Conrardy *et al.* (2014) tested 6 bats sampled in Kenya for the presence of adenoviruses, rhabdoviruses and paramyxoviruses, all samples tested negative.

In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Mops pumilus*: Astroviruses and Coronaviruses.

In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against dengue 2 virus (DENV-2) and non-specific Flaviviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 to 1999, for antibody to SARS-CoV in sera in 35 individuals from Limpopo Province, South Africa, none were tested positive (0/35) and 18 individuals from Mpumalanga Province, South Africa, none tested positive (0/18) and one individual from Bandundu Province, DRC, not tested positive (0/1). Tong *et al.* (2009) report the detection of coronavirus RNA from faecal material of this species in Kenya and was found to be distantly related to the human coronavirus 229E.

Anthony *et al.* (2017b: Suppl.) mention the alpha-coronavirus: Charephon_CoV_KY22. Nziza *et al.* (2019: 156) reported this virus in a rectal swap from a bat from Rwanda. Shapiro *et al.* (2021a: 423) recovered very similar viruses from three bats in Eswatini.

For the two Congos, Kumakamba *et al.* (2021: 7) reported four out of 65 bats to test positive for coronaviruses.

Lane *et al.* (2022: 221) found the following viruses in bats from Ethiopia: Chaerephon bat coronavirus/Kenya/KY22/2006, Chaerephon bat coronavirus/Kenya/KY41/2006, Eidolon bat coronavirus and PREDICT_PMV-24.

Filoviridae
Ebolavirus
EFSA AHAW Panel (EFSA Panel on Animal Health and W (2017: 5) refer to Swanepoel *et al.* (1996), who experimentally inoculated the virus in this bat.

Goldstein *et al.* (2018: 1084) described a new *Ebolavirus* from three Sierra Leonan *Mops pumilus* and one *M. condylurus*: Bomali virus (BOMV). They were sampled in human dwellings in small villages in the Bomali district. This virus might infect humans, but it is not known (yet) whether it is virulent in humans too.

Flaviviridae
Flavivirus
Bukalasa bat virus
Williams *et al.* (1964) report the isolation of the virus in Uganda, 1964, from the salivary glands of *Mops pumilus*. Reported by de Jong *et al.* (2011: 10) and Luis *et al.* (2013: suppl).

Dakar bat virus
Kemp *et al.* (1974) report the isolation of the virus from Nigeria, 1974, from the salivary glands and organ pools of *Mops pumilus*. Reported by de Jong *et al.* (2011: 10) and Luis *et al.* (2013: suppl).

Denque virus
Bonilla-Aldana *et al.* (2020: 3) reported *Chaerephon pumilus* as one of the species which carried this virus.

Entebbe bat virus
Peat and Bell (1970) report the isolation of the virus in Uganda, 1957, from the salivary glands of *M. pumilus*. Reported by de Jong *et al.* (2011: 10).

Zika virus (ZIKV)
Malmlov *et al.* (2019: 2) refer to Shepherd and Williams (1964) who examined 44 *pumilus* specimens in Uganda, of which 16 had antibodies against ZIKV.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 25 Tanzanian *Mops pumilus* specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus). This study was also referred to by Bunuma *et al.* (2025: 6), who indicated that no other studies covering the period 1993 - 2023 wa able to find rabies viruses in Tanzanian bats. Kia *et al.* (2014: 1) tested 33 specimens from Kanke (Nigeria), and found one of them to test positive for Lagos bat virus and one for Shimoni bat virus.

Togaviridae
Alphavirus
de Jong *et al.* (2011: 10) reported Chikungunya virus occurring on *M. pumilus*. Luis *et al.* (2013: suppl.) also reported this virus but used "*Tadarida pumila*" as name for the bat.

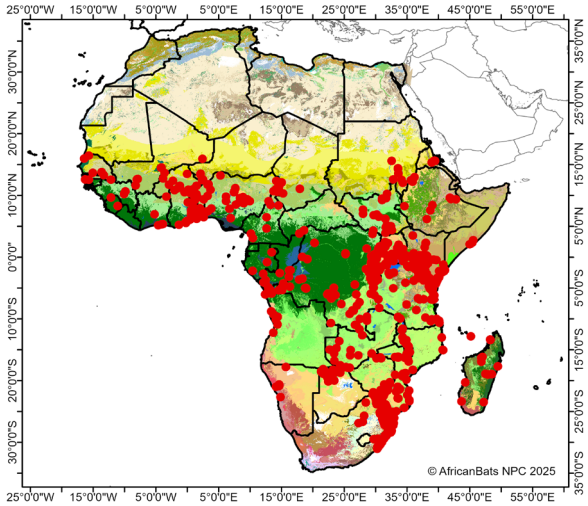

Figure 180. Distribution of *Mops (Chaerephon) pumilus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Equatorial Guinea, Eritrea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Kenya, Madagascar, Malawi, Mali, Mayotte, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Mops (Chaerephon) pusillus (Miller, 1902)

1838.	*Nyctinomus pusilus:* Lesson, Compléments de Buffon, ed 2, Paris, 1: 328. Publication date: 1838. (Lapsus).
1879.	*Nyctinomus pumilus:* Gunther. Publication date: 1879.
*1902.	*Nyctinomus pusillus* Miller, Proc. Biol. Soc. Wash., 15: 245. Publication date: 16 December 1902. Type locality: Seychelles: Aldabra Island. [Goto Description]. Holotype: USNM 20991: ♀, skull and alcoholic. Collected by: Dr. William Louis Abbott. Holotype: USNM 37852: ad ♀, skull and alcoholic. Collected by: Dr. William Louis Abbott. Alcoholic catalogued: 30 June 1893, skull catalogued: 12 February 1900. Poole and Schantz (1942: 120) also mention the number as 20991/37852, and furthermore indicate "Type designated by No. 37852/20997, an error for 20991/37852".
1971.	*Tadarida pumila:* Hayman and Hill. Publication date: 1971.
1981.	*Tadarida (Chaerephon) pumila:* Freeman. Publication date: 1981.
2004.	*Chaerephon pumila:* Louette. Publication date: 2004.
2004.	*Tadarida pumilus:* Louette. Publication date: 2004.
2007.	*Chaerephon pusillus:* Goodman and Ratrimomanarivo. (Name Combination).
2020.	*Mops pusillus:* Simmons and Cirranello, BatNames.org. (Current Combination).
?	*Chaerephon pumila:*
?	*Chaerephon pumilus:*
?	*Mops (Chaerephon) pusillus:* (Current Combination).

TAXONOMY:
Included in *pumilus* by a large number of authors, but its status has been revised by Goodman and Ratrimomanarivo (2007: 391) and Goodman *et al.* (2010a: 21). Naidoo *et al.* (2016: 639) suggested that *pusillus* evolved from the continental *pumilus* ancestor when dispersing over the Mozambique Channel to the Comoro archipelago.

COMMON NAMES:
Czech: morous seychelský. English: Seychelles Free-tailed bat. French: Tadaride des Seychelles. German: Seychellen Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Assessed as Vulnerable (VU D2 ver 3.1 (2001)) as there are only two (2) severely fragmented subpopulations occurring on five island areas (Comoros and Aldabra Atoll). Increasing risk of extreme weather events caused by climate change as well as sea level rise could very quickly affect the species' population, decreasing their numbers substantially and drive the species to a Critically Endangered Status (Bielsa *et al.*, 2020).

Assessment History
Global
2020: VU D2 ver 3.1 (2001) (Bielsa *et al.*, 2020).
2014: LC ver. 3.1 (2001) as a synonym of *Chaerephon pumilus* (Mickleburgh *et al.*, 2014b).

MAJOR THREATS:
Comoros is amongst the countries with the highest rate of deforestation per year, with 3.9% of forests being lost annually (Sewall *et al.*, 2011b; UNDP 2007), and there is very little natural forest remaining (Hawlitscheck *et al.*, 2011). Furthermore, there has been little conservation attention and protection of these forests, which hold a lot of endemic biodiversity (Sewall *et al.*, 2011b). Therefore, it is presumed that a lot of the natural roosting sites of *M. pusillus* have been lost through deforestation.

As a result, this species seems to prefer roosting in non–natural locations, such as under the roofs of buildings. Infrastructure maintenance and renovation is therefore a threat to the majority of their known roosting sites (Goodman *et al.*, 2010a; van Dinther, 2014).

This species is restricted to Aldabra Atoll and the Comoros Archipelago, and it is therefore under threat of climate change related events such as destructive storms. Furthermore, with Aldabra Atoll lying lowly 8m above sea level, they are at risk of losing habitat due to sea level rise (Bielsa *et al.*, 2020).

CONSERVATION ACTIONS:
The Aldabra Atoll is a UNESCO World Heritage Site as well as a Special Reserve (Mickleburgh *et al.*, 1992; Hutson, 2004a) and has been a legally protected special reserve since 1981. Aldabra Atoll is managed by the Seychelles Islands Foundation.

Bielsa *et al.* (2020) report that some local and international organizations such as Dahari, Action Comores and Action Comores International are attempting to mitigate some of the threats of the biodiversity of Comoros, through - for example - reforestation. Nonetheless, unsustainable use of resources continues, mostly due to the population's reliance on their exploitation for fuel wood and farmland.

Currently, there is no monitoring or research of the species underway. Rigorous monitoring is needed to get a population estimate and trend data. Protection and monitoring of known roost sites of both subpopulations is also recommended. Furthermore, as the species has only just been split from *Chaerephon pumilus* in Madagascar and the African continent, and its genus has recently been changed again, more genetic research is likewise recommended (Bielsa *et al.*, 2020).

GENERAL DISTRIBUTION:
M. pusillus was restricted to the Seychelles, but recent molecular work (Goodman *et al.*, 2010a) indicates that the populations on the Comore Islands should assigned to *M. pusillus* and not *M. pumilus*.

Louette (2004) recorded as "*Tadarida pumilus*" occurs on at least three of the Comore Islands (Grande Comore, Anjouan, and Mayotte. Goodman *et al.* (2010c: 126) also recorded "*Charephon pusillus*" from Moheli. Its known elevational range is 15 to 250 m on Grande Comore, 5 to 410 m on Anjouan, 5 to 10 m on Moheli, and 10 to 90 m on Mayotte (Goodman *et al.*, 2010c: 126).

Native: Comoros (Louette, 2004; Goodman *et al.*, 2010c: 126); Seychelles (Goodman *et al.*, 2010c: 126).

GEOGRAPHIC VARIATION:
Based on Cyt *b* analyses, Tidière *et al.* (2022: 1, 7) found a weak, geographically based genetic structure in *Chaerephon pusillus*. The animals from Grande Comore, Mohéli and Anjouan were slightly different from those captured on Mayotte.

ROOST:
On the Comoros, Goodman *et al.* (2010c: 127) did not find a single roost in a natural location, but rather all were synanthropic (see also Wilkinson *et al.*, 2012: 160). The roosts sites were often in the attics of public buildings (schools, civic centres, and hospitals).

MIGRATION:
Goodman *et al.* (2010c: 128) interviewing a director of a primary school on Mitsamiouli mentioned that the presence of bats in the school attic is very seasonal, and as the cold season approaches the site is abandoned.

POPULATION:
Structure and Density
There are only two known subpopulations of this species, on Aldabra Atoll, and on the Comoros Archipelago. Although data are limited, the species is inferred to have a declining population (Bielsa *et al.*, 2020). There is very limited data about the population of *M. pusillus* on Aldabra Atoll. The first specimens identified as *M. pusillus* were collected in 1893 by Abbot (1894). The specimens that were collected and/or examined in later years match the descriptions made of those first collected (Hutson, 2004a). This species of bat has been recorded in three islands from Aldabra Atoll. On Picard, the species has been recorded along and near the settlement (Hill, 1971a; van Dinther, 2014). On Malabar, there is records of them being caught in Middle Camp hut by Passe Horaeau, the eastern channel of the Atoll (SIF photographs). On Grande Terre, the southern island they have been recorded in the Takamaka Grove area (Hill, 1971a), south east of the island and away from the coast, as well as at Anse Mais, in the south west of the island, by the coast (Hill, 1971a; van Dinther, 2014). This is not to say that this species does not occur on Polymnie, the fourth largest island of the Atoll, but merely that it has not yet been recorded there. Polymnie is the island that is least visited on the atoll, with no regular monthly monitoring. *Mops pusillus* is known to fly

as much as 80km between islands in the Comoros (Goodman *et al.*, 2010a), and it is therefore presumed that they occur across the entirety of the Aldabra Atoll.

A roost was found in a tree hollow in 1986 (van Dinther, 2014) by the settlement on Picard, and between 10-20 individuals were seen around Anse Mais, (Grande Terre) between 2013 and 2014 (date not specified) (van Dinther, 2014), suggesting a roost might be nearby. In October 2013, 12 individuals were spotted roosting in the roof of one of the houses at the Settlement, Picard Island (van Dinther, 2014). Counts of individuals leaving and coming back to the roost were done regularly, and by February 2014, the numbers had increased to 38 as a result of breeding. In March 2014, a storm hit the island, and the numbers of individuals roosting under the roof increased to 60 - presumably another roost location had been damaged during the storm and the individuals joined the house roost. By October 2014, when the counts ceased, there were over 100 individuals roosting under the roof (van Dinther, 2014). In June 2018, a roost was again heard in the same house, and monthly monitoring of five (5) houses across the settlement began, where it was believed they might be roosting. The principal roost began with about 100 individuals in June 2018, and had about 150 in November 2018, potentially indicating an increase due to breeding, although no other signs of pupping were recorded. After May 2019, no bats were recorded entering or leaving the roosting site of this house (Sanchez and A'Bear, 2020).

Another roost was identified under the laundry building roof in January 2019, and monthly monitoring began then. At most, this roost was recorded having about 50 individuals, and it was still active in January 2020 when the monitoring ceased (Sanchez and A'Bear, 2020). Bielsa *et al.* (2020) recommends more extensive surveys would need to be carried out on Aldabra Atoll to get a population estimate.

There is also not enough data about the population in the Comoros to have an estimate, but this species is confirmed to occur on all four main islands of the Comoros (Grande Comore, Anjouan, Moheli and Mayotte) (Goodman *et al.*, 2010a). All roosts found during 2006/2007 were in synanthropic locations, with none being found in natural hollows or crevices (Goodman *et al.*, 2010a). It is believed that with wide-scale renovation of infrastructure in Mayotte, a lot of roosts that resided in the old buildings were lost (Goodman *et al.*, 2010c). It is reported that *M. pusillus* and *M. leucogaster* in Mayotte share roosting sites, but molecular and morphological genetic analyses show that they act as good biological species (Goodman *et al.*, 2010a, O'Brian, 2011).

On Aldabra, the population might be fewer than 250 animals (Mickleburgh *et al.*, 2008dr; IUCN, 2009, as "*Chaerephon pumilus*").

Trend
2020: Decreasing (Bielsa *et al.*, 2020)..

REPRODUCTION AND ONTOGENY:
Goodman *et al.* (2010c: 126) provide data that indicates possible inter island seasonal variation in breeding in the Comoros. On 14 November 2006, all of the 10 individuals caught in a colony in central Moroni were female and all reaching term in their pregnancy with single embryos measuring 17 - 20 mm. The same colony was visited on the 28 March 2007, an additional 10 individuals were captured, all of which were females of which five had placental scars, four assumed to be sub-adults without placental scars, and one had a tiny embryo. Juste (unpublished data in Goodman *et al.* (2010c: 127)) report that the site was visited in December 2005, and all of the 20 individuals caught were female. As no males were caught on the two visits with a 5 month difference, Goodman *et al.* (2010c: 127) presumes that this site is a maternity colony.

Between 20 November and 26 November 2006, Goodman *et al.* (2010c: 127) visited five different *M. pusillus* colonies on Anjouan and in contrast to the Moroni site, these colonies contained both males and females. At three of the sites on Anjouan, females outnumbered males with a consistent sex ratio in each case of 0.5, and at one site the sex ratio was 1.0, and the fifth site it was 1.6. Goodman *et al.* (2010c: 127) found at all the colonies, the breeding females were reaching term, with embryos ranging in crown-rump length from 17 - 23 mm, and at one site neonates were present. Of the 25 males captured at the Anjoun sites, all were adult, only seven (28 %) had scrotal testes and convoluted epididymides. The only evidence of non-synchronized breeding in *M. pusillus* on Anjouan was a free-flying animal captured at Patsi on 20 November with a single embryo measuring 1 mm in crown rump length.

Goodman *et al.* (2010c: 127) report on a visit between 28 November and 2 December 2006 that two separate colonies on Moheli were visited and both male and females were captured and the sex ratios were 0.57 and 0.66. At the first colony visited 28 November, of the seven females captured, four had recently given birth and were

lactating and three had single embryos measuring 24 mm in crown-rump length. At the second site visited on the 2 December, all the females were still pregnant with single embryos and with crown-rump length of 19 - 22 mm. Of the males handled from these two colonies, three of 12 (25 %) were in breeding condition with largely scrotal testes with enlarged epididymides.

On Mayotte, between 27 February and 1 March 2007, two colonies were visited and both had males and females, not one of the females showed signs of active reproduction, in several cases the females had remaining lactation tissue and placental scars or large mammae and placental scars, indicating that they had recently terminated a breeding period, also none of the males caught were in reproductive condition (Goodman *et al.*, 2010c). Four different colonies were visited on Grande Comore between 29 March and 1 April 2007, and in all cases, both sexes were found in each and the sex ratio varied from 0.15 to 2.3, with one exception none of the individuals showed active signs of reproduction, although many of the females had large mammae and placental scars. The exception was a female captured on the 29 March in oestrous (Goodman *et al.*, 2010c: 127).

PARASITES:
Lagadec *et al.* (2012: 1696) found this species to be infected by *Leptospira* bacteria.

Hutson (2004a: 130) mentions an endemic ectoparasitic polyctenid bug, *Hypoctenes hutsoni* Maa, 1970.

Dick *et al.* (2023: 73) mentioned the following nycteribiid fly has been found on *Chaerephon pusillus*: *Basilia (Basilia) ansifera* Theodor, 1956.

VIRUSES:
Astroviridae
Hoarau *et al.* (2018: 1) tested 58 bats from the Comoros, found none of them to test positive for this group of viruses.

Coronaviridae
Joffrin *et al.* (2020: 5) reported an Alphacoronavirus from a bat from Mayotte.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 20 individuals from the Comoros using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

Rhabdoviridae
Of the 19 bats from Anjouan that were tested by Mélade *et al.* (2016a: 6), two showed seroreactivity to *Lagos bat lyssavirus*, and two of seven other bats showed the same reaction to *Duvenhage lyssavirus*. On Mayotte, one out of three were positive for these two viruses.

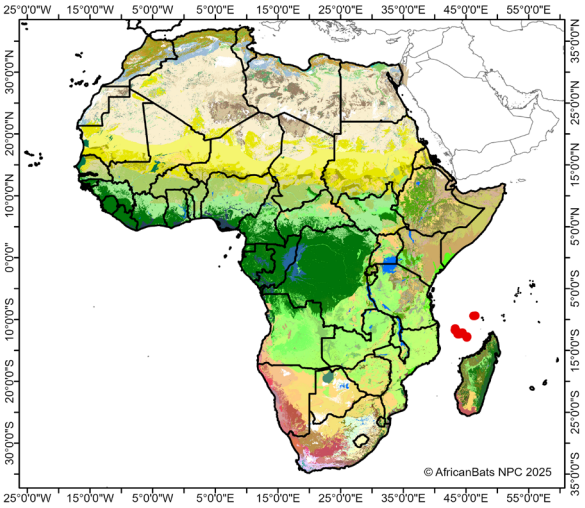

Figure 181. Distribution of *Mops (Chaerephon) pusillus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros, Mayotte, Seychelles.

Mops (Chaerephon) russatus (J.A. Allen, 1917)

*1917. *Chærephon russatus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 458, text fig 25. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Medje [02 25 N 27 18 E, 800 m]. [Goto Description]. Holotype: AMNH 48925: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 8 September 1910; original number: 993. Topotype: MCZ 17386: ♀, skin and skull. Collection date: 8 September 1910. Topotype: MCZ 17387: ♀, skin and skull. Collection date: 8 September 1910.
1989. *Chaerophon russata:* Fenton, Can. J. Zool., 67 (8): 2035. Publication date: 1 August 1989. (Lapsus).
2015. *Chaerophon russatus:* Plumptre, Ayebare, Mugabe, Kirunda, Kityo, Waswa, Matovu, Sebuliba, Behangana, Sekisambu, Mulondo, Mudumba, Nsubuga, Isoke, Prinsloo and Nangendo, Biodiversity surveys of Murchison Falls protected area, 10. Publication date: August 2015. (Lapsus).
2020. *Mops russatus* Simmons and Cirranello, BatNames.org. (Current Combination).
? *Chaerephon russata:* (Alternate Spelling).
? *Chaerephon russatus:* (Name Combination).
? *Mops (Chaerephon) russatus:* (Current Combination).
? *Tadarida russata:* (Name Combination).

TAXONOMY:
See Simmons (2005).

Gregorin and Cirranello (2015: 10) suggest that "*Chaerephon russatus*" is the basalmost branch of the *Chaerephon* + *Mops* clade within the Molossidae.

COMMON NAMES:
Chinese: 赤犬吻蝠. Czech: morous guinejský. English: Russet Wrinkle-lipped bat, Russet Free-tailed Bat. French: Tadaride rousse. German: Rostfarbene Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Mickleburgh *et al.*, 2008bu; IUCN, 2009; Mickleburgh *et al.*, 2019k).

Assessment History
Global
2018: DD ver 3.1 (2001) assessed as *Chaerephon russatus* (Mickleburgh *et al.*, 2019k). 2008: DD ver 3.1 (2001) assessed as "*Tadarida russata*" (Mickleburgh *et al.*, 2008bu; IUCN, 2009). 2004: NT ver 3.1 (2001) assessed as "*Chaerephon russata*" (Mickleburgh *et al.*, 2004aj; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is presumably threatened by habitat loss in parts of its West African range, although further studies are needed to confirm this (Mickleburgh *et al.*, 2008bu; IUCN, 2009; Mickleburgh *et al.*, 2019k).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bu) [in IUCN (2009)] and Mickleburgh *et al.* (2019k) report that there appear to be no direct conservation measures in place. The species has been recorded from the Hell's Gate National Park in Kenya and Tai National Park in Côte d'Ivoire. Further studies are needed into the distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:
Mops russatus has only been recorded from a dozen or so, widely dispersed, localities. It has been recorded from the Tai National Park in Côte d'Ivoire in the west to the Hell's Gate Canyon National Park in Kenya.

Native: Cameroon; Congo (The Democratic Republic of the); Côte d'Ivoire (Beaucournu and Fahr, 2003: 157); Ghana; Guinea (1st record: Decher *et al.*, 2016: 275); Kenya; Uganda (Plumptre *et al.*, 2015: 10).

POPULATION:
Structure and Density
It is believed to be a quite rare species that occurs in small colonies (Mickleburgh *et al.*, 2008bu; IUCN, 2009; Mickleburgh *et al.*, 2019k).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019k). 2008: Unknown (Mickleburgh *et al.*, 2008bu; IUCN, 2009).

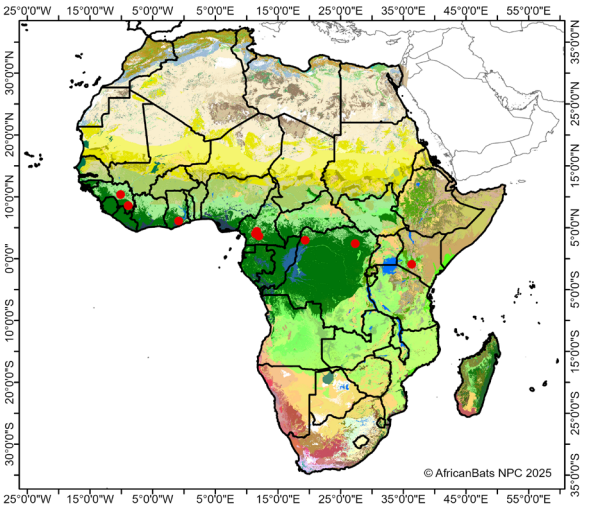

Figure 182. Distribution of *Mops (Chaerephon) russatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Guinea, Kenya.

Mops (Chaerephon) shortridgei (Thomas, 1926)

*1926. *Chaerephon (Lophomops) shortridgei* Thomas, Proc. zool. Soc. Lond., 1926, I: 289. Publication date: 29 April 1926. Type locality: Namibia: NW Ovamboland: 32 mi NW of Rehoboth Mission Station: Ukualukasi [17 32 S 14 37 E, 3 400 ft]. [Goto Description]. Holotype: NHMUK 1925.12.4.24: skin and skull. Collected by: Captain Guy Chester Shortridge; original number: 1389. - Etymology: I have named this striking species in honour of Capt. Shortridge, to whose energy and enthusiasm the great success of the South West African collecting expeditions has been almost wholly due, and who was greatly struck by its remarkable appearance (see Thomas, 1926).

1941. *Chaerephon shortridgei:* J. Eric Hill and Carter, Bull. Am. Mus. Nat. Hist., 78 (1): 57. Publication date: 25 July 1941. (Name Combination).
2023. *Mops shortridgei:* Simmons and Ciranello, Zenodo, 19. Publication date: 8 March 2023. (Name Combination).
? *Mops (Chaerephon) shortridgei:* (Current Combination).

TAXONOMY:
Considered a valid species by Hill and Carter (1941: 57), Peterson *et al.* (1995: 159), Goodman and Cardiff (2004: 236) and Simmons and Cirranello (2023a: 19; 2023b: 19)

COMMON NAMES:
Czech: morous namibijský

CONSERVATION STATUS:
Assessment History
NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004ak; IUCN, 2004).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Namibia.

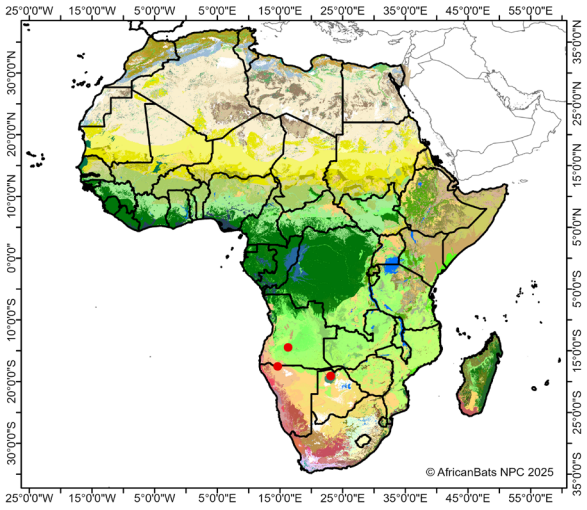

Figure 183. Distribution of *Mops (Chaerephon) shortridgei*.

†*Mops kerio* Gunnell and Manthi, 2018

*2018. *Mops kerio* Gunnell and Manthi, J. Hum. Evol., p "6", fig 6Bj. Publication date: 6 April 2018. Type locality: Kenya: Kanapoi Bat Site [02 18 00 N 36 04 00 E]. Holotype: NMK KP-69821. The holotype consists of a M^2. - Etymology: Referring to the Kerio river that flows through the Kanapoi area (Gunnell and Manthi, 2018: "6").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene (Brown *et al.*, 2019: Suppl.)

Subgenus *Mops (Mops)* Lesson, 1842

*1842. *Mops* Lesson, Nouv. Tabl. Regn. Anim. Mammifères, 18. Publication date: 1842. - Comments: Type species: *Mops indicus* Lesson, 1842 (=*Molossus mops* de Blainville, 1840; Genotype *Mops indicus* Lesson = *Dysopes mops* F. Cuvier; listed in synonymy of *Nyctinomus* by Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 251; but listed as a genus with distinct characters by Thomas, 1913, J. Bombay Nat. Hist. Soc., 22, p. 91). - Etymology: From the masculine German substantive *Mops*, meaning "pug", a small companion dog resembling a bulldog, corresponding to the French "carlin" and the Italian "carlino"; the name refers to the wrinkled lips characteristic of the genus *Mops* and the family Molossidae. According to one seemingly erroneous interpretation, from the Malaysian substantive *mòps*, meaning "bat" (see Lanza *et al.*, 2015: 293). (Current Combination).
1917. *Allomops* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 470, text-fig 12 - 15. Publication date: 29 September 1917 [Goto Description]. - Comments: Type species: *Chærephon (Allomops) osborni* Allen, 1917 (=*Nyctinomus condylurus* A. Smith, 1833).
1951. *Tadarida (Mops):* Ellerman and Morrison-Scott. (Name Combination).
? *Mops (Mops):* (Name Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Chad, Kenya, South Sudan, Tanzania, Uganda.

Mops (Mops) condylurus (A. Smith, 1833)

*1833. *Nyctinomus Condylurus* A. Smith, S. Afr. Quart. J., ser 2, 1 (2): 54. Publication date: November 1833. Type locality: South Africa: KwaZulu-Natal: Port Natal [=Durban], near [29 52 S 31 00 E]. [Goto Description]. - Etymology: From the masculine scientific Latin adjective made up of the masculine Greek substantive "*κονδύλς*" (kóndylos), meaning "knob, knuckle" and the feminine Green substantive "*oúrá*" (ūrá), meaning "tail" as, according to Smith (1833: 54) the tail is "[…] enlarged and wrinkled at the point" (see Lanza *et al.* (2015: 298).

1864. *Dysopes hepaticus* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 31 (7): 14. Type locality: South Sudan: Bahr-el-Ghazal province: Country of the Req natives: Djur River [08 35 19 N 28 26 46 E]. [Goto Description]. - Comments: Meester *et al.* (1986: 74): "Allen (1939a), who regards it as a synony of *bivittata*. Hayman and Hill (1971) regard it as unidentifiable, but point out that Kock (in litt) believes that it probably represents *condylurus*. The latter view is expressed also by Kock (1969a) and Koopman (1975)".

1870. *Nyctinomus angolensis* Peters, J. Sci. mat. phys. nat., ser 1, 3 (10): 124. Publication date: December 1870. Type locality: Angola: Quenza river [= Quanza River] [09 20 S 13 00 E]. [Goto Description]. Holotype: ZMB 4904: ad ♂, skull and alcoholic. Collected by: Toulson (Museum Bocage). Formerly Mus. Bocage; see Turni and Kock (2008: 70). - Comments: Considered a synonym of *leucostigma* by Peterson *et al.* (1995: 168). Roberts (1951: 97), and Ansell and Dowsett (1988: 47) assigned it to Gunther, 1870, 1871. According to Meester *et al.* (1986: 74) "Günther 1871, Zoological Record (1870): 8. Quenza River [="?Cuanza River], Angola. Usually wrongly attributed to Peters, 1870, but see Cabrera and Ruxton, Ann. Mag. Nat. Hist., (9) 17: 595, 1926." According to Peterson *et al.* (1995)? "Kaudern, 1915: Ark. Zool., 9 (18): 77", but Peters, 1870 according to Simmons (2005).

1911. *Chærephon emini* Wroughton, Ann. Mag. nat. Hist., ser 8, 8 (46): 458. Publication date: 1 October 1911. Type locality: Sudan: Rosieres [11 52 N 34 23 E]. - Comments: Not of de Winton, 1901: see Meester *et al.* (1986: 74).

1917. *Chærephon (Allomops) osborni:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 470. Publication date: 29 September 1917. (Name Combination, Lapsus).

1917. *Mops (Allomops) osborni* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 470, 473, text-fig 12 - 14, 26. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Kinshasa (near Leopoldville) [04 18 S 15 18 E, 350 m]. [Goto Description]. Holotype: AMNH 49230: ad ♂, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 22 December 1914; original number: 2570. Paratype: AMNH 49244: ad ♀. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition.

1936. *Mops angolensis wonderi* Sanborn, Field Mus. Nat. Hist., Zool. Ser., (362) 20 (14): 114. Publication date: 15 August 1936. Type locality: Mali: 7 km E Bamako: Sotuba [12 36 N 07 55 W]. [Goto Description]. Holotype: FMNH 42138: ad ♀, skin and skull. Collected by: Frank C. Wonder; collection date: 13 April 1934; original number: 814. - Comments: Considered a valid subspecies by Grubb *et al.* (1998: 93).

1939. *Mops osborni occidentalis* Monard, Arq. Mus. Bocage, 10: 78. Publication date: March 1939. Type locality: Guinea-Bissau: Mansoa [12 04 N 15 19 W]. [Goto Description]. Syntype: MHNG 1326.010: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 234. Syntype: MHNG 861.045: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 215. Syntype: MHNG 861.046: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 217. Syntype: MHNG 861.047: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 218. Syntype: MHNG 861.048: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 225. Syntype: MHNG 861.049: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 228. Syntype: MHNG 923.019: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11 December 1937; original number: 231. Syntype: NMBA 5268: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11-12 December 1937; original number: 226. See Oakeley (1998: 2). From Mansoa (see Monard, 1939: 78). Syntype: NMBA 5269: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11-12 December 1937; original number: 275. See Oakeley (1998: 2). From Mansoa (see Monard, 1939: 78). Syntype: RMCA 15307: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 1937; original number: 223. From Mansoa (see Monard, 1939: 78). Syntype: RMCA 15308: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; original number: 498. From Contubo-el (see Monard, 1939: 78). - Comments: The type locality is either Mansoa [12 04 N 15 19 W], Contubo-el [12 22 N 14 34 W] or Pitche [12 20 N 13 57 W]. Monard (1939: 78) does not mention a holotype, but a series of specimens from Mansoa (14), Cotubo-el (5) and Pitche (9).

1939. *Mops osborni occidentalis f. fulva* Monard, Arq. Mus. Bocage, 10: 80. Publication date: March 1939. Type locality: Guinea-Bissau: Mansoa [12 04 N 15 19 W]. [Goto Description]. Syntype: NMBA 5270: ♀, alcoholic (skull not removed). Collected by: Dr. Albert Monard; collection date: 11-12 December 1937; original number: 232. Monard (1939: 80) mentions a series of 10 specimens (nrs 228 to 237, 5 MM + 5 FF) from Mansoa and 1 M (nr 781) from Pitche. Syntype: RMCA 15309: ♂, alcoholic (skull not removed). Collected by: Dr. Albert Monard; original number: 229. Monard (1939: 78) mentions a larger series: nrs 215 to 227, 275 (13 MM + 1 F from Mansoa); 494 to 498 (1 M + 4 FF) from Contubo-el; 77. - Comments: The type locality is either Mansoa [12 04 N 15 19 W] or Pitche [12 20 N 13 57 W]. Grubb *et al.* (1998: 93) indicate that Monard's quadrinominal name was validated, in accordance with International Code of Zoological Nomenclature Articke 45 (g)(ii)(1), by its use as a trinomial (Freeman (1981b: 159). Monard (1939: 80) mentions a series of 10 specimens (nrs 228 to 237, 5 ♂♂ + 5 ♀♀) from Mansoa and 1 ♂ (nr 781) from Pitche.

1942. *Mops angolensis orientis* G.M. Allen and Loveridge, Bull. Mus. comp. Zool., 89 (4): 151, 166. Publication date: February 1942. Type locality: Tanzania: SE Tanzania, Mtwara, Rovuma river: Kitaya. [Goto Description]. Holotype: MCZ 38829: ad ♂, skin and skull. Collected by: Professor Arthur Loveridge; collection date: 3 April 1939. See Allen and Loveridge (1942: 166). Helgen and McFadden (2001: 146) also mention 9 paratypes (MCZ 38826 - 38828, 38830 - 38835 (4 FF+ 5 MM, skin and skull): see Helgen and McFadden (2001: 145). Paratype: MCZ 38826: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38827: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38828: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38830: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38831: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38832: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38833: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38834: Collected by: Professor Arthur Loveridge. Paratype: MCZ 38835: Collected by: Professor Arthur Loveridge. - Comments: Possibly valid as a subspecies.

1962. *Tadarida angolensis:* Tauffliеb, Bull. Inst. Rech. Sci. Congo, 1: 112. (Name Combination).

1979. *Tadarida condylura:* Ansell, The Puku, 3: 13. (Name Combination).

1981. *Mops osborni fulva:* Freeman, Field. Zool., ns 7: 159. (Name Combination).

2018. *Mops orientis:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Name Combination).

2021. *Mops chondylurus:* Ohimain, Curr. Opin. Pharmacol.. Publication date: 3 August 2021. (Lapsus).
? *Mops (Mops) condylurus:* (Name Combination, Current Combination).
? *Mops angolensis:*
? *Mops condylura angolensis:* (Name Combination, Alternate Spelling).
? *Mops condylura condylura:* (Name Combination, Alternate Spelling).
? *Mops condylura orientis:* (Name Combination, Alternate Spelling).
? *Mops condylura osborni:* (Name Combination, Alternate Spelling).
? *Mops condylurus orientis:* (Name Combination).
? *Mops condylurus osborni:* (Name Combination).
? *Mops condylurus wonderi:* (Name Combination).
? *Mops condylurus:* (Name Combination).
? *Tadarida (Mops) condylura:* (Name Combination).
? *Tadarida condylura condylura:* (Name Combination).
? *Tadarida condylura osborni:* (Name Combination).

TAXONOMY:



Figure 184. An adult female *Mops (Mops) condylurus* caught at Mlawula-NR, Swaziland.

Includes *angolensis* and *leucostigma* but see Peterson *et al.* (1995: 168).

In their analyses, Ammerman *et al.* (2012: 20) found that *Mops condylurus* from clusters with *M. leucostigma* from Madagascar when present, and these two form a close relationship with African *Chaerephon* and not other *Mops*. They also indicate that the two species separated from one another less than 2 million years ago (Ammerman *et al.*, 2012: 23).

COMMON NAMES:

Afrikaans: Angola-losstertvlermuis, Angolase Losstervlermuis. Chinese: 安哥拉犬吻蝠. Czech: morous angolský. English: Angolan Mops Bat, Knob-tailed Mops Bat, Angolan Free-tailed Bat, Knob-tailed Nyctinome. French: Tadaride d'Angola, Molosse d'Angola. German: Angola-Bulldoggfledermaus, Centralafrikanische Doggengrämler. Italian: Carlìno condilùro. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego de cauda livre.

ETYMOLOGY OF COMMON NAME:

Originally described from the former Natal province, it might more appropriately have been called the Natal free-tailed bat, but this name is taken by *Mormopterus acetabulosus*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Gunnell *et al.* (2015a: 20) report on a right distal humerus from a Pleistocene deposit at Olduvai Gorge (Tanzania), which they assigned to *Mops* cf. *M. condylurus*.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008af; IUCN, 2009; Monadjem *et al.*, 2017ab).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Mops condylurus*] (Monadjem *et al.*, 2017ab). 2008: LC ver 3.1 (2001) [assessed as *Tadarida condylura*] (Mickleburgh *et al.*, 2008af; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004aq; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016b). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

There are no major threats to this species. Some colonies roosting within buildings are possibly threatened by general persecution (Mickleburgh *et al.*, 2008af; IUCN, 2009; Monadjem *et al.*, 2017ab).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008af) [in IUCN (2009)] and Monadjem *et al.* (2017ab) report that this species is present in a number of protected areas. No direct conservation actions are currently needed for the species as a whole.

GENERAL DISTRIBUTION:

Mops condylurus is widely distributed over much of sub-Saharan Africa. It ranges from Senegal,

the Gambia and Mali in the west, to the Sudan, Ethiopia and Somalia in the east; from here it ranges southwards through much of eastern and southern Africa, as far south as eastern South Africa and Swaziland. The species appears to be largely absent from the Congo Basin.

Monadjem *et al.* (2010d) does not record any specimens occurring in Namibia.

Besides *Mops condylurus*, Taylor *et al.* (2018b: 63) also mention *Mops* cf. *condylurus* from Angola, whose echolocation calls do not match any known species.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,057,626 km^2. In the RSA, Babiker Salata (2012: 49) found that its distribution is stongly associated with the mean temperature of the coldest quarter.

Native: Angola (Lopes and Crawford-Cabral, 1992; Monadjem *et al.*, 2010d: 543; Taylor *et al.*, 2018b: 62); Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Monadjem *et al.*, 2010d: 543); Burkina Faso (Kangoyé *et al.* (2012: 6025; 2015a: 618); Burundi; Cameroon (Bakwo Fils *et al.*, 2014: 4); Congo (Bates *et al.*, 2013: 336); Congo (The Democratic Republic of the) (Allen, 1917; Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 543); Côte d'Ivoire; Eswatini (Monadjem *et al.*, 2010d: 544, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 141); Gambia (Emms and Barnett, 2005: 50); Ghana; Guinea (Fahr *et al.*, 2006b: 245; Decher *et al.*, 2016: 275); Guinea-Bissau (Seabra, 1900a; Monard, 1939; Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 75); Kenya; Liberia (Fahr, 2007a: 104); Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 823; Monadjem *et al.*, 2010d: 543); Mali; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 543; Monadjem *et al.*, 2010c: 382); Namibia; Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; South Africa (De Graaf, 1960; Monadjem *et al.*, 2010d: 544); Sudan;Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62); Zambia (Monadjem *et al.*, 2010d: 544); Zimbabwe (Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 3422).

Presence uncertain: Madagascar.

Dental Formula:

Dorst (1949: 47-48, fig 2) discussed the milk dentition of this species (as *Mops angolensis*) and indicated that the incisors are quite different from both the canines and premolars, as the prior are tricuspid and the latter are peg-like.

Detailed morphology:

Brain

Amrein *et al.* (2007) from specimens collected from Bénin reported sparse proliferating cell activity, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus, with doublecortin (DCX) they detected young migrating neuron in the subgrannular layer of the hippocampus. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. No NeuroD was detected in the hippocampal granule cells (Amrein *et al.*, 2007).

Functional morphology:

Maloney *et al.* (1999: 385) indicate that *M. condylurus* is well adapted to tolerated high ambivalent temperatures, which may enable them to exploit thermally challenging roost sites and allow them to survive in habitats where less stressful roosts are limited. In some of these roosts, the temperature can reach over 40° C, and the bat's body temperature may exceed 43* C (Bronner *et al.*, 1999: 7; Czenze *et al.*, 2021: 2).

Buffenstein *et al.* (1999: 15) found that urine voided prior to feeding in summer was 22% more concentrated than that in autumn, suggesting that periods of exposure to high temperatures were more stressful. The urine produced was up to eight times more concentrated than plasma.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 18.0 Pa, aspect ratio 9.1 for a wingspan of 36 cm and a wing area of 142 cm^2 and a body mass of 26 g.

Sexual dimorphism:

Chaverri *et al.* (2018: 1944) [referring to Bouchard, 2001b] indicates that the sexes can be distinguished by scent produced from the interaural and muzzle glandular areas.

Echolocation:

Bohmann *et al.* (2011: 1) [referring to Monadjem *et al.* (2010d)] mention peak frequencies between 26 - 35 kHz. Schoeman and Waddington (2011: 291) mention a peak frequency of 24.8 ± 1.5 kHz and a duration of 15.7 ± 2.1 ms for specimens from Durban, South Africa. From the same area, Naidoo *et al.* (2011: 23) mention a F_{peak} of 25.8 ± 0.5 kHz and a duration of 6.8 ± 1.8 ms.

In Swaziland, Taylor *et al.* (2013b: 18) recorded the following parameters for 6 calls: F_{max}: 34.8 ± 2.78 (31.5 - 38.6) kHz, F_{min}: 25.8 ± 1.79 (23.9 - 28.2) kHz, F_{knee}: 30.2 ± 2.16 (27.4 - 32.4) kHz, F_{char}: 27.3 ± 1.98 (24.9 - 29.3) kHz, duration: 5.5 ± 1.40 (3.4 - 7.2) ms. Additional values reported by Monadjem *et al.* (2017c: 179) are: F_{min}: 25.1 ± 1.68 (23.5 - 26.1) kHz, F_{knee}: 30.1 ± 2.03 (28.1 - 32.1) kHz, F_c: 27.3 ± 1.56 (25.9 - 28.8) kHz and duration: 4.3 ± 2.08 (2.2 - 6.4) ms. These calls could be detected up to 30 m away.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 30 (27 - 32) kHz.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg range (RSA): F_{min}: 24 - 28 kHz, F_{char}: 25 - 29 kHz, F_{knee}: 27 - 32 kHz, slope: 40 - 160 OPS, duration: 3 - 7 ms. From the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded 6 calls with: F_{char}: 29.12 ± 0.70 kHz, F_{max}: 30.72 ± 1.52 kHz, F_{min}: 28.45 ± 0.50 kHz, F_{knee}: 29.82 ± 0.97, duration: 15.44 ± 3.78 ms, at 5.57 ± 1.11 calls/sec.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 29.12 ± 0.70 kHz, F_{max}: 30.72 ± 1.52 kHz, F_{min}: 28.45 ± 0.50 kHz.

Five calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 30.74 ± 2.64 kHz, F_{min}: 27.88 ± 4.69 kHz, F_{knee}: 30.12 ± 1.92 kHz, F_{char}: 29.00 ± 1.49 kHz, slope: 11.60 ± 12.27 OPS, duration: 7.09 ± 3.46 ms.

From Maroua, Cameroon, Manga Mongombe (2012: 79) and Bakwo Fils *et al.* (2018: 4) reported for 12 calls a call type of FM and the following parameters: F_{max}: 37.8 ± 3.8 (33.9 - 41.6) kHz, F_{min}: 34.2 ± 4.9 (30.1 - 40.0) kHz, F_{mean}: 36.4 ± 4.5 (31.0 - 41.0) kHz, F_{knee}: 38.2 ± 4.7 (33.9 - 41.5) kHZ, F_{char}: 33.67 ± 5.1 (30.1 - 40.0) kHz, and duration: 0.78 ± 0.89 (0.57 - 0.88) ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 26.7 kHz, F_{start}: NA kHz, F_{end}: NA kHz, Band width: NA kHz, and duration: 10 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 12 bats: F_{max}: 34.5 ± 4.44 kHz, F_{min}: 27.89 ± 3.95 kHz, F_{knee}: 31.59 ± 3.22 kHz, F_{char}: 29.03 ± 2.8 kHz, slope: -480.97 ± 2206.86 OPS, duration: 3.88 ± 1.71 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 26 *Mops condylurus* calls from the Kruger Park (RSA): F_{min}: 25.4 ± 1.4 (22.5 27.2) kHz, Duration: 4.6 ± 1.2 (2.9 8.6) ms, F_{max}: 38.4 ± 4.9 (28.6 45.4) kHz, F_{knee}: 32.3 ± 4.2 (25.5 42.1) kHz, F_{char}: 29.5 ± 3.2 (25.4 37.9) kHz,

101 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 24 - 28 kHz, F_{max}: 32 - 38 kHz, F_{char}: 25 - 29 kHz, F_{knee}: 27 - 32 kHz and duration 4 - 7 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 29.12 ± 0.70 kHz, F_{max}: 30.72 ± 1.52 kHz and F_{min}: 28.45 ± 0.50 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:

Karyotype

Đulić and Mutere (1973a) described the karyotype as having a diploid number of 2*n* = 48, aFN = 56, BA = 10, X = SM, Y = A. While Smith *et al.* (1986) found that the fundamental number was aFN = 66, BA = 20, this is supported by Rautenbach *et al.* (1993). Koubínová (2013: 7) mentioned: 2*n* = 48 and FN = 54.

The karyotype of an Ethiopian female consists of *2n* = 48, FN = 54, including one pair of large metacentrics, four pairs of medium sized metacentrics and 19 pairs of acrocentrics; the X chromosome could be one of the metacentrics (Tolera *et al.*, 2021: 126).

Genetics

See Hoofer and Van Den Bussche (2003).

HABITAT:

Noer *et al.* (2012: 1) indicate that *M. condylurus* prefers to forage over sugarcane fields rather than over savanna, riparian forest and urban areas. They also indicated that the bats travel up to 4.8 km from their roosts during their foraging trips. Their activity area ranges from 1,190 to 1,437 ha.

HABITS:

Bouchard (2001b: 109) found that, in scent-choice-experiments, both males and females were able to distinguish the gender of conspecifics as well as the difference between roost mates and strangers. Chaverri *et al.* (2018: 1944) [referring to Ravel *et al.*, 2010] further indicate that there is an inverse relation between

the number of individuals that can be recognized based on olfactory cues and the size of the colony. This would suggest that recognition is based on individual signatures rather than on group signatures.

ROOST:
In the Mount Nimba area, Monadjem *et al.* (2016y: 368) found a roost in the roof of a school at 540 m.

Bronner *et al.* (1999: 1) investigated the roost microclimates in three man-made structures in South Africa. The ambient temperature in these varied from below 10°C to over 40°C, but the bats preferred zones where the temperature was between 35 and 40°C, where they could maintain their basal metabolic rate.

DIET:
Based on DNA analysis of 30 faecal pellets collected between April and May (austral summer) in the Simunye region of Swaziland, Bohmann *et al.* (2011) reported insects from 24 families (belonging to seven orders) being taken as prey. The highest frequency of occurrence was for Lepidoptera (47.6 %), Diptera (26.7 %), and Hemiptera (20 %). Within the Lepidoptera, Noctuidae (Owlet moths - 23.3 %), Nymphalidae (Brush-footed butterflies - 17.6 %) and Geometridae (Geometer moths - 10 %) were found the most. Within the Diptera, it were primarily representatives of Drosophilidae (Pomace flies - 6.5 %) and Muscidae (House flies and alike - 6.5 %). Within the Hemiptera, Lygaeidae (Chinch bugs and seed bugs) and Pentatomidae (Stink bugs) were found in 6.7 % of the pellets.

From Maroua (Cameroon), and based on faecal analyses, Bol A Anong (2013: 32) reported the diet to include Coleoptera (63.49%), Hemiptera (27.64%), Diptera (7.42%), Lepidoptera (0.05%) and Hymenoptera (0.40%).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention "*Tadarida condylura*" to be preyed upon by: African goshawk (*Accipiter tachiro* (Daudin, 1800)), Eurasian hobby (*Falco subbuteo* Linnaeus, 1758), Wahlberg's eagle (*Hieraaetus wahlbergi* (Sundevall, 1851)), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850).

Bronner *et al.* (1999: 8) reported on the presence of an Eastern Tiger Snake (*Telescopus semiannulatus semiannulatus* Smith, 1849) in a colony of *M. condylurus*.

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008af; IUCN, 2009; Monadjem *et al.*, 2017ab).

In Kenya, Lunn *et al.* (2024a: 9) found a relatively balanced male-to-female population composition of 1:1.08, whereas Happold and Happold (1989b: 136) found a ratio of 2.6:1 in Malawi.

Trend
2016: Unknown (Monadjem *et al.*, 2017ab).
2008: Unknown (Mickleburgh *et al.*, 2008af; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Mutere (1968, 1973b: 271) reported that "*T. condylura*" has a bimodal breeding rhythm in Uganda (pregnancies during December-March and June-September and births in March and September), which is correlated with the rainfall pattern (April-May and October-November), and that the gestation period for this species is about two months. He also indicated [in Krutzsch (2000: 95)] that the testicular position (intra-abdominal or scrotal) showed no significant seasonal variation in sperm production.

Happold and Happold (1990b: 568) reported that in southern Malawi, births occurred early in the wet season and at the end of the wet season and that gestation takes about 1.5 months. Births in mid-Malawi occur earlier and in northern Malawi later.

Happold and Happold (1989b: 133) indicate that "*Tadarida condylura*" is monotocous in Malawi, where it has two births per year. They also found that the interval between births decreases with increasing latitude.

Mutere (1973b) mentioned that the pattern of reproduction is not followed by a postpartum oestrous, whereas Happold and Happold (1989b) mention the opposite.

Wyant and Adams (2007) present data on prenatal growth, development, and skeletal ossification, by integrating data from changes in body size, wing area, and skeletogenesis, from specimens collected from east African countries.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births between early September and early May.

Vierhaus (2011: 295) - referring to Kulzer (2005) - mentioned that females can already reproduce in the second half of their first year. Their

pregnancy takes about 85 days and the young leave their mothers after 50 to 60 days.

PARASITES:

BACTERIA

Höhne *et al.* (1975: 505) found *Listeria monocytogenes* bacteria in two out of 234 "*Tadarida condylura*" specimens from Lomé, Togo.

Studying faecal samples from freshly captured bats, Edenborough *et al.* (2020: 5) found bacteria belonging to Proteobacteria, Bacilli, Firmicutes, Gammaproteobacteria, and Actinobacteria.

One out of 70 Nigerian *Mops condylurus* specimens examined by Kamani *et al.* (2021: 4) was infected by *Leptospira interogans*.

PROTOZOA

Lima *et al.* (2012: 858) described a new species of *Trypanosoma* from Mozambican *Mops condylurus*: *T. (Schizotrypanum) erneyi*. This parasite was also found in two unidentified *Tadarida* specimens. This *Trypanosoma* species, as well as *T. livingstonei*, was reported by Babyesiza *et al.* (2025: 4) in bats from Uganda. They also indicate (p. 5) that *T. erneyi* has a high host specificity for bats of the genera *Tadarida* and *Mops*.

ARACHNIDA

Laelapidae

Taufflieb (1962: 112) reported *Chelanyssus aethiopious* Hirst, 1921 from a "*Tadarida angolensis* [=*Mops osborni*]".

Macronyssidae

Orlova *et al.* (2024: 154) mention this species as host for *Chelanyssus aethiopicus* (Hirst, 1921).

Sarcoptidae

Notoedres tadaridae Fain, 1959 was found by Fain and Aellen (1994: 64) on a "*Tadarida condylura*" specimen from Tandara, DRC.

Trombiculidae

Stekolnikov (2018a: 69, 172) reported *Holubicula toroensis* Daniel and Vercammen-Grandjean, 1985 on a bat from Uganda, and *Microtrombicula tadarida* Vercammen-Grandjean, 1965 on a bat from Rwanda.

HEMIPTERA

Cimicidae

Loxaspis miranda Rothschild, 1912 were found in the hollow trunk of a *Borassus* palm containing many dead *T. condylura*, at the Fambani river, near mouth of Zambesi, in Mozambique (Haeselbarth *et al.*, 1966: 10).

SIPHONAPTERA

Ischnopsyllidae

Lagaropsylla idea Smit, 1957 widespread in tropical Africa (Haeselbarth *et al.*, 1966: 1990; Beaucournu and Kock, 1996). *Lagaropsylla leleupi* Smit, 1957 from Bugesera, Burindi (Haeselbarth *et al.*, 1966: 191). *Lagaropsylla obliqua* Smit, 1957 from Sierra Leone, Cameroon and the Congo (Haeselbarth *et al.*, 1966: 191).

Lagaropsylla incerta (Rothschild, 1900) was reported from Madagascar by Beaucournu and Kock (1996).

VIRUSES:

Astroviridae

Viruses belonging to this family were recorded by Waruhiu *et al.* (2017) from these bats in Kenya, in one (out of 52) tested by Hoarau *et al.* (2018: 2) in Mozambique, and in bats from Guinea (Hermida Lorenzo *et al.*, 2021: 6).

Bornaviridae

Hermida Lorenzo *et al.* (2021: 6) reported Carbovirus from Guinean bats.

Bunyaviridae

Sudi *et al.* (2018: 3) refer to Krüger *et al.* (2015), who reported the presence of Lompole virus (LMPV) in *Mops condylurus* from the DRC (although the latter authors didn't identify the bats involved).

Caliciviridae

Viruses belonging to this family were recorded by Waruhiu *et al.* (2017) from these bats in Kenya.

Coronaviridae - Coronaviruses

SARS-CoV

Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in 19 individuals from Limpopo Province, South Africa, three were tested positive (3/19, 15.8 %) and 96 individuals from Mpumalanga Province, South Africa, 11 tested positive (11/96, 11.9 %) (14/115, 12.2 %).

Anthony *et al.* (2017b: Suppl.) mention the alpha-coronavirus Charephon_CoV_KY22. RNA of the same virus (Chaerephon bat coronavirus/Kenya/KY22/2006) was detected by Suu-Ire *et al.* (2022: 6) in one of 25 tested bats from Ghana. They also found RNA of Kenya bat coronavirus/BtKY56/BtKY55 in four bats and PREDICT_PMV-15 in one bat.

Maganga *et al.* (2020: 5) reported Alphacoronaviruses found in bats from Cameroon, Mozambique and South Africa.

For the two Congos, Kumakamba *et al.* (2021: 7) reported eight out of 105 bats testing positive for coronaviruses.

George *et al.* (2022: 4) found 22.3 % of the *Mops condylurus* specimens they sampled in Nigeria containing RNA of Alphacoronaviruses. George *et al.* (2023: 1) found that these viruses represent a unique subgenus only found in molossid bats.

Filoviridae - Filo viruses
Ebolavirus
Muyembe-Tamfum *et al.* (2012: 9) refer to Pourrut *et al.* (2005) who found ZEBOV-specific antibodies in this species.

Saéz *et al.* (2014) indicate that the two-year old boy, who was patient zero for the 2014 Ebola outbreak in West Africa may have been infected while playing in a hollow tree housing a colony of *M. condylurus*. However, Wood *et al.* (2015: 9-10) find "the suggestion that *Mops condylurus* was the source of infection in the index human case in Guinea noteworthy if somewhat speculative." Additionally, Ouattara and Århem (2021: 19 - 20) convincingly argue that the boy wasn't patient zero and hasn't played near the hollow tree. According to their information, the first patient was a sick woman (from either Sierra Leone or Liberia) seeking treatment in the village and who stayed at the boy's family home. Therefore any link to bats becomes at least unlikely.

Goldstein *et al.* (2018: 1084) described a new *Ebolavirus* from three Sierra Leonan *C. pumilus* and one *Mops condylurus*: Bomali virus (BOMV). They were sampled in human dwellings in small villages in the Bomali district. This virus might infect humans, but it is not known (yet) whether it is virulent in humans too.

Forbes *et al.* (2019: 955) reported this virus from one *M. condylurus* from Kenya (out of 16 *M. condylurus* + 92 other bats collected). Kareinen *et al.* (2021: 3008) found three out of 332 tested Kenyan *condylurus* to be infected by BOMV (two from Busia in the west and one from Taita in the east). Karan *et al.* (2019: 1774) reported this virus from three out of 109 *M. condylurus* bats from Guinea. BOMV RNA was furthermore reported from three female Mozambican bats (Lebarbenchon *et al.*, 2022: 2583).

Bokelmann *et al.* (2021: 1) investigated the replication, tolerance, and persistence of Ebola virus in 10 different primary bat cell isolates from *Mops condylurus* and found that the virus could persist for at least 100 days in lung primary cells, which seems to support the hypothesis that this bat is a likely reservoir for the ebolavirus.

Kareinen *et al.* (2023: 1031) examined a limited number of BOMV-positive bats from Kenya and found no substantial pathologies, suggesting that these bats might act as a reservoir species. Düx *et al.* (2024: 1) found BOMV RNA in Tanzanian *Mops condylurus*, supporting this species' role as a reservoir species.

Riesle-Sbarbaro *et al.* (2024: 2) inoculated 22 wild caught *Mops condylurus* specimens with either EBOV, MARV, REST or TAFV viruses and found some potential for horizontal transmission of EBOV as well as evidence of vertical transmission of this virus. This suggests that *Mops condylurus* might be relevant for the maintenance of entzootic cycles if EBOV.

Flaviviridae
Flavivirus
de Jong *et al.* (2011: 10) reported Bukalasa bat virus, Dakar bat virus, Entebbe bat virus. The latter two are also reported by Luis *et al.* (2013: suppl.), Blitvich and Firth (2017: 3). In Uganda, Kading *et al.* (2018: 3) found neutralizing antibodies against Dengue 2 virus (DENV-2) and non-specific Flaviviruses.

Banzi virus
Gonzalez and Banerjee (2022: 10) mentioned this virus.

Dakar virus
Kemp (1975: 616) mentions that this virus was isolated in Nigeria on *M. condylurus* for the first time on 25 January 1966.

Dengue virus
Bonilla-Aldana *et al.* (2020: 3) reported this bat as one of the bats carrying this virus.

Zika virus (ZIKV)
Malmlov *et al.* (2019: 2) refer to Shepherd and Williams (1964) who examined 36 Ugandan *condylurus* specimens of which 26 had antibodies against ZIKV.

Pegivirus (BPgV)
1 of 10 specimens from the Democratic Republic of Congo examined by Quan *et al.* (2013: Table S5) (10.0 %) was infected by clade G type *Pegivirus*. Of the same 10 specimens, 2 were infected by clade K type

Hantaviridae
Weiss *et al.* (2022: 1) reported a new virus from Angolan (and Tanzanian) bats: Kiwira virus,

which also represents the first hantavirus discovered in this bat species.

Paramxoviridae
Viruses belonging to this family were recorded by Waruhiu *et al.* (2017) from these bats in Kenya.

Hermida Lorenzo *et al.* (2021: 6) identified Lophuromys jeilongvirus, Bat paramyxovirus and Avian avulavirus from Guinean bats.

Hoarau *et al.* (2021: Suppl.) reported them also in bats from Mozambique.

Peribunyaviridae
Orthobunyavirus
Fagre and Kading (2019: 4) report that Bunyamwera virus (BUNV) was found either by virus isolation or molecular/serologic evidence.

Retroviridae
Hermida Lorenzo *et al.* (2021: 6) reported Bat gammaretrovirus, Melomys burtoni retrovirus and Squirrel monkey retrovirus from Guinean bats.

In their overview tables, Maganga *et al.* (2014a: 8) and Willoughby *et al.* (2017: Suppl.) reported that the following viruses were already found on *M. condylurus*: Bukalasa bat virus, Dakar bat virus, Entebbe bat virus, Coronavirus (SARS-CoV), Bunyamwera orthobunyavirus, West Nile virus, Yellow fever virus, Zaïre Ebola, Zika virus.

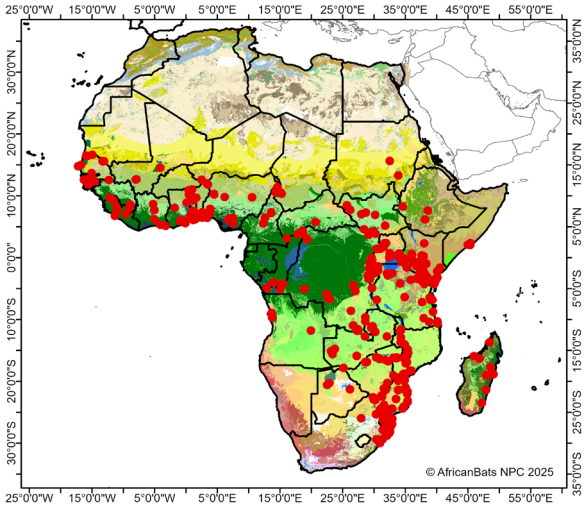

Figure 185. Distribution of *Mops (Mops) condylurus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Mops (Mops) congicus J.A. Allen, 1917

*1917. *Mops congicus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 467, pl 55. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Medje [02 25 N 27 18 E, 800 m]. [Goto Description]. Holotype: AMNH 48893: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 8 September 1910; original number: 966.
? *Mops (Mops) congicus:* (Name Combination, Current Combination).
? *Mops congica:* (Alternate Spelling).
? *Tadarida congica:* (Name Combination).

TAXONOMY:
Does not include *trevori*; see Peterson (1972).

COMMON NAMES:
Czech: morous konžský. English: Medje Mops Bat, Medje Free-tailed Bat, Medje Greater Free-tailed Bat. French: Tadaride de Medje. German: Kongo-Bulldoggfledermaus, Medje-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bp; IUCN, 2009; Monadjem *et al.*, 2017ay).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops congicus*] (Monadjem *et al.*, 2017ay). 2008: LC ver 3.1 (2001) [assessed as *Tadarida congica*] (Mickleburgh *et al.*, 2008bp; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004bx; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is threatened in parts of its range by habitat loss, largely resulting from logging activities and conversion of land to agricultural use

(Mickleburgh *et al.*, 2008bp; IUCN, 2009; Monadjem *et al.*, 2017ay).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bp) [in IUCN (2009)] and Monadjem *et al.* (2017ay) report that it is not known if the species is present in any protected areas. Further studies are needed into the distribution, abundance, natural history, and threats to this poorly known species.

GENERAL DISTRIBUTION:
Mops congicus has been patchily recorded in Central Africa. It is found from southern Cameroon, east into the northern part of the Democratic Republic of the Congo and western Uganda.

Earlier records of this species from Ghana (Koopman, 1993a: 236) and Nigeria (Bergmans, 1977b: 285) are now allocated to *Mops trevori* (Simmons, 2005: 442; Fahr *et al.*, 2006a: 74); Tanshi *et al.*, 2022a: 314).

Native: Cameroon; Congo (The Democratic Republic of the); Uganda.

POPULATION:
Structure and Density
The species has been rarely collected. While a single large colony of approximately several dozen bats has been reported, it is suspected to generally occur in much smaller roosts (Mickleburgh *et al.*, 2008bp; IUCN, 2009; Monadjem *et al.*, 2017ay).

Trend
2016: Unknown (Monadjem *et al.*, 2017ay).
2008: Unknown (Mickleburgh *et al.*, 2008bp; IUCN, 2009).

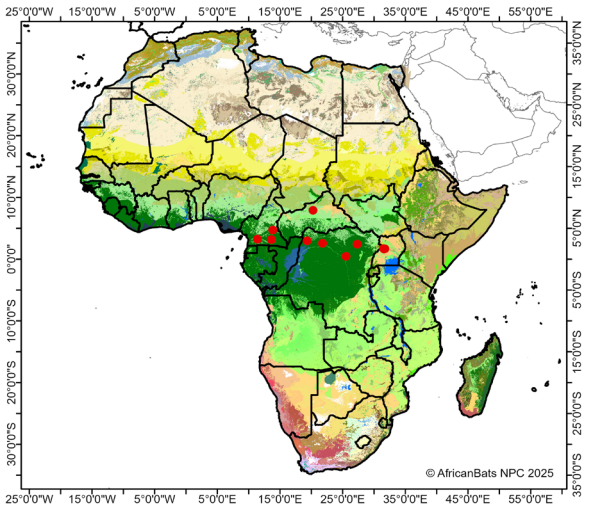

Figure 186. Distribution of *Mops (Mops) congicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Central African Republic, Congo (Democratic Republic of the), Uganda.

Mops (Mops) demonstrator (Thomas, 1903)

*1903. *Nyctinomus demonstrator* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (71): 504. Publication date: 1 November 1903. Type locality: Sudan: Equatoria province: 25 mi (37 km) N of Gondokoro: Mongalla [05 10 N 31 50 E, 500 m]. [Goto Description]. Holotype: NHMUK 1902.7.4.3: ad ♂. Collected by: W.L.S. Loat Esq. Presented/Donated by: W.L.S. Loat Esq.

1917. *Mops (Allomops) faradjius* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 476. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 49222: ad ♂, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 1 November 1913; original number: 3015. - Comments: One of the skull labels mentions 12 January 1913, which probably is an error.

? *Mops (Mops) demonstrator:* (Name Combination, Current Combination).

? *Mops demonstrator:* (Name Combination).

? *Mops demostrator:* (Lapsus).

? *Tadarida (Mops) demonstrator:* (Name Combination).

? *Tadarida demonstrator:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous mongallanský. English: Mongalla Mops Bat, Mongallan Mops Bat, Mongalla Free-tailed Bat. French: Tadaride de Mongalla. German: Mongalla-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bs; IUCN, 2009; Monadjem *et al.*, 2017u).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops demonstrator*] (Monadjem *et al.*, 2017u). 2008: LC ver 3.1 (2001) [assessed as *Tadarida demonstrator*] (Mickleburgh *et al.*, 2008bs; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004az; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
In part of its range this species is threatened by habitat loss, mostly the cutting of larger roosting trees from savanna. It may also be threatened by encroaching desertification in the northern limits of its range (Mickleburgh *et al.*, 2008bs; IUCN, 2009; Monadjem *et al.*, 2017u).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bs) [in IUCN (2009)] and Monadjem *et al.* (2017u) report that this species has been recorded from the Garamba National Park in the Democratic Republic of the Congo (Freeman, 1981b), and may be present in additional protected areas. There is a need to protect suitable large roosting trees in savanna. Further research is needed to better understand the distribution, natural history and major threats to this species.

GENERAL DISTRIBUTION:
Mops demonstrator has been patchily recorded from West Africa (Côte d'Ivoire, Ghana and Burkina Faso) and Central to East Africa (Cameroon, eastern Democratic Republic of the Congo, western Uganda and Sudan).

A record from the Gambia appears to be in error (Koopman, 1989b; Grubb *et al.*, 1998).

Native: Burkina Faso (Kangoyé *et al.*, 2015a: 618); Cameroon; Congo (The Democratic Republic of the); Côte d'Ivoire; Ghana; Sudan; Uganda.

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) reported 2*n* = 48, FN = 54, BA = 8, a submetacentric X chromosome and an acrocentric Y chromosome.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
This species is rarely recorded. Animals are usually found singly or as small groups of up to 12 bats (Mickleburgh *et al.*, 2008bs; IUCN, 2009; Monadjem *et al.*, 2017u).

Trend
2016: Decreasing (Monadjem *et al.*, 2017u). 2008: Decreasing (Mickleburgh *et al.*, 2008bs; IUCN, 2009).

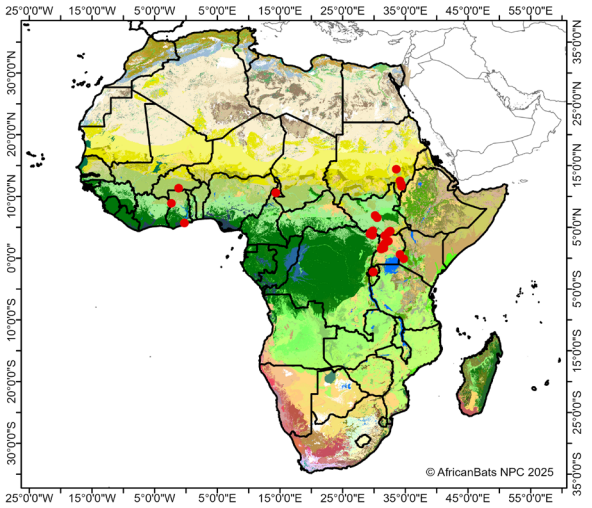

Figure 187. Distribution of *Mops (Mops) demonstrator*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burkina Faso, Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Kenya, Rwanda, South Sudan, Sudan, Uganda.

Mops (Mops) leucostigma (G.M. Allen, 1918)

*1918. *Chaerephon leucostigma* G.M. Allen, Bull. Mus. comp. Zool., 61 (14): 513. Publication date: 27 February 1918. Type locality: Madagascar: Tananarive [=Antananarivo] [18 55 S 47 31 E, 1 300 m]. Holotype: MCZ 16344: ad ♀, skin and skull. Collected by: Dr. Frederik Roelker Wulsin; collection date: December 1915. See Peterson *et al.* (1995: 168); Helgen and McFadden (2001: 145). Paratype: MCZ 16345: ♂, skin and skull. See Helgen and McFadden (2001: 145). - Comments: Ratrimomanarivo *et al.* (2008: 66 - 67) mentions the following: "In his description of *Mops leucostigma*, Allen (1918) cited two specimens - the holotype (MCZ 16344), which was sexed as a 'female' and the paratype (MCZ 16345), which was sexed as a 'male' (also see Helgen & McFadden, 2001). We examined these two specimens. In Allen's description he specifically states, 'The skull is provided with a prominent sagittal crest, which in the type, though partly broken, must have been at least a millimetre high.' This is an accurate description of the MCZ 16344. In members of the genus *Mops* in general (Freeman, 1981) and in *M. leucostigma* specifically (this study), adult males are distinctly larger than adult females and have a prominent and more developed occipital and sagittal crests. Based on size, skull shape, and the development of the occipital and sagittal crests, the holotype is a male and the paratype a female.

Given that all of the collection data for the holotype (MCZ 16344) and paratype (MCZ 16345) are identical, we strongly suspect that the museum labels for these two specimens have been accidentally exchanged before the publication of Allen (1918).".

2018. *Mops leucogaster:* Kemp, López-Baucells, Rocha, Wangensteen, Andriatafika, Nair and Cabeza, Agric. Ecosyst. Environ., 269: 88 (for 2019). Publication date: 1 October 2018. (Lapsus).

? *Mops (Mops) leucostigma:* (Name Combination, Current Combination).

? *Mops condylura leucostigma:* (Name Combination, Alternate Spelling).

? *Mops leucostigma:* (Name Combination).

? *Tadarida (Mops) leucostigma:* (Name Combination).

? *Tadarida leucostigma:* (Name Combination).

TAXONOMY:

Included in *condylurus* by Koopman (1993a: 236), but considered a valid species in *Tadarida (M.)* by Peterson *et al.* (1995: 152) and Russ *et al.* (2001). Considered a valid species in the genus *Mops* by Hutson *et al.* (2001: 34), Goodman and Cardiff (2004: 227), Simmons (2005).

COMMON NAMES:

Czech: morous běloskvrnný. English: Malagasy large white-bellied Free-tailed Bat, Madagascar White-bellied Free-tailed Bat, Malagasy White-bellied Free-tailed Bat, White-shouldered bat. French: Tadaride à queue libre de Madagascar, Grand molosse malgache. German: Gefleckte Bulldoggfledermaus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Gunnell *et al.* (2014: 3) refer to fossils material from the Andrahomana cave on Madagascar.

CONSERVATION STATUS:

Global Justification

This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its large distribution range, and its ability both to tolerate persecution and to persist in a variety of habitats in many parts of its range (Andriafidison *et al.*, 2008m; IUCN, 2009; Monadjem *et al.*, 2017ca).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Mops leucostigma*] (Monadjem *et al.*, 2017ca). 2008: LC ver 3.1 (2001) [assessed as *Tadarida leucostigma*] (Andriafidison *et al.*, 2008m; IUCN, 2009). 2000: DD ver 2.3 (1994).

Regional

None known.

MAJOR THREATS:

In some areas it is hunted for food (Goodman *et al.*, 2008d) or persecuted, but these are not thought to be serious threats (Andriafidison *et al.*, 2008m; IUCN, 2009; Monadjem *et al.*, 2017ca).

CONSERVATION ACTIONS:

Andriafidison *et al.* (2008m) [in IUCN (2009)] report that this species is known from Kirindy CFPF and Parc National de Zombitse-Vohibasia (Goodman *et al.*, 2005a). It is also common in villages adjacent to several protected areas (Goodman *et al.*, 2005a; Russ *et al.*, 2003; Monadjem *et al.*, 2017ca).

GENERAL DISTRIBUTION:

Mops leucostigma is known from Madagascar and the Comoros archipelago (Mohéli and Anjouan islands). On Madagascar it is found from the north to the southwest of the island (Eger and Mitchell, 2003; Peterson *et al.*, 1995) including the islands of Nosy Be and Nosy Komba (Rakotonandrasana and Goodman, 2007: 6). Recorded at an elevation span of 5 to 1,300 m above sea level (Allen, 1918b; Eger and Mitchell, 2003).

Native: Madagascar (Eger and Mitchell, 2003; Peterson *et al.*, 1995; Rakotonandrasana and Goodman, 2007: 6); Comoros (Ratrimomanarivo *et al.*, 2008: 57).

DETAILED MORPHOLOGY:

Baculum

Rakotondramanana and Goodman (2017: 62) describe the baculum as displaying a distinct "m"-shape; length: 0.75 ± 0.097 (0.56 - 0.86) mm, width: 1.09 ± 0.137 (0.83 - 1.35) mm.

FUNCTIONAL MORPHOLOGY:

Amador *et al.* (2019: Suppl.) [referring to Garbutt (2007) and Taylor *et al.* (2012a)] mention a wing loading value of 14.2 Pa, aspect ratio 8.3 for a wingspan of 32 cm and a wing area of 121 cm^2 and a body mass of 18 g.

HABITAT:

Dammhahn and Goodman (2013: 108) indicate that this species' foraging habitat consists of open areas and the area above the forest canopy.

Crowley and Goodman (2025: 4) report it to be widespread in intact and degraded forests, ecotones, agricultural, and urban areas (near forests).

ROOST:
This bat roosts in caves and hollow trees (7 to 25 animals group together) or buildings (group size to 250 bats) (Garbutt, 2022: 96)..

MIGRATION:
Reher *et al.* (2019: 121) found that *M. leucostigma* was only present in the Vintany Cave (southwestern Madagascar) during the rainy season, whereas other species such as *Triaenops menamena* and *Miniopterus mahafaliensis* were present in both the dry and wet season.

DIET:
Rakotondramanana *et al.* (2015: 78) report the following insect orders (by volume percent, by frequency percent): Coleoptera (64.0, 100.0); Lepidoptera (30.0, 100.0); Trichoptera (6.0, 60.0).

Kemp *et al.* (2018: Suppl.) used DNA metacarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Coleoptera, Diptera (*Simulium lineatum* (Meigen, 1804)), Lepidoptera (*Anthozela* sp., *Celsumaria elongata* Brown, 2017, *Spodoptera mauritia* (Boisduval, 1833)), Blattodea, Hemiptera (*Yanga guttulata* (Signoret, 1860)), Ephemeroptera, Sarcoptiformes, Orthoptera, Hymenoptera, Mesostigmata, Trombidiformes, Trichoptera.

Todilahy *et al.* (2022: 127, 130) investigated the diet based on fecal pellets and found representatives of Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, and Diptera. In adult males and juveniles of both sexes, Coleoptera were the most abundant, whereas Hymenoptera formed the main part of the diet in adult females (see also Crowley and Goodman, 2025: 28).

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of two individuals in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

POPULATION:
Structure and Density
The population and local abundance of this species are not known (Andriafidison *et al.*, 2008m; IUCN, 2009; Monadjem *et al.*, 2017ca).

Trend
2016: Unknown (Monadjem *et al.*, 2017ca).
2008: Unknown (Andriafidison *et al.*, 2008m; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Six bats collected at Sarahandrano on 6 May 2021, five were females of which three had large mammae, one had small mammae and the last one was lactating. The male specimen had enlarged testicles and convoluted epididymes.

PARASITES:
ARACHNIDA
Macronyssidae
Orlova *et al.* (2024: 154) mention this species as host for *Chelanyssus aethiopicus* (Hirst, 1921).

SIPHONAPTERA
Ischnopsyllidae
Duchemin *et al.* (2022: 1077) reported the presence of *Lagaropsylla hoogstraali* Smit, 1957 and *Lagaropsylla idae* Smit, 1957.

VIRUSES:
Astroviridae
Three bats from Madagascar were found to harour viruses of this family (Hoarau *et al.*, 2021: Suppl.).

Paramyxoviridae
Specimens from this species tested by Wilkinson *et al.* (2014: 8270) were found to be positive for paramyxoviruses.
11 out of 68 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

Rhabdoviridae
Mélade *et al.* (2016a: 6) tested 20 bats for *Lagos bat lyssavirus* and found positive reactions in two of them.

UTILISATION:
See Goodman *et al.* (2008d).

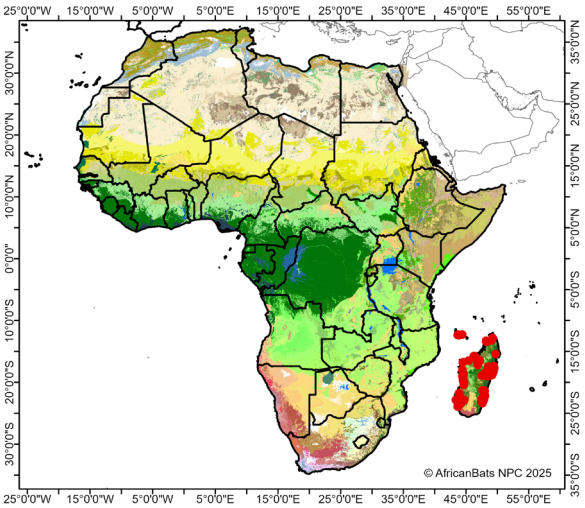

Figure 188. Distribution of *Mops (Mops) leucostigma*.

Comoros, Madagascar.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Mops (Mops) midas (Sundevall, 1843)

*1843. *Dysopes Midas* Sundevall, Kongl. Svenska Vet.-Akad. Hand., ser 3, 30: 207, pl 2, fig 7 [for 1842]. Publication date: 1843. Type locality: Sudan: Blue Nile Province: E-bank White Nile: Valid Sohey [= Wad Shala]: restricted by Turni and Kock (2008: 68). [14 34 N 13 48 E]. [Goto Description]. Syntype: NHMUK 1846.6.2.20: ad ♂, skin and skull. Formerly Stockholm Museum (ZSM no. 523), locality: Bahr el Abiad. See Turni and Kock (2008: 68). Syntype: NRM 590521:; collection date: 1 June 1937. Syntype: NRM 630520:; collection date: 1837. Syntype: ZMB 535: skin only. Collected by: Hedenborg; collection date: 1831 - 1835. From [Dar] Sennar, Sudan; see Turni and Kock (2008: 68). Syntype: ZSM |TS237|: Collected by: Hedenborg; collection date: 1846. See Turni and Kock (2008: 68). Syntype: ZSM |TS612|: skin only. Collected by: Hedenborg; collection date: 1836. See Turni and Kock (2008: 68). - Comments: Horáček *et al.* (2000: 137) mention "Bahr-el-Abiad, White Nile" as type locality. Meester *et al.* (1986: 73): "Bahr-el-Abiad (White Nile), Sudan. Kock (1969a: 154) suggests that the type locality is at Jebel el Funj, between the White and Blue Nile, and Koopman (1975, and in litt.) restricts it to the east (not west, as shown in 1975: 429) bank of the White Nile at 11 45 N 33 30 E, Blue Nile Province, Sudan."). El-Rayah (1980: 264) believes the restriction to Jebel el Funj is incorrect as Sundevall described the type locality as Bahr el-Abiad which is the area south of Omdurman (15 19 N 32 29 E) and commonly known as Bahar Abiad and restricts the type locality to the vicinity of Jebel Aulia (15 19 N 32 31 'E). For a deeper discussion on the type locality, see Turni and Kock (2008: 68). - Etymology: According to a legend the mythological King Midas of Phrygia offended Apollo, so the god turned Midas' ears into those of a donkey, i.e. in very long ears; which in this species are relatively large (see Lanza *et al.*, 2015: 304).
? *Mops (Mops) midas:* (Name Combination, Current Combination).
? *Mops midas:* (Name Combination).
? *Tadarida (Mops) midas:* (Name Combination).
? *Tadarida midas:* (Name Combination).

TAXONOMY:



Figure 189. A female *Mops (Mops) midas* (TM 48104) caught at Makalali Game Reserve, Limpopo Province, South Africa.

Dunlop (1999), following Koopman (1994), recognizes two subspecies: *M. m. midas* (Sundevall 18437) occurring over most of the range and *M. m. miarensis* (Grandidier, 1869) occurring in Madagascar (Peterson *et al.* (1995). Although *miarensi* has previously been considered a subspecies endemic to the island of Madagascar (Simmons (2005), Ratrimomanarivo *et al.* (2007) found no distinctive or taxonomically definitive differences between populations of *Mops midas* occurring on the African continent and Madagascar.

COMMON NAMES:

Afrikaans: Midas se losstertvlermuis, Midas-losstertvlermuis. Chinese: 米达犬吻蝠. Czech: morous oslí. English: Midas Mops Bat, Midas Bat, Midas Free-tailed Bat, Sundevall's Free-tailed Bat, Midas Groove-cheeked Bat. French: Tadaride Midas, Molosse Midas, Tadarida de Midas, Molosse de Midas. German: Midas-Bulldoggfledermaus, Sennaarische Doggengrämler. Italian: Carlìno Mìda. Malawian: Liputiputi, Ndemiya, Namzeze.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

No known fossils (Dunlop, 1999).

CONSERVATION STATUS:

Global Justification

This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread but patchy distribution. The species is locally hunted and persecuted, but it is not thought to be declining fast enough to place it in a higher category of threat (Jenkins *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017ag).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Mops midas*] (Monadjem *et al.*, 2017ag). 2008: LC ver 3.1 (2001) [assessed as *Tadarida midas*] (Jenkins *et al.*, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004ax; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Taylor *et al.*, 2016a). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
This species is thought to be locally threatened by general persecution, collection for food and habitat loss (Jenkins *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017ag).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008a) [in IUCN (2009)] and Monadjem *et al.* (2017ag) report that there is a need to protect large trees and other known roosting sites for this species (this does not apply to populations on Madagascar). In Madagascar, it is known from Beza Mahafaly and Zombitse-Vohibasia National Parks.

GENERAL DISTRIBUTION:
Mops midas is a widespread lowland, savanna species ranging from West Africa eastwards to East Africa and southwards into southern Africa. It has been recorded from the Arabian Peninsula. It is present on Madagascar (including the island of Nosy Be), where it is generally distributed in the drier western and southern habitats of the island below 150 m asl (Ratrimomanarivo *et al.*, 2007). In South Africa, the species' distribution is mostly affected by precipitation seasonality (Babiker Salata, 2012: 49). Taylor *et al.* (2018b: 63) predict that the species might also occur in Angola.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 441,324 km^2.

Native: Benin; Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 544); Burkina Faso (Kangoyé *et al.*, 2015a: 618); Burundi; Central African Republic; Chad; Congo (The Democratic Republic of the); Eritrea (Lavrenchenko *et al.*, 2004b: 133); Eswatini (Shapiro and Monadjem, 2015: "1", Monadjem *et al.*, 2021: 5)): Ethiopia; Gambia; Ghana; Kenya; Madagascar (Peterson *et al.*, 1995; Rakotonandrasana and Goodman, 2007: 6); Malawi (Ansell and Dowsett, 1988: 47; Monadjem *et al.*, 2010d: 544); Mali; Mozambique; Namibia (Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 544); Niger; Nigeria; Rwanda; Saudi Arabia; Senegal; South Africa (Monadjem *et al.*, 2010d: 544); Sudan; Tanzania; Togo; Uganda; Zambia (Ansell, 1973; Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 544); Zimbabwe (Monadjem *et al.*, 2010d: 544).

BIOGEOGRAPHY:
Samonds *et al.* (2012: 5356) indicate that *M. midas* seems to have migrated multiple times between the African continent and Madagascar.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Dunlop (1999).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Dunlop (1999).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 62) describe the baculum as an elongated rod, which has a notable twist to the mid-shaft in a lateral view. The distal tip is rounded, and the proximal tip terminates in a blunt point length: 1.90 ± 0.091 (1.80 - 2.05) mm, width: 0.39 ± 0.058 (0.32 - 0.46) mm.

Other
For a description of the crania, teeth, ears and tragus, and wingshape and aspect ratio see Dunlop (1999).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 11.4 Pa, aspect ratio 8.9 for a wingspan of 46 cm and a wing area of 235 cm^2 and a body mass of 44 g.

SEXUAL DIMORPHISM:
Sexual dimorphism in *M. midas* occurs primarily in the stronger development of the sagittal and lambdoidal crests (Kingdon, 1974; Smithers, 1983; Dunlop, 1999), as well as the greater length and width of the skull (Peterson *et al.*, 1995) in males.

ECHOLOCATION:
See Dunlop (1999) and Taylor (1999b).

In Waterberg, South Africa, Taylor *et al.* (2013b: 18) recorded the following parameters for 6 calls: F_{max}: 14.5 ± 1.45 (12.7 - 16.2) kHz, F_{min}: 12.8 ± 0.82 (11.7 - 13.7) kHz, F_{knee}: 13.8 ± 1.02 (12.5 - 15.0) kHz, F_{char}: 13.1 ± 0.88 (12.0 - 14.0) kHz, duration: 10.3 ± 2.89 (7.8 - 15.8) ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 14 (12 - 15) kHz.

Linden *et al.* (2014: 40) reported the following parameters from the Southpansberg range (RSA): F_{min}: 12 - 14 kHz, F_{char}: 12 - 14 kHz, F_{knee}: 12 - 15 kHz, slope: 32 - 66 OPS, duration: 8 - 16 ms.

At the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded 13 calls: F_{char}: 13.11 ± 1.04 kHz, F_{max}: 14.66 ± 1.46 kHz, F_{min}: 12.33 ± 1.42 kHz, F_{knee}: 13.71 ± 0.98 kHz,

duration: 14.79 ± 3.78 ms, with 4.29 ± 2.73 calls/sec.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 14.23 ± 1.91 kHz, F_{max}: 15.81 ± 2.51 kHz, F_{min}: 13.67 ± 1.83 kHz.

From Swaziland, the following values were reported by Monadjem *et al.* (2017c: 179): F_{min}: 11.8 ± 0.50 (11.3 - 12.5) kHz, F_{knee}: 13.1 ± 1.08 (11.9 - 14.5) kHz, F_c: 12.3 ± 0.72 (11.6 - 13.4) kHz and duration: 14.2 ± 3.89 (9.0 - 20.7) ms.

Weier *et al.* (2020: Suppl.) reported on four calls from the Okavango River Basin with the following characteristics: F_{max}: 18.51 ± 5.52 kHz, F_{min}: 14.78 ± 4.17 kHz, F_{knee}: 16.79 ± 4.44 kHz, F_{char}: 15.27 ± 3.89 kHz, slope: 25.69 ± 20.05 OPS, duration: 10.63 ± 5.28 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 20 bats: F_{max}: 18.69 ± 0.81 kHz, F_{min}: 17.09 ± 2.01 kHz, F_{knee}: 18.39 ± 0.66 kHz, F_{char}: 17.49 ± 0.67 kHz, slope: -120.48 ± 998.33 OPS, duration: 5.67 ± 3.18 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Tabls S1) had a duration of 7.43 ± 1.98 ms, F_{min}: 14.67 ± 1.19 kHz, F_{max}: 16.52 ± 0.80 kHz, F_{knee}: 16.06 ± 0.64 kHz and F_{char}: 15.03 ± 0.62 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 7 *Mops midas* calls from the Kruger Park (RSA): F_{min}: 13.7 ± 1.8 (11.7 17.3) kHz, Duration: 9.6 ± 2.2 (6.0 13.2) ms, F_{max}: 15.8 ± 2.5 (12.8 18.9) kHz, F_{knee}: 14.4 ± 2.0 (12.1 17.9) kHz, F_{char}: 14.2 ± 1.9 (12.1 17.6) kHz, 45 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 12 - 14 kHz, F_{max}: 13 - 16 kHz, F_{char}: 12 - 14 kHz, F_{knee}: 12 - 15 kHz and duration 8 - 16 ms.

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) described the karyotype as having a diploid number of 2*n* = 48, aFN = 66, BA = 20, X = SM, Y = A, this is supported by Rautenbach *et al.* (1993).

HABITAT:
See Dunlop (1999).

HABITS:
See Dunlop, 1999).

ROOST:
See Dunlop (1999).

Happold and Happold (2023: 124) indicate that, in the DRC, these bats roost in groups of about a dozen, whereas in Botswana and Zimbabwe the colony size can reach several hundreds. In Madagascar, colonies in old buildings can contain up to 600 bats (Garbutt, 2022: 96).

MIGRATION:
May make local migrations, as they only appear in parts of their range (northeastern Congo) at the end of the dry season (Allen *et al.*, 1917; Dunlop, 1999).

DIET:
In the Limpopo province (RSA), Taylor *et al.* (2017b: 246, 252 - 254) found 93 prey items spread over seven insect orders: Lepidoptera (100 % [found in all faecal pellets] and covering 17 families: *Synemon austera* + *Talanga sexpunctalis* + *Antaeotricha* sp. + *Elachista* sp. + *Araeopteron* sp. + *Dyops subdifferens* + *Eublemma* sp. + *Peridrome orbicularis* + *Spargaloma sexpunctata* + *Eutelia polychorda* + *Lophoptera* sp. + *Phlegetonia callichroma* + *Acanthovalva inconspicuaria* + *Achrosis pyrrhularia* + *Aethalura punctulata* + *Cabera AH02SA* + *Chiasmia interrupta* + *Ennominae* sp. + *Eupithecia* sp. + *Isturgia arizeloides* + *Isturgia roraria* + *Isturgia pulinda* + *Scopula atricapilla* + *Hyblaea puera* + *Gonometa postica* + *Sena* sp. + *Sena prompta* + *Xenopseustis* sp. + *Acronicta psi* + *Adisura marginalis* + *Athetis ignava* + *Bastilla torrida* + *Bryophila AH01Pe* + *Chasmina lispodes* + *Chasmina* sp. + *Condica parista* + *Copitarsia* + *Cortyta canescens* + *Enmonodia capensis* + *Grammodes stolida* + *Harrisimemna trisignata* + *Heterochroma BioLep767* + *Hypotacha* sp. + *Leucania BioLep10* + *Leucania BioLep162* + *Leucania multilinea* + *Leucania Poole05* + *Leucania porphyrodes* + *Mythimna consanguis* + *Mythimna convecta* + *Mythimna impura* + *Mythimna oxygala* + *Mythimna nigrisparsa* + *Mythimna obsoleta* + *Mythimna* sp. + *Niphonyx segregata* + *Hadenini* sp. + *Ophiusa tirhaca* + *Pandesma robusta* + *Paratrachea laches* + *Pericyma atrifusa* + *Polia piniae* + *Rhesala moestalis* + *Spodoptera exigua* + *Tycomarptes* sp. + *Xanthodes malvae* + *Garella nilotica* + *Maurilia arcuata* + *Meganola dentata* + *Meganola baracoana* + *Pseudosomera noctuiformis* + *Stenoptilia* sp. + *Phycitinae* + *Copaxa lavendera* + *Pseudautomeris irene* + *Agrius convolvuli* + *Cochylidia implicitana* + *Platphalonidia felix* + unmatched), Coleoptera (67 % - *Cybister tripunctatus* + unmatched), Hemiptera (29 % - *Macrorhaphis acuta* + *Nezar viridula* + unmatched), Diptera, Orthoptera (Tettigoniinae), Blattodea (25 % - *Pycnoscelus* sp. + unmatched) and Neuroptera (29 % - unmatched).

PREDATORS:
Malan *et al.* (2022: 167) reported two individuals found in pellets from a South African bat hawk (*Macheiramphus alcinus* Bonaparte, 1850.
The barn owl (*Tyto alba* (Scopoli, 1769)) is another predator (Garbutt, 2022: 96).

POPULATION:
Structure
Verschuren (1957) found females outnumbered males in the roost at a ratio of four to one.

Density
Smithers, 1983) reported *M. midas* roosting in groups of up to several hundred; however, Verschuren, 1957) only recorded groups of 10-20 individuals leaving roosts. In Madagascar, no large colonies have been found and it is thought to be a locally common species with a patchy distribution. The maximum recorded colony was near Amboasary of 600 individuals (Jenkins *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017ag).

Trend
2016: Decreasing (Monadjem *et al.*, 2017ag).
2008: Decreasing (Jenkins *et al.*, 2008a; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
See Dunlop (1999).

REPRODUCTION AND ONTOGENY:
See Dunlop (1999).

Krutzsch (2000: 127) indicates that this species is polyoestrous.

Happold and Happold (1990b: 568) reported that in Malawi, births occur at the end of the wet season.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] suggest that the birth season runs from December to March.

MATING:
See Dunlop (1999).

PARASITES:
ARARCHNIDA
Several mites have been recorded for this species, including *Chelanyssus aethiopicus* (Family Macronyssidae) and *Nycteriglyhus tadaridae* (Family Rosensteiniidae) (Anciaux de Faveaux, 1971; 1976a). Bat fleas (Siphonaptera) have also been recorded (Dunlop, 1999). *Lagaropsylla hoogstraali* (Ischnopsyllidae: Ischnopsyllinae) was found amongst a batch of fleas taken from *M. midas* in the Kruger National Park, South Africa in the Pafuri area (Segerman and Braack, 1988).

Argasidae
Orlova *et al.* (2024: 155) reported this species as host for *Argas vespertilionis* (Latreille, 1802).

SIPHONAPTERA
Ischnopsyllidae
Lagaropsylla hoogstraali Smit, 1957 from Rwanda (Haeselbarth *et al.*, 1966: 190), and Madagascar (Hastriter, 2016: 17).

VIRUSES:
Astroviridae
Hoarau *et al.* (2021: Suppl.) reported one Madagascan bat testing positive for viruses of this family.

Circoviridae
Vidovszky *et al.* (2023: Suppl.) found Bat associated cyclovirus 3 in a DRC bat identified as *Mops* cf. *midas*.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in 15 individuals from Limpopo Province, South Africa, none were tested positive (0/15). One out of two specimens tested by Geldenhuys *et al.* (2013: 517) in Makhado, Limpopo, RSA was found to be positive for CoV.

Positive testing bats were also reported from Madagascar by Hoarau *et al.* (2021: Suppl.).

Lane *et al.* (2022: 221) found PREDICT_CoV-114 and PREDICT_PMV-175 viruses in Ethiopian bats.

Paramyxoviridae
Mélade *et al.* (2016b: 4) tested 19 Madagascan specimens of which one was positive for paramyxoviruses.

UTILISATION:
In Madagascar, Goodman *et al.* (2008d) found that these bats were caught, cooked and then fed to domestic pigs.

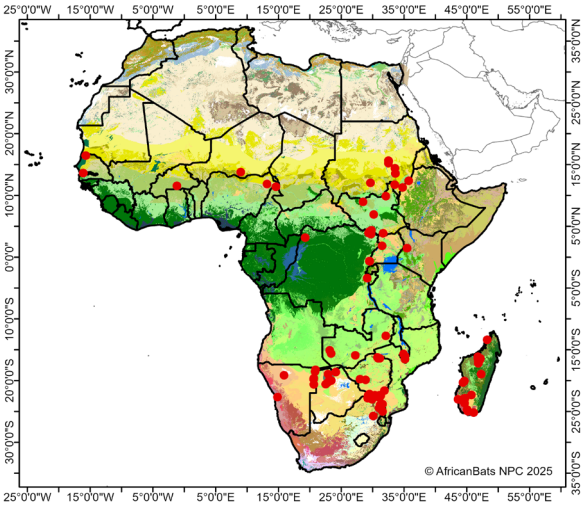

Figure 190. Distribution of *Mops (Mops) midas*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Sudan.

Mops (Mops) midas miarensis (A. Grandidier, 1869)

*1869. *Nyctinomus Miarensis* A. Grandidier, Rev. Mag. Zool., ser 2, 21: 337. Publication date: September 1869. Type locality: Madagascar: between Soua-haze and Soua-hané [sic]: Miari [probably Miary near Tuléar]. [Goto Description]. Holotype: MNHN 29: ad ♀. Holotype: MNHN ZM-MO-1997-1851: ad ♀, alcoholic (skull not removed). Collected by: Alfred Grandidier. See Peterson *et al.* (1995: 174). Number 229 in Rode (1941).

1870. *Nyctinomus unicolor* A. Grandidier, Rev. Mag. Zool., ser 2, 22: 49. Publication date: February 1870. Type locality: Madagascar: "Madagascar". [Goto Description].

? *Mops (Mops) midas miarensis:* (Name Combination, Current Combination).

? *Mops miarensis:* (Name Combination).

? *Mops midas miarensis:* (Name Combination).

GENERAL DISTRIBUTION:
E, SW, S Madagascar.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Mops (Mops) midas midas (Sundevall, 1843)

*1843. *Dysopes Midas* Sundevall, Kongl. Svenska Vet.-Akad. Hand., ser 3, 30: 207, pl 2, fig 7 [for 1842]. Publication date: 1843. Type locality: Sudan: Blue Nile Province: E-bank White Nile: Valid Sohey [= Wad Shala]: restricted by Turni and Kock (2008: 68). [14 34 N 13 48 E]. [Goto Description]. Syntype: NHMUK 1846.6.2.20: ad ♂, skin and skull. Formerly Stockholm Museum (ZSM no. 523), locality: Bahr el Abiad. See Turni and Kock (2008: 68). Syntype: NRM 590521:; collection date: 1 June 1937. Syntype: NRM 630520:; collection date: 1837. Syntype: ZMB 535: skin only. Collected by: Hedenborg; collection date: 1831 - 1835. From [Dar] Sennar, Sudan; see Turni and Kock (2008: 68). Syntype: ZSM |TS237|: Collected by: Hedenborg; collection date: 1846. See Turni and Kock (2008: 68). Syntype: ZSM |TS612|: skin only. Collected by: Hedenborg; collection date: 1836. See Turni and Kock (2008: 68). - Comments: Horáček *et al.* (2000: 137) mention "Bahr-el-Abiad, White Nile" as type locality. Meester *et al.* (1986: 73): "Bahr-el-Abiad (White Nile), Sudan. Kock (1969a: 154) suggests that the type locality is at Jebel el Funj, between the White and Blue Nile, and Koopman (1975, and in litt.) restricts it to the east (not west, as shown in 1975: 429) bank of the White Nile at 11 45 N 33 30 E, Blue Nile Province, Sudan."). El-Rayah (1980: 264) believes the restriction to Jebel el Funj is incorrect as Sundevall described the type locality as Bahr el-Abiad which is the area south of Omdurman (15 19 N 32 29 E) and commonly known as Bahar Abiad and restricts the type locality to the vicinity of Jebel Aulia (15 19 N 32 31 'E). For a deeper discussion on the type locality, see Turni and Kock (2008: 68). - Etymology: According to a legend the mythological King Midas of Phrygia offended Apollo, so the god turned Midas' ears into those of a donkey, i.e. in very long ears; which in this species are relatively large (see Lanza *et al.*, 2015: 304).

? *Mops (Mops) midas midas:* (Name Combination, Current Combination).

? *Mops midas midas:* (Name Combination).

? *Tadarida midas midas:* (Name Combination).

GENERAL DISTRIBUTION:
Continental Africa; Arabia.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Burkina Faso, Cameroon, Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Namibia, Niger, Nigeria, Senegal,

South Africa, South Sudan, Sudan, Uganda, Zambia, Zimbabwe.

Mops (Mops) niangarae J.A. Allen, 1917

*1917. *Mops niangaræ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 468. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Niangara [03 24 N 27 52 E]. [Goto Description]. Holotype: AMNH 48901: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 12 December 1910; original number: 1313. - Etymology: Referring to the locality where the type specimen was found.
? *Mops (Mops) niangarae:* (Name Combination, Current Combination).
? *Mops niangarae:* (Current Spelling).
? *Tadarida congica niangarae:* (Name Combination).

TAXONOMY:
Peterson (1972) and Thorn *et al.* (2009: 68) included this species in *trevori*. Hayman and Hill (1971) listed it as a subspecies of *Tadarida congica* (= *Mops congicus*). Freeman (1981b: 111, 159) considered it a distinct species pending collection of additional specimens.

Additional studies are needed into the systematic status of *Mops niangarae*, especially with regards to its relationship to *M. trevori* (see Hayman and Hill, 1971; Peterson, 1972; Freeman, 1981b; Simmons, 2005).

COMMON NAMES:
Czech: morous niangaranský. English: Niangara Mops Bat, Niangaran Mops Bat, Niangara Free-tailed Bat. French: Tadaride du Niangara. German: Niangara-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy, and lack of recent information on its extent of occurrence, ecological requirements and threats (Mickleburgh *et al.*, 2008bq; IUCN, 2009; Mickleburgh *et al.*, 2014; Mickleburgh *et al.*, 2019l).

Martin *et al.* (2022: Suppl.) point out that this taxon is known from the holotype only, which was collected in 1917, and should possibly be considered as Critically Endangered (Possibly Extinct) or Extinct.

Assessment History
Global
2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019l). 2014: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2014). 2008: DD ver 3.1 (2001) [assessed as *Tadarida niangarae*] (Mickleburgh *et al.*, 2008bq; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004bj; IUCN, 2004). 2002: CR B1+2c (Mickleburgh *et al.*, 2002a: 22). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are currently unknown (Mickleburgh *et al.*, 2008bq; IUCN, 2009; Mickleburgh *et al.*, 2014; Mickleburgh *et al.*, 2019l).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bq) [in IUCN (2009)], Mickleburgh *et al.* (2014) and Mickleburgh *et al.* (2019l) report that it is not known if the species is present in any protected areas. Additional studies are needed into the distribution, natural history and threats to this little-known bat.

GENERAL DISTRIBUTION:
Mops niangarae is known only from the holotype collected from "Niangara, northeastern Belgian Congo" (Democratic Republic of the Congo near the border with Sudan) (Allen *et al.*, 1917; Lang and Chapin, 1917a).

Native: Congo (The Democratic Republic of the) (Allen *et al.*, 1917; Lang and Chapin, 1917a).

POPULATION:
Structure and Density
It is known only from the holotype (Mickleburgh *et al.*, 2008bq; IUCN, 2009; Mickleburgh *et al.*, 2014; Mickleburgh *et al.*, 2019l).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019l). 2014: Unknown (Mickleburgh *et al.*, 2014). 2008: Unknown (Mickleburgh *et al.*, 2008bq; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

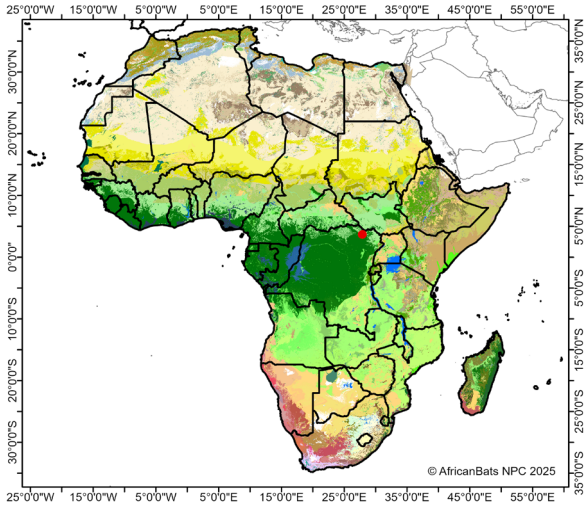

Figure 191. Distribution of *Mops (Mops) niangarae*.

Mops (Mops) niveiventer Cabrera and Ruxton, 1926

*1926. *Mops angolensis niveiventer* Cabrera and Ruxton, Ann. Mag. nat. Hist., ser 9, 17 (103): 594. Publication date: 1 May 1926. Type locality: Congo (Democratic Republic of the): Kasai Occidental province: St. Joseph de Luluabourg [=Kananga] [ca. 05 53 S 22 26 E, 610 m]. [Goto Description]. Holotype: NHMUK 1926.7.6.109: ♀, skin and skull. Collection date: 16 April 1924; original number: 409.

1937. *Mops chitauensis* J.Eric Hill, Am. Mus. Novit., 916: 2, 3, text-fig 1. Publication date: 17 April 1937. Type locality: Angola: Malange district: Chitau [11 15 S 17 01 E, 4 930 ft]. [Goto Description]. Holotype: AMNH 88116: ad ♂, skin and skull. Collected by: Lee S. Bradley and the Phipps-Bradley Expedition; collection date: 10 February 1933; original number: 676.

1975. *Tadarida nivieventer:* Fenton, Life Sci. Occ. Pap., R. Ont. Mus., 104: 23. (Lapsus).

? *Mops (Mops) niveiventer:* (Name Combination, Current Combination).

? *Mops niveiventer:* (Name Combination).

? *Tadarida (Mops) niveiventer:* (Name Combination).

? *Tadarida niveiventer:* (Name Combination).

TAXONOMY:
Koopman (1993a) suggested that *niveiventer* is possibly a subspecies of *demonstrator*. Here considered a distinct species following Simmons (2005).

COMMON NAMES:
Czech: morous sněhobílý. English: White-bellied Mops Bat, White-bellied Free-tailed Bat. French: Tadaride à ventre blanc. German: Weißbauch-Bulldoggfledermaus. Portuguese: Morcego de cauda livre de ventre branco.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Cotterill, 2008f; IUCN, 2009; Monadjem and Cotterill, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops niveiventer*] (Monadjem and Cotterill, 2017c). 2008: LC ver 3.1 (2001) [assessed as *Tadarida niveiventer*] (Cotterill, 2008f; IUCN, 2009). 2004: LC ver 3.1 (2001) (Cotterill, 2004f; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is locally threatened in parts of its range, often through general deforestation and the conversion of suitable habitat by shifting agricultural practices (Cotterill, 2008f; IUCN, 2009; Monadjem and Cotterill, 2017c).

CONSERVATION ACTIONS:
Cotterill (2008f) [in IUCN (2009)] and Monadjem and Cotterill (2017c) report that there appear to be no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. Further studies are needed into the distribution and systematics of this species.

GENERAL DISTRIBUTION:
Mops niveiventer is present in Central Africa and parts of Southern Africa. It has been recorded

from eastern Angola, southern Democratic Republic of the Congo, northern Zambia, Rwanda, northern Mozambique and possibly from Malawi.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 722,774 km^2.

Records from Botswana and Madagascar are definitely *condylurus* (see Hayman and Hill, 1971: 61; Meester *et al.*, 1986: 74; Simmons, 2005).

Native: Angola (Monadjem *et al.*, 2010d: 544); Burundi; Cameroon (Bol A Anong *et al.*, 2011: 48; Bakwo Fils *et al.*, 2014: 4); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 544); Mozambique (Monadjem *et al.*, 2010d: 544); Rwanda; Tanzania; Zambia (Ansell, 1973; Monadjem *et al.*, 2010d: 544).
Presence uncertain: Malawi.

The record from Cameroon is probably doubtful (Jakob Fahr, pers. comm.).

DENTAL FORMULA:
Dorst (1957b: 134) indicated the milk dentition of *Mops angolensis niveiventer* shows some differences with the dentition of *Mops angolensis* he described previously (Dorst, 1949), a fact he attributed to it being a different geographic race. However, the latter form is currently considered to belong to a separate species: *Mops (Mops) condylurus*. The upper milk toothrow of *niveiventer* consists of three functional teeth which are reduced to pegs, and two additional, vestigial teeth. In the lower toothrow there are three incisors of different shape and a remarkably developed canine. There is also one premolar, which is clearly developed, but not functional as it doesn't erupt through the gum. This tooth is resorbed in the young.

ECHOLOCATION:
From Maroua, Cameroon, Manga Mongombe (2012: 79) and Bakwo Fils *et al.* (2018: 4) reported a FM call type for 10 calls and the following parameters: F_{max}: 37.7 ± 2.9 (32.2 - 40.8) kHz, F_{min}: 34.1 ± 2.6 (29.9 - 37.6) kHz, F_{mean}: 35.9 ± 2.8 (31.1 - 39.3) kHz, F_{knee}: 37.6 ± 2.7 (32.1 - 40.8) kHZ, F_{char}: 34.1 ± 2.6 (30.1 - 37.6) kHz, and duration: 0.74 ± 0.10 (0.65 - 0.95) ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 20.3 kHz, F_{start}: NA kHz, F_{end}: NA kHz, Band width: NA kHz, and duration: 8.1 ms.

DIET:
In fecal pellets from Maroua (Cameroon), Bol A Anong (2013: 32) found Coleoptera (64.75%), Hemiptera (25.00%), Diptera (9.53%) and Lepidoptera (0.23%).

POPULATION:
Structure and Density
This is a locally common species that can be found in large colonies of up to hundreds of individuals within buildings, but is more often present in smaller numbers (Cotterill, 2008f; IUCN, 2009; Monadjem and Cotterill, 2017c).

Trend
2016: Unknown (Monadjem and Cotterill, 2017c).
2008: Unknown (Cotterill, 2008f; IUCN, 2009).

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023: 75) mentioned that *Nycteribia schmidlii scotti* Falcoz, 1923 has been found on *Mops niveiventer* from the DRC.

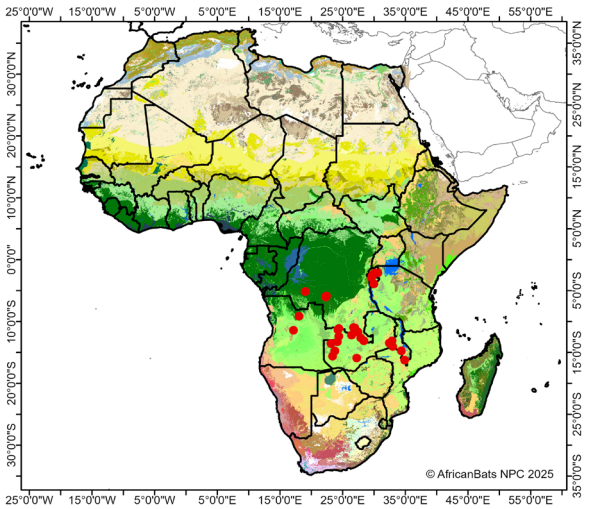

Figure 192. Distribution of *Mops (Mops) niveiventer*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Congo (Democratic Republic of the), Malawi, Mozambique, Rwanda, Zambia, Zimbabwe.

Mops (Mops) trevori J.A. Allen, 1917

*1917. *Mops trevori* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 469, pl 48, fig 2. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 49250: ad ♀, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 29 September 1912;

original number: 1954. - Etymology: In honour of John B. Trevor, a Trustee of the American Museum of Natural History and Chairman of the Committee on African Exploration, whose enthousiasm and generosity in support of the Congo Expedition contributed to its success (see Allen, 1917: 469).
1996. *Mops trevoli:* Kityo and Kerbis, J. East Afr. Nat. Hist., 85: 63. (Lapsus).
? *Mops (Mops) trevori:* (Name Combination, Current Combination).
? *Tadarida trevori:* (Name Combination).

TAXONOMY:
Formerly included in *niangarae*; see Freeman (1981b: 111, 159).

COMMON NAMES:
Czech: morous Trevorův. English: Trevor's Mops Bat, Trevor's Free-tailed Bat, Trevor´s Bat. French: Tadaride d'Allen, Tadaride de Trevor. German: Trevors Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since, although it has been recorded over a very wide area, there are only very few records, and very little is known about its status, threats and habitat requirements (Mickleburgh *et al.*, 2008bv; IUCN, 2009; Mickleburgh *et al.*, 2014a; Mickleburgh *et al.*, 2019e).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019e). 2014: DD ver 3.1 (2001) [assessed as *Mops trevori*] (Mickleburgh *et al.*, 2014a). 2008: DD ver 3.1 (2001) [assessed as *Tadarida trevori*] (Mickleburgh *et al.*, 2008bv; IUCN, 2009). 2004: VU A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004aw; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is generally threatened by habitat loss, resulting from the conversion of land to agricultural use, and the extraction of firewood and timber (Mickleburgh *et al.*, 2008bv; IUCN, 2009; Mickleburgh *et al.*, 2014a; Mickleburgh *et al.*, 2019e).

Siddig (2014: 548) also mentions that the conflicts between Sudan and South Sudan, in combination with droughts play an important role.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bv) [in IUCN (2009)], Mickleburgh *et al.* (2014a) and Mickleburgh *et al.* (2019e) who report that there appear to be no direct conservation measures in place, however, it has been recorded from some protected areas. Further studies are needed into the distribution, natural history and threats to this little-known bat.

GENERAL DISTRIBUTION:
Mops trevori has been patchily recorded in parts of West and Central Africa. In West Africa It has been recorded from Guinea, Côte d'Ivoire, Comoe in Ghana, and Agege in Nigeria. In Central Africa it has been recorded from the Central African Republic, parts of eastern Democratic Republic of the Congo and western Uganda.

Native: Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire; Ghana; Guinea; Nigeria; Sierra Leone (Weber *et al.*, 2019: 28 - first record); Sudan; Uganda (Kityo and Kerbis, 1996: 63).

POPULATION:
Structure and Density
Little is known about the abundance of this apparently rare species, but it is presumed that colony size is likely to be small (Mickleburgh *et al.*, 2008bv; IUCN, 2009; Mickleburgh *et al.*, 2014a; Mickleburgh *et al.*, 2019e).

Trend
2018: Decreasing (Mickleburgh *et al.*, 2019e). 2014: Decreasing (Mickleburgh *et al.*, 2014a). 2008: Decreasing (Mickleburgh *et al.*, 2008bv; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
One of two females reported from Sierra Leone by Weber *et al.* (2019: 28) was pregnant on 25 March.

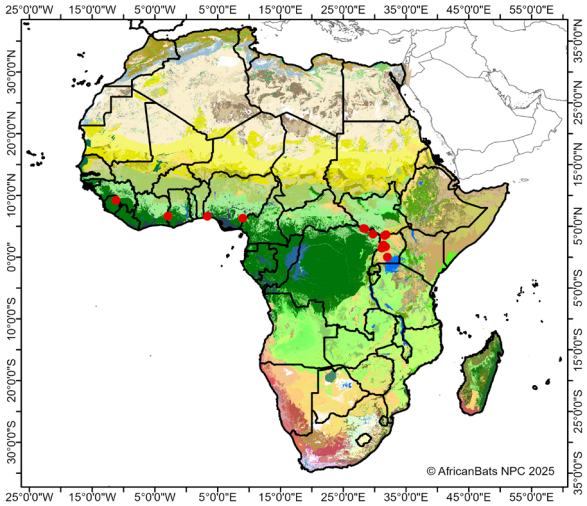

Figure 193. Distribution of *Mops (Mops) trevori*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Nigeria, Sierra Leone, South Sudan, Uganda.

Subgenus *Mops (Ornatomops)* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, 2025

*2025. *Ornatomops* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, Ecol. Evol., 15 (5): 6. Publication date: 14 May 2025. - Etymology: From the Latin word 'ornatus' meaning 'ornament' and and *mops* is from a Malayan word that means 'bat' (Torrent *et al.*, 2025a: 7)...

TAXONOMY:
Torrent *et al.* (2025a: 1) collected a male bat in continental Equatorial Guinea which closely resembled three female specimens of *Mops tomensis* collected on São Tomé. This species was believed to be endemic to that Gulf of Guinea island. These bats showed a major genetic and morphological likeness with *Mops gallagheri* described from the DRC (and which is known from one male specilmen). These features separated them from the other African *Mops* species and resulted in the description of this new subgenus.

Torrent *et al.* (2025a: 9) indicate that this subgenus forms a clade in between *Chaerephon* and *Mops*.

Currently recognized species of the subgenus *Ornatomops* ***gallagheri*** (Harrison,1975); ***tomensis*** (Juste and Ibañez, 1993).

GENERAL DISTRIBUTION:
This subgenus is only known from three localities in Central Africa: São Tomé Island, mainland Equatorial Guinea and the DRC (Torrent *et al.*, 2025a: 9)..

Mops (Ornatomops) gallagheri (Harrison, 1975)

*1975. *Tadarida (Chaerephon) gallagheri* Harrison, Mammalia, 39 (2): 313. Type locality: Congo (Democratic Republic of the): Kivu province: 30 km SW Kindu: Scierie Forest [03 10 S 25 46 E]. [Goto Description]. Holotype: HZM 1.7797: ♂. Collected by: Major Michael Desmond Gallagher; collection date: 14 November 1974; original number: MDB-3256. Holotype: NHMUK 1976.207: ad ♂. Collected by: Major Michael Desmond Gallagher; collection date: 14 November 1974; original number: MDG-3256. Formerly HZM 1.7797. - Etymology: In honour of Major M.D. Gallagher, the collector of the type specimen.
2020. *Mops gallagheri:* Simmons and Cirranello, BatNames.org. (Current Combination).
2025. *Mops (Ornatomops) gallagheri:* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, Ecol. Evol., 15 (4): 6. Publication date: 14 May 2025. (Current Combination).
2025. *Mops Ornatomops gallagheri:* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, Ecol. Evol., 15 (5): 6. Publication date: 14 May 2025. (Lapsus).
? *Chaerephon gallagheri:* (Name Combination).
? *Mops (Chaerephon) gallagheri:* (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous kivuský. English: Gallagher's Wrinkle-lipped Bat, Gallagher's Free-tailed Bat, Zaïre Gland-tailed Bat. French: Tadaride de

Gallagher, Molosse du Zaïre. German: Gallaghers Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Mickleburgh *et al.*, 2008ag; IUCN, 2009; Mickleburgh *et al.*, 2019c).

Assessment History
Global
2018: DD ver 3.1 (2001) assessed as "*Chaerephon gallagheri*" (Mickleburgh *et al.*, 2019c). 2008: DD ver 3.1 (2001) assessed as "*Tadarida gallagheri*" (Mickleburgh *et al.*, 2008ag; IUCN, 2009). 2004: CR D ver 3.1 (2001) (Mickleburgh *et al.*, 2004ai; IUCN, 2004). 2002: CR: B1+2c (Mickleburgh *et al.*, 2002a: 22). 1996: CE (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are unclear. It may be threatened by habitat loss, through the conversion of forest to agricultural use and timber extraction, however, this needs to be confirmed (Mickleburgh *et al.*, 2008ag; IUCN, 2009; Mickleburgh *et al.*, 2019c).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ag) [in IUCN (2009)] and Mickleburgh *et al.* (2019c) report that there are no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. Additional studies are needed into the distribution, abundance, natural history and threats to this poorly known species.

GENERAL DISTRIBUTION:
Mops gallagheri has only been recorded from the type locality of 'Scierie Forest, 30 km of southwest Kindu, Kivu' in the Democratic Republic of the Congo. It may range more widely distributed, however, other surveys in the general area have not recorded this species.

Native: Congo (The Democratic Republic of the) (Gallagher and Harrison, 1977; Harrison, 1975a).

POPULATION:
Structure and Density
There is little information on the abundance of this species (Mickleburgh *et al.*, 2008ag; IUCN, 2009; Mickleburgh *et al.*, 2019c).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019c). 2008: Unknown (Mickleburgh *et al.*, 2008ag; IUCN, 2009).

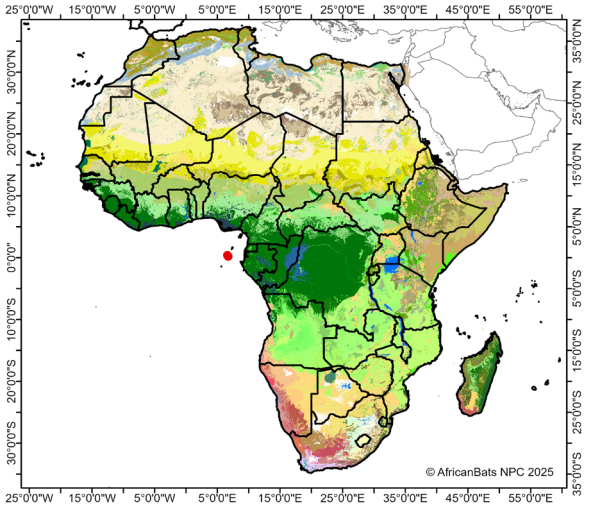

Figure 194. Distribution of *Mops (Ornatomops) gallagheri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

Mops (Ornatomops) tomensis (Juste and Ibáñez, 1993)

*1993. *Tadarida (Chaerephon) tomensis* Juste and Ibáñez, J. Mamm., 74 (4): 901, figs 1 - 2. Publication date: November 1993. Type locality: São Tomé and Príncipe: São Tomé Island: 3 km NW Guadalupe: Praia das Conchas [00 24 N 06 37 E]. [Goto Description]. Holotype: EBD 18256M: ♀, complete skeleton. Collected by: Javier Juste and Antonio Ayong; collection date: 22 April 1988; original number: B7085. Paratype: EBD 17371M: ♀. Collected by: Javier Juste and Carlos J. Ibáñez Uargui; collection date: 11 April 1988. From Agua Izé. Paratype: EBD 17734M: ♀. Collected by: Javier Juste and Antonio Ayong; collection date: 22 April 1988. - Etymology: Referring to the island of São Tomé, where the species occurs.
2020. *Mops tomensis:* Simmons and Cirranello, BatNames.org. (Current Combination).
2025. *Mops (Ornatomops) tomensis:* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, Ecol. Evol., 15 (5): 7. Publication date: 14 May 2025. (Current Combination).
2025. *Mops Ornatomops tomensis:* Torrent, Garin, Aihartza, Méndez-Rodríguez, Alene and Juste, Ecol. Evol., 15 (5): 7. Publication date: 14 May 2025. (Lapsus).
? *Chaerephon tomensis:* (Name Combination).
? *Mops (Chaerephon) tomensis:* (Current Combination).
? *Tadarida tomensis:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous tomášský. English: São Tomé Free-tailed Bat. French: Tadaride de São Tomé. German: São Tomé-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN B1ab(iii) ver 3.1 (2001)) because its extent of occurrence is less than 1000 km^2 (933 km^2), all individuals are in a single location (the island of São Tomé). There is continuing decline in the extent and quality of its lowland habitat (Mickleburgh *et al.*, 2008dl; IUCN, 2009), mainly due to coastal development, including tourism activities, conversion of land to agricultural use and possible port construction (Monadjem *et al.*, 2019d).

Assessment History
Global
2016: EN B1ab(iii) ver 3.1 (2001) assessed as "*Chaerephon tomensis*" (Monadjem *et al.*, 2019d). 2008: EN B1ab(iii) ver 3.1 (2001) assessed as "*Tadarida tomensis*" (Mickleburgh *et al.*, 2008dl; IUCN, 2009). 2004: CR B1ab(I,iii) ver 3.1 (2001) (Mickleburgh *et al.*, 2004cy; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is believed to be threatened by general habitat loss resulting from coastal development, including tourism activities, conversion of land to agricultural use and possible port construction. The possible impact of recent oil extraction activities near the cost is of concern (Monadjem *et al.*, 2019d). The species may be competing with the much more abundant species *Mops pumilus* (J. Juste *pers. comm.,* 2008 in Mickleburgh *et al.*, 2008dl in IUCN, 2009), with further studies into this relationship needed (Mickleburgh *et al.*, 2008dl; IUCN, 2009; Monadjem *et al.*, 2019d)..

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dl) [in IUCN (2009)] and Monadjem *et al.* (2019d) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:
Mops tomensis has been recorded from two lowland localities, Praia das Conchas (3 km NW of Guadalupe) and Agua Izé, in the northern part of São Tomé Island, of São Tomé and Príncipe. Extensive surveys have not located the species elsewhere on the island.

Native: São Tomé and Príncipe [São Tomé] (Rainho *et al.*, 2010a: 40).

ECHOLOCATION:
Rainho *et al.* (2022: 605) reported the following parameters for 26 calls from Sáo Tomé tentatively assigned to this species: F_{min}: 21.0 ± 1.1 (19.0 - 22.4) kHz, F_{max}: 23.0 ± 1.1 (20.4 - 25.5) kHz, F_{maxE}: 22.1 ± 1.0 (19.9 - 24.1) kHz, duration: 16.3 ± 1.7 (12.7 - 19.9) ms and interpulse interval: 350.7 ± 97.2 (137.0 - 558.5) ms.

HABITAT:
On São Tomé, Castro-Fernandes *et al.* (2024: 2) reported this species to be an open-space forager.

POPULATION:
Structure and Density
It seems to be a very rare species that, despite considerable trapping effort, is currently only known from the type series of three specimens (Mickleburgh *et al.*, 2008dl [in IUCN, 2009]; Monadjem *et al.*, 2019d; Rainho *et al.*, 2022: 607).

Trend
2016: Decreasing (Monadjem *et al.*, 2019d). 2008: Decreasing (Mickleburgh *et al.*, 2008dl; IUCN, 2009).

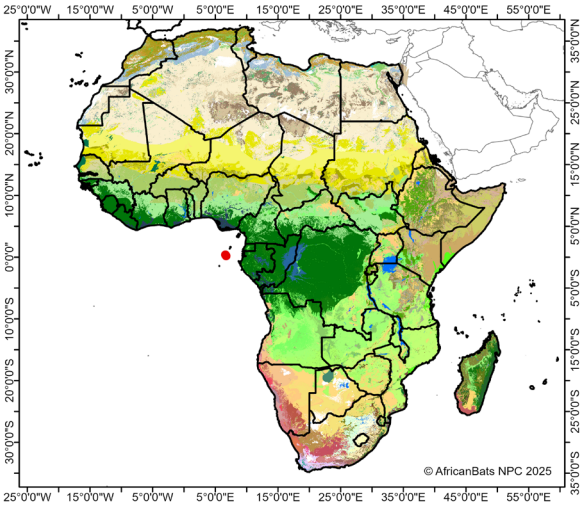

Figure 195. Distribution of *Mops (Ornatomops) tomensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
São Tomé and Príncipe.

†*Mops rusingae* (Arroyo-Cabrales, Gregorin, Schlitter and Walker, 2002)

*2002. *Tadarida rusingae* Arroyo-Cabrales, Gregorin, Schlitter and Walker, J. Vert. Paleont., 22 (2): 382. Type locality: Kenya: Rusinga Island, west; KNM Locality 114 [00 20 S 34 06 E]. [Goto Description]. - Comments: Hiwegi formation; late Early Miocene, ca. 17.5 - 18.0 Ma. - Etymology: The species name is derived from the specific locality where the holotype was collected, Rusinga Island (see Arroyo-Cabrales *et al.*, 2002).
2003. *Tadarida (Mops) rusingae:* Czaplewski, Morgan and Naeher, Acta Chiropt., 5 (1): 65. (Name Combination).
2008. *Mops rusingae:* Van Cakenberghe and Seamark, African Chiroptera Report. Publication date: July 2008. (Name Combination, Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
The holotype was found in the Hiwegi formation; late Early Miocene (Burdigalian - Brown *et al.*, 2019: Suppl.) deposits, dating between 17.5 to 18.0 Mya (Arroyo-Cabrales *et al.*, 2002).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

†*Mops turkwellensis* Gunnell and Manthi, 2018

*2018. *Mops turkwellensis* Gunnell and Manthi, J. Hum. Evol., p"5", "6", fig 6C. Publication date: 6 April 2018. Type locality: Kenya: Kanapoi Bat Site [02 18 00 N 36 04 00 E]. Holotype: NMK KP-69820. The holotype consists of a left M^2. - Etymology: Referring to the Turkwell river, which flows into Lake Turkana north of Kanapoi (Gunnell and Manthi, 2018: "6").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene (Brown *et al.*, 2019: Suppl.)

Subgenus *Mops (Xiphonycteris)* Dollman, 1911

*1911. *Xiphonycteris* Dollman, Ann. Mag. nat. Hist., ser 8, 7 (38): 210. Publication date: 1 February 1911 [Goto Description]. - Comments: Type species: *Xiphonycteris spurrelli* Dollman, 1911.
? *Mops (Xiphonycteris):* (Name Combination, Current Combination).
? *Tadarida (Xiphonycteris):* (Name Combination).

TAXONOMY:
Currently recognized species: ***bakarii*** Stanley, 2008, ***brachypterus*** (Peters, 1852), ***nanulus*** J. A. Allen, 1917, ***petersoni*** (El Rayah, 1981), ***spurrelli*** (Dollman, 1911) and ***thersites*** (Thomas, 1903).

Mops (Xiphonycteris) bakarii Stanley, 2009

*2008. *Mops bakarii* Stanley, Acta Chiropt., 10(2): 184, Figs 2 -6. Publication date: December 2008. Type locality: Tanzania: Pemba Island, Kipangani Village: in attic of hospital [4.96487 S 39.71456 E, 12m]. Holotype: FMNH 192895: ad ♂, skin and skull. Collected by: William ("Bill") T. Stanley; collection date: 5 August 2006; original number: WTS 7307. Paratype: FMNH 192824: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7312. Paratype: FMNH 192825: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7313. Paratype: FMNH 192826: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7327. Paratype: FMNH 192827: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7328. Paratype: FMNH 192828: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7329. Paratype: FMNH 192829: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7335. Paratype: FMNH 192830: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7336. Paratype: FMNH 192831: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7337. Paratype: FMNH 192832: ad ♀. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7338. Paratype: FMNH 192833: ad ♀. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7339. Paratype: FMNH 192834: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7345. Paratype: FMNH 192835: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7347. Paratype: FMNH 192836: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7348. Paratype: FMNH 192894: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7306. Paratype: FMNH 192896: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7308. Paratype: FMNH 192897: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7322. Paratype: FMNH 192898: ad ♂.

Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7331. Paratype: FMNH 192899: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7332. Paratype: FMNH 192900: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7333. Paratype: FMNH 192901: ad ♂. Collected by: William ("Bill") T. Stanley; collection date: 5 - 6 August 2006; original number: WTS 7334. - Etymology: In honour of Dr. Bakari Asseid, director of the Department of Commercial Crops, Fruits and Forestry, Zanzibar, to recognize his significant contributions to the conservation of natural habitats and biota of Zanzibar (including both Pemba and Unguja Islands) (see Stanley, 2008: 185).

? *Mops (Xiphonycteris) bakarii:* (Name Combination, Current Combination).

COMMON NAMES:
Czech: morous Stanleyův. German: Bakaris Bulldoggfledermaus, Pemba-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Shapiro (2017) report this species is listed as Data Deficient due to only one known locality and lack of further data, while population size is not known.

Assessment History
Global
2016: DD ver. 3.1 (2001) [assessed as *Mops bakarii*] (Shapiro, 2017).

Regional
None known.

MAJOR THREATS:
Specific threats to this species are known at present (Shapiro, 2017).

CONSERVATION ACTIONS:
Shapiro (2017) report there are no specific conservation measures are in place for this species.

GENERAL DISTRIBUTION:
O'Brien (2011: 288) reports it from Pemba.

POPULATION:
Structure and Density
There is no information about the species population size and population trend (Shapiro, 2017).

Trend
2016: Unknown (Shapiro, 2017).

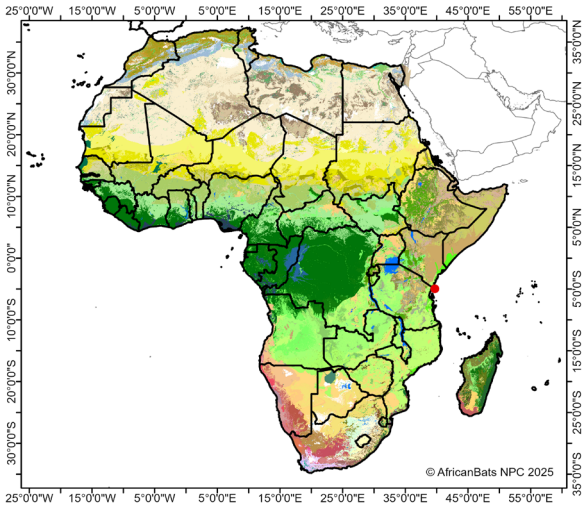

Figure 196. Distribution of *Mops (Xiphonycteris) bakarii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Tanzania.

Mops (Xiphonycteris) brachypterus (Peters, 1852)

*1852. *Dysopes brachypterus* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 59, pl 15, fig 1. Publication date: 1852. Type locality: Mozambique: Mozambique Island [15 03 S 40 46 E]. [Goto Description]. Holotype: ZMB 536/85537: ad ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008) [skin: ZMB 536 + skull: ZMB 85537 (=An 16356)]. Neotype: ROM 46721: ad ♂, skin and skull. Collected by: Terence Michael Shortt and A.E. Williams; collection date: 24 June 1968; original number: SG301. - Etymology: From the Greek adjective "*βραχύς*" (brakhìs), meaning "short" and the Greek neuter substantive "*πτερόν*" (pteròn), meaning "wing"; but actually the species' wings are not particularly short (see Lanza *et al.*, 2015: 295).

1877. *Nyctinomus [(Nyctinomus)] brachypterus:* Dobson, Proc. zool. Soc. Lond., 1876, IV: 722. Publication date: April 1877. (Name Combination).

1908. *Nyctinomus leonis* Thomas, Ann. Mag. nat. Hist., ser 8, 2 (10): 373. Publication date: 1 October 1908. Type locality: Sierra Leone: "Sierra Leone". [Goto Description]. Holotype: NHMUK 1862.12.23.3: ad ♂, skin and skull. Presented/Donated by: J. Brown Esq. (Specimen "c" of Dobson's catalogue).

1917. *Nyctinomus ochraceus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 455. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Medje [02 25 N 27 18 E, 800 m]. [Goto Description]. Holotype: AMNH 48821: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 16 March 1910; original number: 745.

1939. *Mops leonis:* G.M. Allen, Bull. Mus. comp. Zool., 83: 108. Publication date: February 1939. (Name Combination).

1980. *Tadarida (Mops) brachyptera:* El-Rayah, Systematics of African molossid bats of the subgenus *Xiphonycteris* of the genus *Tadarida* (Molossidae: Chiroptera) - PhD Thesis - University of Toronto:, 231.

? *Chaerephon leonis ochraeus:*

? *Mops (Xiphonycteris) brachypterus:* (Name Combination, Current Combination).
? *Mops brachypterus leonis:* (Name Combination).
? *Mops brachypterus ochraceus:* (Name Combination).
? *Mops brachypterus:* (Name Combination).
? *Tadarida brachyptera leonis:* (Name Combination).
? *Tadarida brachyptera:* (Name Combination).
? *Tadarida leonis leonis:*
? *Tadarida leonis ochraeus:*
? *Tadaride brachyptera:* (Name Combination).
? *Xiphonycteris leonis:*

TAXONOMY:
Includes *leonis*; see El-Rayah (1981: 6). Stanley (2008: 190) points out that *brachypterus* is in need of revision, since the dental features (e.g., size of upper canines and first upper premolar) differ between for the holotype and continental specimens attributed to it.

Monadjem *et al.* (2016y: 368) and Herkt *et al.* (2017: Appendix S9) found differences in the ecological niches and a clear geographic gap between the distribution areas of *brachypterus* and *leonis sensu stricto*, but as genetic tests evaluating the distinct species status are still lacking, they are still considered to represent the same species.

COMMON NAMES:
Castilian (Spain): Murciélago Guanero. Chinese: 短翼犬吻蝠. Czech: morous krátkokřídlý. English: Sierra Leone Mops Bat, Short-winged Mops Bat, Sierra Leone Free-tailed Bat, White-fingered Free-tailed Bat. French: Tadaride de Peters, Tadaride à doigts blancs. German: Kurzflügel-Bulldoggfledermaus, Kurzflügeligen Doggengrämler. Italian: Carlìno brachìttero.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bo; IUCN, 2009; Monadjem *et al.*, 2017az).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops brachypterus*] (Monadjem *et al.*, 2017az). 2008: LC ver 3.1 (2001) [assessed as *Tadarida brachyptera*] (Mickleburgh *et al.*, 2008bo; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as *Mops brachypterus*] (Mickleburgh *et al.*, 2004bo; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The species is threatened in parts of its range by deforestation, presumably mostly through logging and mining activities and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008bo; IUCN, 2009; Monadjem *et al.*, 2017az).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bo) [in IUCN (2009)] and Monadjem *et al.* (2017az) report that it is not known if the species is present in any protected areas. Further studies are needed into the taxonomy, distribution, natural history, and threats to this species.

GENERAL DISTRIBUTION:
Mops brachypterus ranges widely from West Africa to the East African coast. In West Africa, it is distributed from the Gambia and Sierra Leone in the west, through to Nigeria and Cameroon in the east. From Cameroon, it occurs patchily eastwards through the Congo Basin to Uganda, and to coastal parts of Kenya, Tanzania (including the islands of Unguja [=Zanzibar] [where its presence is questioned according to O'Brien (2011: 289)] and Mafia) and Mozambique in the south.

Native: Cameroon; Central African Republic; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 543); Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Guinea (Simons *et al.*, 2014: 284); Kenya; Liberia; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 543); Nigeria; Sierra Leone; Tanzania; Togo.

Presence uncertain: Zanzibar (Stanley, 2008: 191).

Bates *et al.* (2013: 339) reject the presence of this species in the Republic of Congo.

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) described the karyotype as having a diploid number of 2*n* = 48, aFN = 54, BA = 8, and a presumably submetacentric X (one female studied).

HABITAT:
Monadjem *et al.* (2016y: 368) captured this bat flying over small forest streams in the Mount Nimba area, at altitudes between 450 and 550 m.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008bo; IUCN, 2009; Monadjem *et al.*, 2017az).

Trend
2016: Unknown (Monadjem *et al.*, 2017az).
2008: Unknown (Mickleburgh *et al.*, 2008bo; IUCN, 2009).

PARASITES:
Apanaskevich and Tomlinson (2020: 602) described a new tick (*Haemaphysalis latitudinis* (Ixodidae) from multiple hosts, including a *Mops brachypterus* from Adiopodoumé, Côte d(Ivoire.

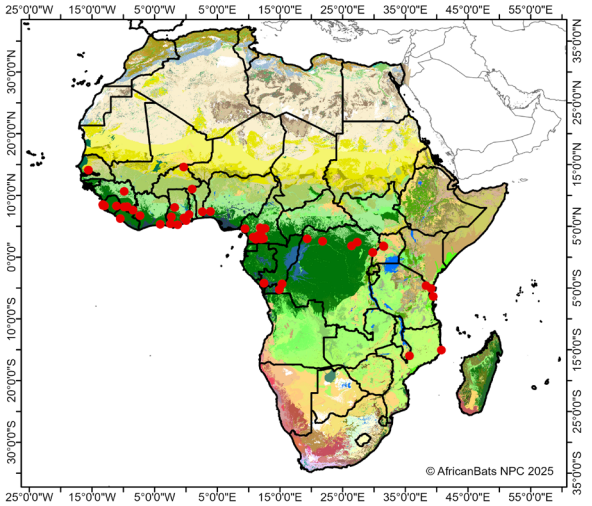

Figure 197. Distribution of *Mops (Xiphonycteris) brachypterus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Guinea, Liberia, Malawi, Mozambique, Nigeria, Rwanda, Senegal, Sierra Leone, Tanzania, Uganda.

Mops (Xiphonycteris) nanulus J.A. Allen, 1917

*1917. *Mops (Allomops) nanulus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 477. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Niangara [03 24 N 27 52 E]. [Goto Description]. Holotype: AMNH 48864: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 12 December 1910; original number: 1318. Topotype: AMNH 48860: ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 48861: ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 48862: ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 48863: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 48865: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition.
1940. *Mops calabarensis* Hayman, in: Sanderson, Trans. Linn. Soc. Lond., 24 (7) 1: 677. Publication date: January 1940. Type locality: Nigeria: Eastern region, Calabar: Ikotmbo [05 03 N 18 19 E, 50 ft]. Holotype: NHMUK 1939.318: ♂, skin and skull. Collected by: Ivan Terrance Sanderson; collection date: 18 September 1932; original number: 3.
1940. *Mops nannulus:* Sanderson, Trans. Linn. Soc. Lond., 24 (7) 1: 677. Publication date: January 1940. - Comments: Lapsus (see Grubb *et al.* (1998: 96). (Lapsus).
2015. *Mops annulus:* Gunnel, Butler, Greenwood and Simmons, Am. Mus. Novit., 3846: 34. Publication date: 16 December 2015. (Lapsus).
? *Mops (Xiphonycteris) nanulus:* (Name Combination, Current Combination).
? *Mops cf. nanulus DMR-2017*
? *Mops nanulus:* (Name Combination).
? *Tadarida nanula calabarensis:* (Name Combination).
? *Tadarida nanula:* (Name Combination).

TAXONOMY:
Distinction from *spurrelli* not certain; see Koopman (1989a).

COMMON NAMES:
Chinese: 侏犬吻蝠. Czech: morous trpasličí. English: Dwarf Mops Bat, Dwarf Free-tailed Bat. French: Tadaride naine. German: Zwerg-Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017l).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops nanulus*] (Monadjem *et al.*, 2017l). 2008: LC ver 3.1 (2001) [assessed as *Tadarida nanula*] (Mickleburgh *et al.*, 2008w; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004o; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
In general, there are no threats to this widespread and somewhat adaptable species. In parts of its range it is locally threatened by habitat loss, primarily deforestation resulting from logging operations and the conversion of land to agricultural use (Mickleburgh *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017l).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008w) [in IUCN (2009)] and Monadjem *et al.* (2017l) report that it is not known if the species is present in any protected areas. Further studies are needed into the distribution, abundance, natural history, and threats to this species.

GENERAL DISTRIBUTION:
Mops nanulus is widely, but patchily, recorded in West, Central and East Africa. It ranges from Sierra Leone and Guinea in the west, through West Africa to Cameroon, and from here east to southern Sudan, Uganda, and western Kenya with an additional record from western Ethiopia and as far south as the southern portion of the Democratic Republic of the Congo. Start (1969: 222) suggests that the species' range might have been more continuous during the Pleistocene when there was a higher degree of rainfall, resulting in a continuous belt of lowland forest between Congo and Kenya.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Cameroon; Congo (The Democratic Republic of the) (Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 544); Côte d'Ivoire; Ethiopia; Gambia (Emms and Barnett, 2005: 50; Simmons, 2005); Ghana; Guinea (Fahr *et al.*, 2006a: 73; Decher *et al.*, 2016: 276); Kenya (Start, 1969: 220); Liberia (Fahr, 2007a: 104); Nigeria; Sierra Leone; Sudan; Uganda.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Start (1969: 221) indicates that there appears to be a general cline from pale-winged red forms in the west to dark-winged brown ones in the east, although this is not absolute.

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) reported 2*n* = 48, FN = 54, BA = 8, a submetacentric X chromosome and an acrocentric Y chromosome.

POPULATION:
Structure and Density
This is a common species (Mickleburgh *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017l).

Trend
2016: Unknown (Monadjem *et al.*, 2017l). 2008: Unknown (Mickleburgh *et al.*, 2008w; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Start (1969: 221) reports on six female specimens collected in West Pokot (Kenya) between 25 and 29 August 1967, of which five were carrying well developed embryos, whereas the sixth was lactating.

Weber *et al.* (2019: 28) reported one pregnant female from Sierra Leone on 26 March.

Krutzsch (2000: 127) indicates that "*Tadarida (Mops) nanulus*" is polyoestrous.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Guinea, Kenya, Nigeria, Sierra Leone, South Sudan, Togo, Uganda.

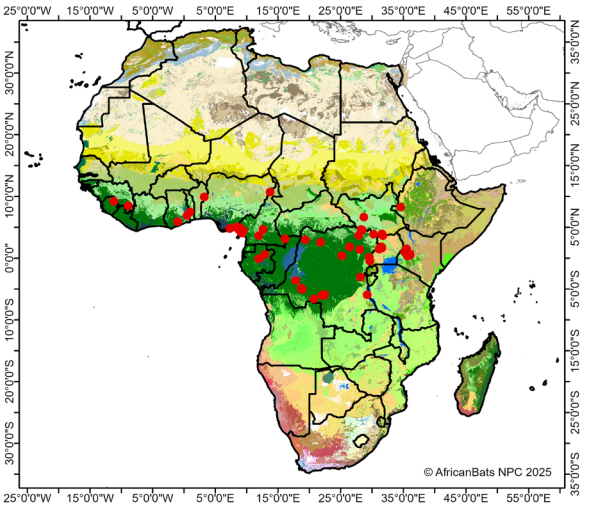

Figure 198. Distribution of *Mops (Xiphonycteris) nanulus*.

Mops (Xiphonycteris) petersoni (El Rayah, 1981)

*1981. *Tadarida [(Xiphonycteris)] petersoni* El Rayah, Life Sci. Occ. Pap., R. Ont. Mus., 36: 3, figs 1 - 2. Publication date: 11 December 1981. Type locality: Cameroon: Kumba, 15 km S [04 39 N 09 26 E]. [Goto Description]. Holotype: ROM 55813: ad ♂, skull and alcoholic. Collected by: Randolph Lee Peterson; collection date: 27 January 1970; original number: 0364. See El-Rayah (1981: 3). Paratype: AMNH 236332: ♂, skin and skull. 6 km SE Eseka(03°35'N 10°44'E) (See El-Rayah, 1981: 3). Paratype: AMNH 236333: ♂, skin and skull. 6 km SE Eseka(03°35'N 10°44'E) (see: El-Rayah, 1981: 3). Paratype: AMNH 241075: ♂, skin and skull. Near Okola (04°00'N 11°33'E) (see El-Rayah, 1981: 3). Paratype: AMNH 241076: ♂, skin and skull. 30 km E Nanga Emboko (04°38'N 12°21'E) (see El-Rayah, 1981: 3). Paratype: AMNH 241078: ♀, skin and skull. 30 km E Nanga Emboko (04°38'N 12°21'E) (see El-Rayah, 1981: 3). - Etymology: In honour of Randolph L. Peterson, collector of the type specimen.

? *Mops (Xiphonycteris) petersoni:* (Name Combination, Current Combination).

? *Mops petersoni:* (Name Combination).

? *Tadarida petersoni:* (Name Combination).

TAXONOMY:

Described in *Tadarida (Xiphonycteris)*, but see comments under *Tadarida* and *Mops*.

COMMON NAMES:

Czech: morous kamerunský. English: Peterson's Mops Bat, Peterson's Free-tailed Bat. French: Tadaride de Peterson. German: Petersons Bulldoggfledermaus.

CONSERVATION STATUS:

Global Justification

Listed as Near Threatened because this species is likely in significant decline (but probably at a rate of less than 30% over a 15 year period; i.e., three generations) because of ongoing loss of its primary forest habitat, which makes the species close to qualifying for Vulnerable (Mickleburgh *et al.*, 2010).

Assessment History

Global

2021: NT A2c ver 3.1 [assessed as *Mops petersoni*] (Bakwo Fils *et al.*, 2021a). 2010: NT ver 3.1 (2001) [assessed as *Mops petersoni*] (Mickleburgh *et al.*, 2010). 2008: VU A4c ver 3.1 (2001) [assessed as *Tadarida petersoni*] (Mickleburgh *et al.*, 2008bt; IUCN, 2009). 2004: VU A4c ver 3.1 (2001) (Mickleburgh *et al.*, 2004av; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

The species is considered to be threatened by loss and degradation of forest habitats within its known range, largely through the conversion of land to agricultural use and the extraction of firewood and timber (Mickleburgh *et al.*, 2008bt; IUCN, 2009; Mickleburgh *et al.*, 2010).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2010) and Bakwo Fils *et al.* (2021a: 5) repeat what was stated by Mickleburgh *et al.* (2008bt) [in IUCN (2009)] who report that there appear to be no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. There is a need to maintain areas of suitable forest within the range of this species. Further studies are needed into the distribution, abundance, breeding biology and general ecology of this species.

GENERAL DISTRIBUTION:

Mops petersoni has only been recorded from Ghana and Cameroon (with type locality at '15 km S Kumba'), with no records from the intervening countries of Togo, Benin and Nigeria. Koopman (1993a) included "perhaps Sierra Leone" as part of the distribution, however, J. Fahr (*pers. comm.*, 2004 in Mickleburgh *et al.*, 2008bt; IUCN, 2009) indicates that there is no evidence of the species' presence. The specimen involved was re-identified as belonging to *Mops brachypterus*.

Native: Cameroon; Ghana.

Presence uncertain: Sierra Leone (Koopman, 1993a).

MOLECULAR BIOLOGY:

Karyotype

Smith *et al.* (1986) reported 2*n* = 48, FN = 54, BA = 8, a submetacentric X chromosome and an acrocentric Y chromosome.

HABITAT:

This species is only from rainforest (Bakwo Fils *et al.*, 2021a: 5), and possibly entering the Northern Rainforest–Savanna Mosaic (Happold, 2013cf: 526).

POPULATION:

Structure and Density

It is considered to be a very rare species (Mickleburgh *et al.*, 2008bt; IUCN, 2009; Mickleburgh *et al.*, 2010).

Trend
2021: Decreasing (Bakwo Fils *et al.*, 2021a). 2010: Unknown (Mickleburgh *et al.*, 2010). 2008: Unknown (Mickleburgh *et al.*, 2008bt; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Ghana.

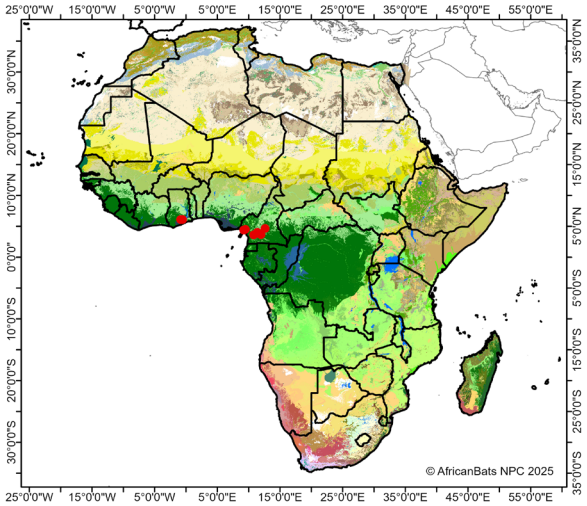

Figure 199. Distribution of *Mops (Xiphonycteris) petersoni*.

Mops (Xiphonycteris) spurrelli (Dollman, 1911)

*1911. *Xiphonycteris spurrelli* Dollman, Ann. Mag. nat. Hist., ser 8, 7 (38): 211. Publication date: 1 February 1911. Type locality: Ghana: Western province: 60 mi (90 km) W Kumasi: Bibianaha [=Bibiani] [06 28 N 02 20 W, 720 ft]. [Goto Description]. Holotype: NHMUK 1911.1.11.1: ad ♂. Collected by: Dr. H.G.F. Spurrell; collection date: 8 December 1910; original number: 34. - Etymology: In honour of dr. H.G.F. Spurrell, who collected the type specimen, and provided many rare and unique West-African mammals to National Collection (see Dollman, 1911: 211).
1973. *Xiphonycteris spurelli:* Eisentraut, Bonn. zool. Monogr., 3: 47. (Lapsus).
? *Mops (Xiphonycteris) spurelli:* (Lapsus).
? *Mops (Xiphonycteris) spurrelli:* (Name Combination, Current Combination).
? *Mops spurrelli:* (Name Combination).
? *Tadarida spurelli:* (Lapsus).
? *Tadarida spurrelli:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous sahelský. English: Spurrell's Mops Bat, Spurrell's Free-tailed Bat. French: Tadaride de Spurell. German: Spurrells Bulldoggfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dm; IUCN, 2009; Monadjem *et al.*, 2017ak).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops spurrelli*] (Monadjem *et al.*, 2017ak). 2008: LC ver 3.1 (2001) [assessed as *Tadarida spurrelli*] (Mickleburgh *et al.*, 2008dm; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cm; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The species is locally threatened by deforestation, often through conversion of land to agricultural use or by extraction of timber and firewood (Mickleburgh *et al.*, 2008dm; IUCN, 2009; Monadjem *et al.*, 2017ak).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dm) [in IUCN (2009)] and Monadjem *et al.* (2017ak) report that there appear to be no direct conservation measures in place for this species, and it is not known if the species is present within any protected areas. There is a need to maintain areas of suitable forest habitat for this species. Additional studies are needed into the distribution of this species.

GENERAL DISTRIBUTION:
Mops spurrelli ranges through parts of West and Central Africa. It occurs from Sierra Leone in the west, through Liberia, Guinea, Côte d'Ivoire and Togo, to Cameroon, Equatorial Guinea (Bioko and Rio Muni), the Central African Republic with

a record from the eastern part of The Democratic Republic of the Congo. It is possibly present in other countries, such as Benin, Nigeria and Congo, however, this needs to be confirmed.

Native: Cameroon; Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire; Equatorial Guinea (Bioko); Ghana; Guinea (Fahr and Ebigbo, 2003: 128); Liberia; Sierra Leone; Togo.

Presence uncertain: Benin; Congo; Nigeria.

MOLECULAR BIOLOGY:
Karyotype
Smith *et al.* (1986) reported 2*n* = 48, FN = 64, BA = 18, a submetacentric X chromosome for a female.

HABITAT:
At Mount Nimba, Monadjem *et al.* (2016y: 368) recorded this species over small streams and swamps at altitudes between 450 and 600 m.

POPULATION:
Structure and Density
Within Central Africa this is a very common species and is believed to have quite large colonies (Mickleburgh *et al.*, 2008dm; IUCN, 2009; Monadjem *et al.*, 2017ak).

Trend
2016: Unknown (Monadjem *et al.*, 2017ak). 2008: Unknown (Mickleburgh *et al.*, 2008dm; IUCN, 2009).

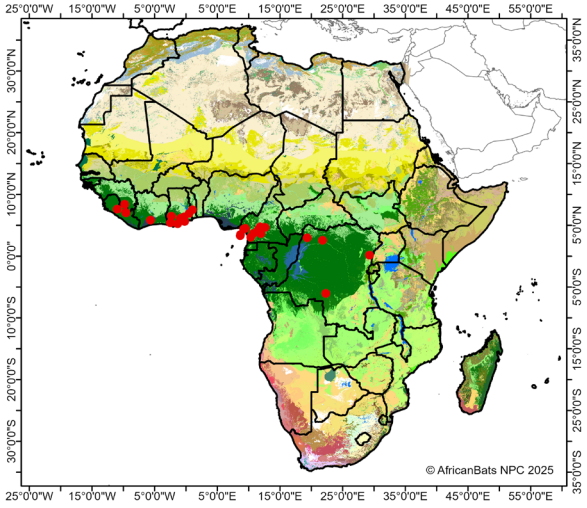

Figure 200. Distribution of *Mops (Xiphonycteris) spurrelli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ghana, Liberia, Sierra Leone, Togo.

Mops (Xiphonycteris) thersites (Thomas, 1903)

*1903. *Nyctinomus thersites* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (72): 634. Publication date: 1 December 1903. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1904.2.8.4: ad ♂. Collected by: George Latimer Bates Esq. 3 specimens: see Thomas (1903e: 635). - Etymology: Thersites was one of the members of the Greek army against Troy. He tried to stir up the army against its leaders, for which he got beaten by Odysseus. His name is a scorn: naughty boy. He was an excessive thwaddler, with deformed legs, feet, and bent over shoulders, a pointed head and thin flaky hair.
1917. *Mops (Allomops) occipitalis* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 474, text-fig 15. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Avakubi [01 18 N 27 32 E]. [Goto Description]. Holotype: AMNH 48851: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 13 February 1914; original number: 2487.
1973. *Tatarida theresites:* Eisentraut, Bonn. zool. Monogr., 3: 113. (Lapsus).
2018. *Mops therisites:* Gunnell and Manthi, J. Hum. Evol., Suppl. Publication date: 6 April 2018. (Lapsus).
2021. *Mops thersithes:* Kadjo, Niamien, Akpatou, and Brou, Int. J. Fauna Biol. Stud., 8 (5): 25. Publication date: September-October 2021. (Lapsus).
? *Mops (Xiphonycteris) thersites:* (Name Combination, Current Combination).
? *Mops (Xyphonycteris) thersites:* (Lapsus).
? *Mops thersites:* (Name Combination).
? *Tadarida (Mops) thersites:* (Name Combination).
? *Tadarida thersites thersites:* (Name Combination).
? *Tadarida thersites:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Chinese: 无畏犬吻蝠. Czech: morous spílavý. English: Railer Mops Bat, Railer Bat. French: Tadaride de Railer. German: Thersites' Bulldoggfledermaus. Portuguese: Morcego de railer.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Gunnell *et al.* (2015a: 22) report on a number of humeri from a Pleistocene deposit at Olduvai Gorge (Tanzania), which they assigned to *Mops* cf. *M. thersites*.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dn; IUCN, 2009; Monadjem *et al.*, 2017al).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Mops thersites*] (Monadjem *et al.*, 2017al). 2008: LC ver 3.1 (2001) [assessed as *Tadarida thersites*] (Mickleburgh *et al.*, 2008dn; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cl; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is locally threatened by habitat destruction, often through conversion of land to agricultural use or timber extraction (Mickleburgh *et al.*, 2008dn; IUCN, 2009; Monadjem *et al.*, 2017al).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dn) [in IUCN (2009)] and Monadjem *et al.* (2017al) report that there appear to be no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. Additional studies are needed into the distribution of this species.

GENERAL DISTRIBUTION:
Mops thersites has been recorded from much of Western and Central Africa. It ranges from Sierra Leone in the west, through West Africa (where it has been recorded from most countries) to Cameroon, and from here south into southern parts of the Democratic Republic of the Congo, and east into Uganda, Rwanda and western Kenya. It is present on Bioko Island, Equatorial Guinea.

Native: Cameroon; Central African Republic; Congo (The Democratic Republic of the) (Schouteden, 1944; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 544); Côte d'Ivoire; Equatorial Guinea [Bioko]; Gabon; Ghana; Guinea (Fahr *et al.*, 2006b: 245; Denys *et al.*, 2013: 284); Kenya; Liberia (Fahr, 2007a: 104); Nigeria; Rwanda; Sierra Leone; Uganda.

Presence uncertain: Mozambique and Zanzibar.

Bates *et al.* (2013: 339) reject the presence of this species in the Republic of Congo as Malbrant and Maclatchy (1949) only suggested it might occur in that country and subsequent authors did not provide supporting records.

MOLECULAR BIOLOGY:
Karyotype
Denys *et al.* (2013: 284) report the karyotype for a single female specimen from the Guinean Mount Nimba area attributed to this species as: 2*n* = 48, NFa = 70, including four pairs of metacentric, eight pairs of subtelocentric, 11 pairs of acrocentric autosomes and a middle-sized submetacentric X chromosome.

HABITAT:
This species was captured by Monadjem *et al.* (2016y: 368) in the Mount Nimba area above water in forested and open habitats between 450 and 880 m.

In the Yapi Daniel private forest (Côte d'Ivoire), this bat was the most abundant species in the wetland area (Kadjo *et al.*, 2021: 26).

POPULATION:
Structure and Density
It appears to be quite abundant in parts of its range (Mickleburgh *et al.*, 2008dn; IUCN, 2009; Monadjem *et al.*, 2017al).

Trend
2016: Stable (Monadjem *et al.*, 2017al). 2008: Stable (Mickleburgh *et al.*, 2008dn; IUCN, 2009).

PARASITES:
HEMIPTERA
Polyctenidae
Hypoctenes clarus Jordan, 1922, from near Kribi, Cameroon and Ghana (Haeselbarth *et al.*, 1966: 18; Szentiványi *et al.*, 2022: 6).

SIPHONAPTERA
Ischnopsyllidae
Lagaropsylla oblique Smit, 1957 from Sierra Leone, Cameroon and the Congo (Haeselbarth *et al.*, 1966: 191).

VIRUSES:
Filoviridae - File viruses
Marburgvirus
Weiß (2013: 58, 66) found antibodies against MARV in one *M. thersites* from the Taï National Park (Côte d'Ivoire).

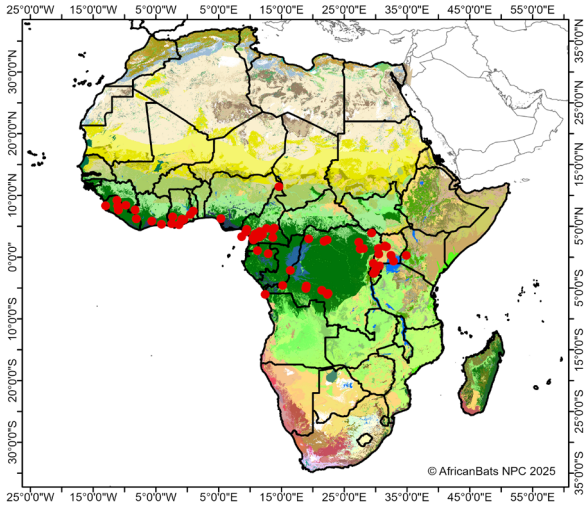

Figure 201. Distribution of *Mops (Xiphonycteris) thersites*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Rwanda, Sierra Leone, Togo, Uganda.

Genus ***Mormopterus*** Peters, 1865

*1866. *Mormopterus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 258. - Comments: Type species: *Nyctinomus (Mormopterus) jugularis* Peters, 1865. - Etymology: From the Greek "*mormopterus*" meaning phantom- or ghost-winged or winged goblin (Flannery, 1990: 367; 1995a: 408). - Phonetics: morm-op'-te-rus, morm-op-ter'-us. (Current Combination).
? *Tadarida (Mormopterus):* (Name Combination).

TAXONOMY:
Meester *et al.* (1986) state that this treatment of *Mormopterus* is provisional; it has been regarded as a subgenus of *Tadarida* (Hayman and Hill, 1971) or as a valid genus that includes *Platymops* and *Sauromys* as subgenera (Freeman, 1981b; Legendre, 1984), and the extralimital *Micronomus* as either a subgenus (Legendre loc. cit.) or a synonym (Freeman, 1981b; Peterson, 1985).

Bronner *et al.* (2003) mention that the status of *Sauromys*, described as a monotypic subgenus of the extralimital (to southern Africa) *Platymops* for the South African flat-headed free-tailed bat, remains unclear. Peterson (1965) raised it to generic rank, a treatment endorsed by many subsequent authors, and corroborated by a limited multivariate analysis of wing bone and cranial characteristics (Peterson, 1985). However, morphometric studies by Freeman (1981b) and Legendre (1984) concluded that it is a subgenus of *Mormopterus*, a position followed by Koopman (1993a, 1994). Simmons (2005) retains *Sauromys* as a valid genus in the 3rd Edition of Mammal Species of the World, a treatment we favour because of the unique ecology and morphology of *S. petrophilus*. The separation between *Mormopterus* and *Sauromys* is also supported by the analysis of the Rag2 data by Ammerman *et al.* (2013: 309).

Meester *et al.* (1986) furthermore state that it was originally described as a subgenus, but this genus was regarded as a synonym of *Platymops* by Shortridge (1942), Roberts (1951) and Ellerman *et al.* (1953). Harrison (1962) retains it as a subgenus, while Peterson (1965) raises it to generic rank, in which he is followed by Hayman and Hill (1971), Smithers (1971), Corbet and Hill (1980) and Rautenbach (1982). However, Freeman (1981b), followed by Koopman (1982) and Legendre (1984), conclude that both *Sauromys* and *Platymops* are subgenera of *Mormopterus*. We take the view that both *Platymops* and *Sauromys* are valid genera.

From their molecular study, Lamb *et al.* (2010: 203; 2011: 10) found that *M. jugularis* and *M. francoismoutoui* form a monophyletic clade (dated about 31.2 MYR), whereas a third member of the genus (the New World *M. kalinowskii*) seems more related to the South American *Nyctinomops laticaudatus* and *Nyctinomops aurispinosus*.

Goodman *et al.* (2022: 1904) indicate that as *jugularis* was the first species associated with the genus *Mormopterus* this genus name should be restricted to the species occurring in the western Indian Ocean area (= Malagasy region).

The analysis of the recombination activating gene 2 (Rag2) sequence data led Ammerman *et al.* (2013: 307) to conclude that the genus *Cheiromeles* is the most basal lineage within the

Molossinae, and that *Mormopterus* is a sistergroup of the rest of the Molossinae.

Key in Jacobs and Fenton (2002, Mammalian Species, 703).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Mormopterus*: ***acetabulous*** (Hermann, 1804); *doriae* K. Andersen, 1907 – Sumatra (Indonesia) (Simmons, 2005: 445); ***francoismoutoui*** Goodman, Jansen Van Vuuren, Ratrimomanarivo, Probst and Bowie, 2008; ***jugularis*** (Peters, 1865); *kalinowskii* (Thomas, 1893) – Peru, northern Chile (Simmons, 2005: 445); *minutus* (Miller, 1899) – Cuba (Simmons, 2005: 445); *phrudus* Handley, 1956 – Peru (Simmons, 2005: 4435).

COMMON NAMES:
Czech: Petersovi morousi. English: Phantom-winged Bats, Little Bulldog Bats, Little Mastiff Bats, Little Goblin Bats, Flat-headed Bats, Flat-headed Bulldog Bats, Goblin bats. French: Tadarides. German: Mastino-Fledermäuse.

PARASITES:
ACARI
Myobiidae
Fain (1973: 299) described *Ewingana (Mormomyobia) lamorali* from a *Mormopterus* sp. from Sakaraka (Madagascar)/

UTILISATION:
See Goodman *et al.* (2008d).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Mormopterus acetabulosus (Hermann, 1804)

*1804. *V[espertilio] acetabulosus* Hermann, Obs. Zool. , 19. Publication date: 31 August 1804. Type locality: Mauritius: Port Louis. [Goto Description]. Holotype: MNHN ZM-MO-1984-368: ad? ♀. Collected by: Julien François Desjardins; collection date: 1829; original number: A488. Goodman *et al.* (2008c: 1324) incidcate that the specimen is labeled as type, but was collected 25 years after Hermann (1804) described it. Neotype: FMNH 187489: Collected by: Steven M. Goodman and V. Florens; collection date: 29 October 2006. Mauritius, Black River District, Palma, Palma Cave, 20 16'40.5"S 57 27'14.7"E. Goodman *et al.* (2008c: 1327) designated this as the neotype. Cheke (2009b) rejects the assignment of the neotype by Goodman *et al.* (2008c), based on article 73.1.4 and 75.8 (rules of Nomenclature - ICZN 1999). - Comments: Cheke (2009b: 1) rejects the assignment of the neotype, based on article 73.1.4 (rules of Nomenclature - ICZN 1999), which indicates that Paul Jossigny's drawings made of the specimen that Commerson once had before him in Mauritius should be considered the holotype of Hermann's *Vespertilio acetabulosus*, and that the designation of a neotype by Goodman *et al.* (2008c: 1324) is invalidated by article 75.8. The drawings on which Commerson based himself (and which were referred to by Hermann, 1804: 19) are to be found amongst the Commerson papers, in the folder of other similar drawings at MS 282(II), labelled No. 51 (Moutou, 1982, pers. obs. 2006) in the archives of the Bibiothèque du Muséum; the folder is described in paragraph 73 of Laissus's (1974) catalogue.
1820. *Nyctinomus acetabulosus:* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 117. Publication date: 1820. (Name Combination).
1877. *Nyctinomus [(Mormopterus)] acetabulosus:* Dobson, Proc. zool. Soc. Lond., 1876, IV: 734. Publication date: April 1877. (Name Combination).
? *Molossus acetabulosus:* Commerson. - Comments: Dobson (1877: 734) refers for this combination to Peters (1869a: 402), and suggests it is only a manuscript name. (Name Combination).
? *Mormopterus acetabulosus:* (Name Combination, Current Combination).
? *Tadarida acetabulosus natalensis:* (Name Combination).

TAXONOMY:
See Simmons (2005: 444) and Goodman *et al.* (2008c).

Cheke (2009a: 115) indicates that Jossigny's drawing used by Hermann to describe the species in 1804 is to be considered as the lectotype of the species, which would overrule the need for a neotype as designated by Goodman *et al.* (2008c: 1324).

COMMON NAMES:
Afrikaans: Natalse losstertvlermuis. Czech: morous mauricijský. English: Natal Flat-headed Bat, Natal Wrinkle-lipped Bat, Natal Free-tailed Bat. French: Sauromys du Natal, Tadaride à lèvres ridées, Petit molosse de Port Louis. German: Mauritius Mastino-Fledermaus, Maurizische Doggengrämler.

CONSERVATION STATUS:
Global Justification
Listed as Endangered (EN A2bc; B1ab(iii,v)+2ab(iii,v)) because this species has a restricted range and decline in population size. It occurs in less than five sites on Mauritius. It is restricted to lava tube caves. The population of the species has declined by over 80% during the last 18 years, however the rate of decline over the last three generations is unknown; it is likely that it approached 67% over three generations (11-12 years based on a generation length of 3.9 years; see Pacifici *et al.*, 2013). The major roosting cave system for the species had been

developing into a tourism attraction for the past three years, resulting in loss of over 10,000 bats from a single location.

Assessment History
Global
2016: EN A2bc; B1ab(iii,v)+2ab(iii,v) ver. 3.1 (2001) (Bergmans *et al.*, 2017c). 2014: EN A2b; B1ab(iii)+2ab(iii) ver 3.1 (2001) (Bergmans *et al.*, 2017c). 2008: VU D2 ver 3.1 (2001) (Hutson and Bergmans, 2008; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Hutson and Bergmans, 2004; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
South Africa: 2004: considered a vagrant not assessed, known from single locality (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
It is threatened by disturbance of roosting caves, and the removal of protective grills over the caves for landfill purposes Hutson and Bergmans, 2008; IUCN, 2009; Bergmans *et al.*, 2017c).

CONSERVATION ACTIONS:
Hutson and Bergmans (2008) [in IUCN (2009)] and Bergmans *et al.* (2017c) report that it is not known if the species is present in any protected areas. There is a need to protect cave roosts of this species in Mauritius by re-grilling important sites, cleaning the caves from household waste, education of local community (Bergmans *et al.*, 2017c).

GENERAL DISTRIBUTION:
Mormopterus acetabulosus is endemic to the Mascarene Islands (Mauritius) (see Goodman *et al.*, 2008c: 1316; O'Brien, 2011: 288). Records from Réunion should be assigned to *Mormopterus francoismoutoui*).

There is a single doubtful record for Madagascar (Peterson *et al.*, 1995: 150). Taylor (1998: 60) mentioned a specimen from South Africa (Durban) collected by Andrew Smith in 1833, but also states that no further specimens have been collected since. An old record from between the district of Shoa and Lake Rudolph in southern Ethiopia (Hayman and Hill, 1971: 59), most probably should be attributed to *M. francoismoutoui* (Goodman *et al.*, 2008c: 1325). Furthermore, it is now considered most likely that specimens taken outside of the Mascarene Islands were vagrants.

Monadjem *et al.* (2010d) did not retain this species for south Central Africa, but did mention the specimen from Durban, South Africa in the appendix (p. 545).

Native: Mauritius (Smith, 1833: 54; Meester *et al.*, 1986: 67; Simmons, 2005: 444; Goodman *et al.*, 2008c: 1316).

Presence uncertain: Madagascar (Dobson, 1878; Allen, 1939a; Hayman and Hill, 1971; Meester *et al.*, 1986: 67; Peterson *et al.*, 1995: 150; Simmons, 2005: 444); South Africa (Meester *et al.*, 1986: 67; Taylor, 1998: 60; Taylor, 2000: 75; Simmons, 2005: 444; Monadjem *et al.*, 2010d: 545); Sudan (Freeman, 1981b: 75).

Presence incorrectly assigned: Ethiopia (Hayman and Hill, 1971: 59; Simmons, 2005: 444; Kaipf *et al.*, 2015: 13); Réunion.

ROOST:
Middleton (1998a: 91) mention large colonies occurring in two caves in the Plaine des Roches area (Mauritius), and indicate that elsewhere the colonies seldom reach 2,000 animals.

Bunsy *et al.* (2024) indicated that caves with larger entrances were preferred probably because the bats could be more manoeuvrable and protected from predators.

DIET:
Bunsy *et al.* (2024: 2) mention that *M. acetabulosus* feeds on agricultural pests, including *Cryptophlebia peltastica* (Meyrick, 1921) (Lepidoptera, Tortricidae) and on human disease vectors such as the African Malaria mosquito, *Anopheles gambiae* Giles, 1902.

POPULATION:
Structure and Density
The largest known day roost colony on La Réunion (at Trois Bassins), with estimates from 25,000 to 10,000 individuals, is abandoned in austral winter, and it is not known where these bats spend the winter (Devaux, 2006; Issartel, 2004; Probst, 2003; Goodman *et al.*, 2008c: 1325). Goodman (2007) found bats allocated to this species to be common at several sites on Mauritius. However, Taylor (2016) [in [Bergmans *et al.* (2017c)] found the species to be narrowed to only four caves in Mauritius. Based on the survey it has been estimated that the population decreased by over 80% during the last 18 years and it keeps declining.

Trend
2016: Decreasing (Bergmans *et al.*, 2017c). 2008: Unknown (Hutson and Bergmans, 2008; IUCN, 2009).

Recent research by Bunsy *et al.* (2024) revealed that 17 of the 130 investigated lava cave tunnels contained roosts, whereas only nine were inhabited in the 2017 survey. However, they were unable to determine whether these extra roosts were overlooked previously or whether this was a recent colonisation (or a combination of the two).

PARASITES:
Dietrich *et al.* (2018a: 3) reported the presence of sequences closely related to the bacterium *Leptospira borgpetersenii*.

Laudisoit *et al.* (2012: 739) indicate that the type host for *Araeopsylla martialis* (Rothschild, 1903) (Siphonaptera; Ischnopsyllidae) was originally mentioned as "*Nyctinomus acetabulosus*", but this should actually be *Mormopterus francoismoutoui*.

VIRUSES:
Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 55 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 1 positive results for viral nucleic acids.

Rhabdoviridae
Of 31 specimens tested against *Lagos bat lyssavirus* and *Duvenhage lyssavirus* by Mélade *et al.* (2016a: 6), respectively five and six showed a seroreaction. This was also the case for one out of eight bats tested for *European bat lyssavirus 1*.

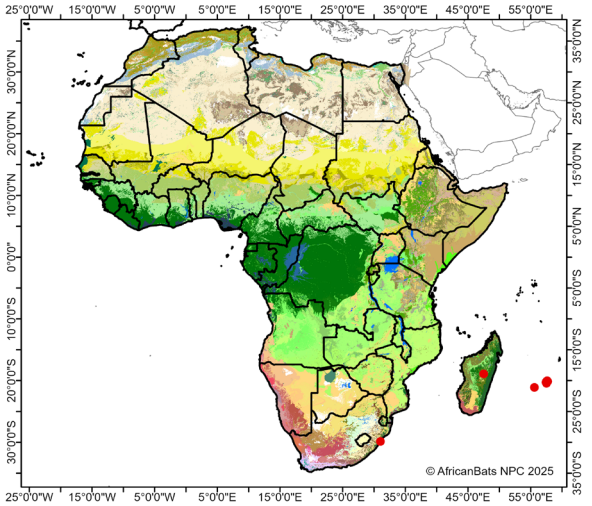

Figure 202. Distribution of *Mormopterus acetabulosus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Ethiopia, Madagascar, Mauritius, Réunion, South Africa.

Mormopterus acetabulosus acetabulosus (Hermann, 1804)

*1804. *V[espertilio] acetabulosus* Hermann, Obs. Zool. , 19. Publication date: 31 August 1804. Type locality: Mauritius: Port Louis. [Goto Description]. Holotype: MNHN ZM-MO-1984-368: ad? ♀. Collected by: Julien François Desjardins; collection date: 1829; original number: A488. Goodman *et al.* (2008c: 1324) incidcate that the specimen is labeled as type, but was collected 25 years after Hermann (1804) described it. Neotype: FMNH 187489: Collected by: Steven M. Goodman and V. Florens; collection date: 29 October 2006. Mauritius, Black River District, Palma, Palma Cave, 20 16'40.5"S 57 27'14.7"E. Goodman *et al.* (2008c: 1327) designated this as the neotype. Cheke (2009b) rejects the assignment of the neotype by Goodman *et al.* (2008c), based on article 73.1.4 and 75.8 (rules of Nomenclature - ICZN 1999). - Comments: Cheke (2009b: 1) rejects the assignment of the neotype, based on article 73.1.4 (rules of Nomenclature - ICZN 1999), which indicates that Paul Jossigny's drawings made of the specimen that Commerson once had before him in Mauritius should be considered the holotype of Hermann's *Vespertilio acetabulosus*, and that the designation of a neotype by Goodman *et al.* (2008c: 1324) is invalidated by article 75.8. The drawings on which Commerson based himself (and which were referred to by Hermann, 1804: 19) are to be found amongst the Commerson papers, in the folder of other similar drawings at MS 282(II), labelled No. 51 (Moutou, 1982, pers. obs. 2006) in the archives of the Bibiothèque du Muséum; the folder is described in paragraph 73 of Laissus's (1974) catalogue.

1823. *Nyctinomus mauritianus* Horsfield, Zoological Research in Java, Part 5, 9th page of text in account of *N. tenuis*. Publication date: January 1823. Type locality: Mauritius: Port Louis. [Goto Description].

? *Mormopterus acetabulosus acetabulosus:* (Name Combination, Current Combination).

ROOST:
On Mauritius, these bats use caves as typical roosting sites (see Wilkinson *et al.*, 2012: 160).

VIRUSES:
Wilkinson *et al.* (2012: 160) found one specimen out of 55 examined on Mauritius, that tested positive for Respirovirus / Morbillivirus / Henipahvirus (RMH) and Paramyxovirinae (PMV)

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Mauritius, Réunion.

Mormopterus acetabulosus natalensis (A. Smith, 1847)

1833. *Nyctinomus dubius* A. Smith, S. Afr. Quart. J., ser 2, 1 (2): 54. Publication date: November 1833. Type locality: South Africa: Cape Province and Natal, between. [Goto Description].

*1847. *Dysopes natalensis* A. Smith, Illustrated Zoology of South African Mammals, pl 49 and text. Publication date: December 1847. Type locality: South Africa: KwaZulu-Natal: Port Natal [=Durban], near [ca. 29 52 S 31 00 E]. - Comments: Dobson (1877: 734) mentions that the original name used by Smith (1847: pl. 49) was *Nyctinomus natalensis*, but this could not be checked yet. If this isn't the case, then this combination should probably be attributed to Dobson (1877). - Etymology: The name reflects the two specimens collected in KwaZulu-Natal.

? *Mormopterus acetabulosus natalensis:* (Name Combination, Current Combination).

TAXONOMY:
Allen (1939a) tentatively treats *dubius* as a species of *Nyctinomus* (= *Tadarida*), remarking that its status is uncertain; Roberts (1951), without giving reasons, regards it as a prior name for *natalensis*. Ellerman *et al.* (1953) are doubtful whether or not the two names are synonymous, and although they list *dubius* in the synonymy of *natalensis* they suggest that it may be necessary to discard the name as not being certainly identifiable. Hayman and Hill (1971: 65) list *dubius* as *incertae sedis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

Mormopterus francoismoutoui Goodman, Jansen Van Vuuren, Ratrimomanarivo, Probst, Bowie, 2008

*2008. *Mormopterus francoismoutoui* Goodman, Jansen Van Vuuren, Ratrimomanarivo, Probst and Bowie, J. Mamm., 89 (5): 1318, figs 2 - 6. Type locality: Réunion: Commune de La Possession: Pont de Balthazar [2056.732S 5519.848E, 40m]. Holotype: FMNH 193986: ad ♂, skull and alcoholic. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006; original number: SMG 15310. Paratype: FMNH 193982: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193983: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193984: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193985: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193987: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193988: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193989: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193990: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193991: ♀, alcoholic (skull not removed). Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 25 September 2006. Paratype: FMNH 193992: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193993: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193994: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193995: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193996: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193997: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193998: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 193999: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194000: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194001: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194002: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194003: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194004: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194005: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194006: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194007: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194008: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194009: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194010: ♂, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194011: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194012: ♀, skull only. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194013: complete skeleton. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194014: complete skeleton. Collected by: Steven M. Goodman and Jean-Michel Probst; collection date: 26 September 2006. Paratype: FMNH 194015: ♂, complete skeleton. Collected by: Steven M. Goodman. Paratype: FMNH 194016: ♀, complete skeleton. Collected by: Steven M. Goodman. Paratype:

FMNH 74208: ♂, alcoholic (skull not removed). Collected by: dr. Gérard J. Morel. Paratype: FMNH 74209: ♀, alcoholic (skull not removed). Collected by: dr. Gérard J. Morel. Paratype: MNHN ZM-MO-1862-362: Collected by: M. Millard. Paratype: MNHN ZM-MO-1865-24: Collected by: Auguste Lantz. Paratype: MNHN ZM-MO-1865-25: Collected by: Auguste Lantz. Paratype: MNHN ZM-MO-1865-26: Collected by: Auguste Lantz. Paratype: MNHN ZM-MO-1981-301: Collected by: Dr. Véto and François Moutou; collection date: 23 March 1979. Paratype: MNHN ZM-MO-1981-302: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: MNHN ZM-MO-1981-303: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: MNHN ZM-MO-1981-304: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: MNHN ZM-MO-1981-305: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: MNHN ZM-MO-1981-306: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: MNHN ZM-MO-1981-307: Collected by: Dr. Véto and François Moutou; collection date: 1 August 1980. Paratype: UMMZ 115813: Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115814: Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115815: Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115816: Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115817: ♀. Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115818: Collected by: Frank B. Gill; collection date: 2 June 1967. Paratype: UMMZ 115819: Collected by: Frank B. Gill; collection date: 2 June 1967. - Etymology: The name *francoismoutoui* is a patronym in honour of Dr. François Moutou of the Unité d'Epidémiologie, Agence Française de Sécurité Sanitaire des Aliments, Maison Alfort, France. Dr. Moutou has made important contributions to the vertebrate fauna of the Mascarene Islands, particularly La Réunion (Goodman *et al.*, 2008c: 1319). (Current Combination).

2013. *Mormopterus francoimoutoui:* Barataud and Giosa, Le Rhinolophe, 19: 151. (Lapsus).

Taxonomy:

Formerly identified as *M. acetabulosus* see Goodman *et al.* (2008c: 1316).

Common Names:

Czech: morous réunionský. English: Reunion Free-tailed bat. French: Petit molosse, Tadaride de La Réunion. German: Reunion Mastino-Fledermaus.

Conservation status:

Global Justification

Goodman *et al.* (2008c: 1325) state it is under no serious threat of population decline in the near future. Augros *et al.* (2015: 372) refer to IUCN (2010) and mention "LC" as status. Goodman (2017f) report that this species is known from numerous sites on La Réunion, which include large maternity and day roosting colonies in caves and numerous synanthropique roost sites, such as under bridges and in houses, churches, and the principal airport (Dietrich *et al.*, 2015b). No clear threats are known.

Assessment History

Global

2016: LC ver. 3.1 (2001) (Goodman, 2017f).

Regional

None known.

Major threats:

No threats identified by Goodman (2017f). However, Aguillon *et al.* (2023: 10) [referring to Augros *et al.* (2015)] mention that displacement from its roosts might be an issue, due its excrement and musky smell leading to considerable nuisance for humans.

Conservation actions:

On the basis of territorial legislation, all bats on La Réunion are protected by law (Arrêté of 17 April 1981 and of 17 February 1989) (Goodman *et al.*, 2008c: 1325). More details are needed on the ecology, bioacoustics, and dispersal patterns of La Réunion bats (Goodman, 2017f).

General distribution:

Mormopterus francoismoutoui has been recorded from a variety of localities on La Réunion from sea level to about 2,000 m (Moutou, 1982; Goodman *et al.*, 2008c).

Native: Réunion (Goodman *et al.*, 2008c: 1316).

Biogeography:

Aguillon *et al.* (2024: 1) estimated that these bats arrived on Reunion during a single colonisation event about 175,000 years ago, after which an in-situ diversification and evolution of divergent ancestral lineages took place. The population appeared to have expanded about 55,000 years ago.

General description of external morphology:

Mormopterus francoismoutoui is a relatively large member of the genus *Mormopterus*. Its dorsal body fur is short and dense with a rich dark brown color and its ventrum is slightly paler. Wing membrane and uropatagium are brownish black and show no noticeable change in pigmentation across their surface area. In adult males, there is a large glandular sac on the ventral portion of the lower neck; this gland is absent in females (Goodman *et al.* (2008c).

An albino specimen was reported by Ramasindrazana *et al.* (2014: 103) and Lucati and López-Baucells (2016: Suppl.).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^1/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 30

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2008c): The skull of *M. francoismoutoui*, as with most other members of this genus, is not noticeably flattened and has a long rostrum and well-developed lachrymal tubercles. The postorbital processes are well developed and distinctly shaped. The palatal emargination is well developed, similar to character state 4 for variable C65 of Freeman (1981b). Basisphenoid pits are present, but are not prominent, and there is a pronounced extension of the palatal spine descending onto the palatine bone.

SEXUAL DIMORPHISM:
The study by Aguillon *et al.* (2023: 9) showed that a subtle, but significant sexual dimorphism exitsted in the length of the forearm, with males being the larger. Adult females, on the other hand, had a higher BCI than males.

ECHOLOCATION:
Barataud and Giosa (2013: 150) analysed 253 sequences from *M. francoismoutoui* specimens on Réunion and found Fsub start: 64 ± 24.3 kHz, F_{end}: 41.5 ± 6.1 kHz, bandwidth: 24 ± 22.1 kHz, F_{max}: 45 ± 8.1 kHz and duration: 11.2 ± 2.9 ms.

MOLECULAR BIOLOGY:
Genetics
Dietrich *et al.* (2019: 6) developed 12 polymorphic molecular markers to facilitate further investigations into population genetics of this species.

Using mitochondrial DNA and microsatellite markers, Aguillon *et al.* (2024: 8) identified 410 haplotypes (in 603 sequences) for *mt*DNA and 1135 genotypes (in 1136 individuals) for the microsatellites.

HABITS:
The holotype and associated specimens roosting in the expansion joint of a bridge were observed to roost in a vertical position (head down) in very narrow crevices (Goodman *et al.*, 2008c: 1319).

ROOST:
Found in a variety of different roost sites, ranging from natural caves to synanthropic situations (Goodman *et al.*, 2008c). The holotype and associated specimens were extracted by hand from the expansion fissures in the lower portion of a concrete bridge (Goodman *et al.*, 2008c). Moutou (1982) found the species to roost in the crevices found in the rock faces around the island. It is also associated with a variety of human structures, including open roofs, roof slats, and window shutters (Goodman *et al.*, 2008c).

Augros *et al.* (2015: 374) provide an overview of 112 roosts, of which 74 (66 %) were artificial.

Aguillon *et al.* (2023: 2, 5) mention that the roosts are monospecific and can contain few hundred to tens of thousands of individuals. In one cave (of about 30 m^3), the authors estimated the number of bats possibly reaching 100,000 (based on a density of 900 bats/m^2). The roost size started to increase in October and reached its maximum around January-February (in one case by a factor of 400). Hoarau *et al.* (2023: 2) mention that the cave was only used from October to June, and that the females leave this cave about one month after parturition. From January onwards, the cave is primarily inhabited by newborns and juveniles.

MIGRATION:
The bats abandon Trois Bassins (with estimates of 10,000 to 25,000 individuals) during the austral winter, and it is not known where these bats spend the winter (Probst, 2003; Issartel, 2004; Devaux, 2006; Goodman *et al.*, 2008c).

POPULATION:
Structure and Density
The largest known day roost colony on La Réunion (at Trois Bassins), with estimates from 10,000 to 25,000 individuals, is abandoned in austral winter, and it is not known where these bats spend the winter (Devaux, 2006; Issartel, 2004; Probst, 2003; Goodman *et al.*, 2008c: 1325) [as *M. acetabulosus*]. While Goodman (2017f) report that this species is not correctly estimated but presumably substantial, with one maternity cave-dwelling colony estimated at 66,500 animals (Ramasindrazana *et al.*, 2014). In urban areas across the island, considerable numbers can be seen foraging at night around outside lighting (Goodman, 2017f).

Joffrin *et al.* (2022: 2) report on a 30 m^3 natural cave on the west coast of Réunion estimated to contain between 40,000 and 50,000 adult bats.

At the juvenile stage, both sexes were in equilibrium, but in adult bats, Aguillon *et al.* (2023: 6, 8) found a bias towards males (56%, based on captures at 19 roosts). A female biased sex ratio was found in the largest maternity roost. A sex ratio in favour of females was also observed during the summer (October to

December), whereas during the winter (June - July) more males were found.

Aguillon *et al.* (2024: 11) calculated that a major expansion of the population started about 55,000 years ago, and lasted for about 10,000 years. They also indicated that the population decline started about 500 years ago, well before humans colonised the island (about 350 years ago). Unfortunately, no data is available for the last few decades (p. 13).

Trend
2016: Increasing (Goodman, 2017f). 2008: Unknown (Hutson and Bergmans, 2008; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Aguillon *et al.* (2023: 2, 8, 10) mention that parturition takes place between December and February and this occurred in just a few roosts (one in a huge natural cave where bat density is very high, a second in an electric building (releasing heat), and a third under a sheet metal roof (accumulating heat during the day), all of these conditions probably offering warm conditions), but flying juveniles were observed in almost all roosts between January and September. Based on the structure of the epiphyses, juveniles were no longer identifiable after July (Aguillon *et al.*, 2023: 3).

MATING:
Aguillon *et al.* (2023: 11, 8) found that mating occurred in March and was followed by a seven month delay before the start of pregnancy. Most of the males were reproductively active from late January to early April, whereas 5 % were active in October.

PARASITES:
Laudisoit *et al.* (2012: 739) indicate that *M. francoismoutoui* is actually the type host for *Araeopsylla martialis* (Rothschild, 1903) (Syphonaptera; Ischnopsyllidae) and not "*Nyctinomus acetabulosus*".

Dietrich *et al.* (2015b: 4280) found similar infection dynamics for *Leptospira* bacteria and paramyxoviruses, which showed peak infections during late pregnancy and two months after the initial birth period. Both pathogens, however, did not seem to interact with one another.

Guernier *et al.* (2016: 1) found *M. francoismoutoui* on Réunion to be infected by *Leptospira borgpetersenii* bacteria, which also infect humans. However, these bacteria had different haplotypes, indicating that the bats do not have any role in human infections. Dietrich *et al.* (2018a: 2) mention the bacterium to be closely related to *L. borgpetersenii*.

VIRUSES:
Hoarau *et al.* (2023: 3) reported on co-infections. They found bats that were infected by both corona and paramyxoviruses (0.7 %), and to a lesser extent by corona and astroviruses (0.3 %) or by paramyxo and astrovirusesn (0.1 %) but never by the three.

Niu and McKee (2025: 232) mentioned that the shedding of viruses in this species has a clear seasonal pattern, with a peak in the weaning period, when neonates matured into juveniles. For Coronaviruses, the major peaks occurred in February and March, but there was also a minor peak in December, which aligned with the parturition season.

Astroviridae
Joffrin *et al.* (2021) reported on astroviruses collected from guano samples over a 28 month period.

Coronaviridae
Two bats tested by Hoarau *et al.* (2021: Suppl.) were posifive for viruses of this family. Joffrin *et al.* (2022: 1, 4) found virus shedding pulses during late pregnancy (December-January) and within two months of parturition (February-March).

Orthoherpesviridae/Herpesviridae
Aguillon *et al.* (2025: 1) reported a rapid herpesvirus (HSV) infection of juveniles (< 6 months). The prevalence of HSV was slightly lower in large colonies, but Aguillon *et al.* (2025: 6) indicated that this was linked to the presence of large numbers of juvenile bats, which showed low infection rates. The mean shedding prevalence in adults was 96.2 ± 0.65 %, whereas this in juveniles was 15.03 ± 5.66 % at the time they started to fly, but reached 60.67 ± 7.82 % after 6 months.

Paramyxoviridae
Nieto-Rabiela *et al.* (2019: Suppl.) reported Bat paramyxovirus to be present.
Data collected by Aguillon *et al.* (2025: 1) suggest that juveniles have a longer protection by maternal antibodies.

Rhabdoviridae
A large amount of bats from La Réunion were tested for lyssaviruses by Mélade *et al.* (2016a: 6), which resulted in the following numbers: *Lagos bat lyssavirus*: 3 seroreactions for 121 bats; *Duvenhage lyssavirus*: 14/117, and *European bat lyssavirus 1*: 9/82.

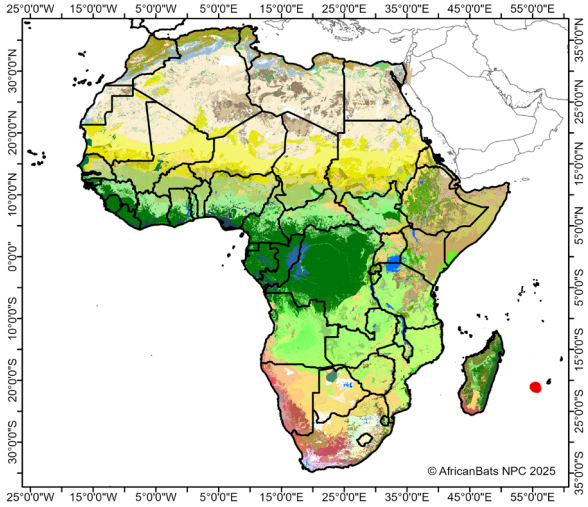

Figure 203. Distribution of *Mormopterus francoismoutoui*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Réunion.

Mormopterus jugularis (Peters, 1865)

*1865. *Nyctinomus (Mormopterus) jugularis* Peters, in: Sclater, Proc. zool. Soc. Lond., 1865, II: 468. Publication date: October 1865. Type locality: Madagascar: Antananarivo (formerly Tananarive) [18 55 S 47 31 E]. Holotype: ZMB 2977: ad ♂, skull and alcoholic. Collected by: Harry R. Caldwell. Presented/Donated by: William Lutley Sclater. See Turni and Kock (2008: 70).

1877. *Nyctinomus [(Mormopterus)] albiventer* Dobson, Proc. zool. Soc. Lond., 1876, IV: 733. Publication date: April 1877. Type locality: Madagascar: "Madagascar". [Goto Description]. Holotype: NHMUK 1863.12.26.1: ♀. - Comments: Type: NHMUK ???, ad ♀, alcoholic, purchased.

? *Mormopterus albiventer:*

? *Mormopterus jugularis:* (Name Combination, Current Combination).

TAXONOMY:
See Simmons (2005: 445).

COMMON NAMES:
Czech: morous Petersův. English: Peters's Goblin bat, Peters's Wrinkle-lipped Bat, Peters' Wrinkle-lipped Bat. French: Sauromys à jugulaire, Sauromys de Peters, Tadaride de Madagascar. German: Madagaskar Mastino-Fledermaus. Japanese: Pita-ohiki-koumori.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Muldoon *et al.* (2009: 1114) report on subfossil remains from the Ankilitelo fauna (late Holocene, appr. 500 years ago).
Gunnell *et al.* (2014: 3) refer to fossil material from Tsimanampetsotsa (one tooth and a few pieces of a forelimb according to Sabatier and Legendre (1985: 23)), Ankilitelo, and Andrahomana on Madagascar.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread distribution across Madagascar and because it is not thought to be facing any major threats across its range (Andriafidison *et al.*, 2008g; IUCN, 2009; Monadjem *et al.*, 2017cb).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cb). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008g; IUCN, 2009). 1996: VU A2c ver 2.3 (1994) (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is not threatened by loss of native forests because it forages in open areas associated with agriculture. It is locally persecuted when roosting in buildings although this is not yet a major threat. Some colonies are subject to hunting and although this is thought to have resulted in abandonment in at least two cases (Goodman *et al.*, 2008d), harvest levels do not appear a major threat (Andriafidison *et al.*, 2008g; IUCN, 2009; Monadjem *et al.*, 2017cb).

Fernández-Llamazares *et al.* (2018: 273) indicate that *M. jugularis* is often hunted in sacred caves in and around the Tsimanampetsotsa National Park, although in the park, it is generally restricted to periods of famine, e.g., in 2007, when the bats fed 200 people for two months.

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008g) [in IUCN (2009)] and Monadjem *et al.* (2017cb) report that as this species is more commonly found roosting in buildings than natural settings it is not found in many of the protected areas in Madagascar (Goodman *et al.*, 2005a). However, there is no need for any conservation measures at present as this species appears to be widely distributed and is locally abundant.

GENERAL DISTRIBUTION:
Mormopterus jugularis is endemic to Madagascar (Peterson *et al.*, 1995) and very widespread (but patchy) across the island with a known distribution extending from the coast up to the high plateau at 1,400 m in Anjozorobe (J. Ranivo *pers. comm.,* in Andriafidison *et al.*, 2008g; IUCN, 2009).

Native: Madagascar (Peterson *et al.*, 1995; Simmons, 2005: 445)

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 62) describe the baculum of this species as proportionately broad at the proximal, rounded base and tapering to a rounded distal tip. In lateral view, the structure has a slight curve to the main shaft; length: 0.69 ± 0.015 (0.68 - 0.71) mm, width: 0.24 ± 0.016 (0.22 - 0.26) mm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Garbutt (2007) and Taylor *et al.* (2012a)] mention a wing loading value of 13.4 Pa, aspect ratio 7.9 for a wingspan of 25 cm and a wing area of 80 cm^2 and a body mass of 11 g.

ECHOLOCATION:
Hending *et al.* (2023: 372) reported F_{peak}: 32.6 ± 2.8 kHz, duration: 23 ± 16 ms, and interpulse interval: 195 ± 079 ms.

MOLECULAR BIOLOGY:
Karyotype
Richards *et al.* (2010) reported one male with a 2*n*=48 and a FNa=54. They found one large metacentric, three medium-sized metacentric and 19 acrocentric autosomal pairs. The X chromosome is submetacentric and the Y chromosome is metacentric. FISH using *Myotis* probes was also applied.

Volleth *et al.* (2023b: 6) reported one male with a 2*n*=48 and a FNa=60. The X chromosome was medium-sized submetacentric with the proximal third of the long arm darker stained after C-banding, whereas the Y chromosome was a small submetacentric and nearly completely heterochromatic and about half the size of the X. The difference in FNa number is attributed to the identification of three subtelocentric chromosomal pairs (p. 26).

HABITAT:
Dammhahn and Goodman (2013: 108) indicate that this species' foraging habitat consists of open areas and the area above the forest canopy.

ROOST:
Synantropic structures are the typical roosting sites for this species on Madagascar (Wilkinson *et al.*, 2012: 160). The roosts usually contain less than 100 animals, but a cave in Ankarana housed over 22,000 bats (Garbutt, 2022: 94).

MIGRATION:
Reher *et al.* (2019: 121) found that *M. jugularis* was only present in a southwestern Madagascan cave during the rainy season, whereas other species such as *Triaenops menamena* and *Miniopterus mahafaliensis* were present in both the dry and wet season.

DIET:
Kemp *et al.* (2018: Suppl.) used DNA metacarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Coleoptera (*Xyleborus ferrugineus* (Fabricius, 1801)), Ephemeroptera, Diptera (*Simulium lineatum* (Meigen, 1804), *Culex annulioris* Theobald, 1901, *Culex* MBI-27, *Anopheles squamosus* Theobald, 1901), Lepidoptera (*Meyrickiella homosema* (Meyrick, 1887), *Herpetogramma licarsisalis* (Walker, 1859)), Blattodea, Dermaptera, Hemiptera, Neuroptera, Orthoptera, Sarcoptiformes, Astigmata, Hymenoptera

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of three individuals in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar. Other predators include the barn owl (*Tyto alba* (Scopoli, 1769) and the Madagascar Long-eared Owl (*Asia madagascariensis* (A. Smith, 1834).

POPULATION:
Structure and Density
There are no quantitative data available on populations of this species; however, it is assumed to have a high population size because it is widespread and roosts in large colonies in buildings (Andriafidison *et al.*, 2008g; IUCN, 2009; Monadjem *et al.*, 2017cb).

Trend
2016: Unknown (Monadjem *et al.*, 2017cb).
2008: Unknown (Andriafidison *et al.*, 2008g; IUCN, 2009).

PARASITES:
Lagadec *et al.* (2012: 1696) and Gomard *et al.* (2016: 5) report the presence of *Leptospira* sp bacteria in this species, which, according to Dietrich *et al.* (2018a: 3), were having sequences closely related to *L. borgpetersernii*

Laudisoit *et al.* (2012: 739) refer to Lumaret (1962), who reported the present of *Araeopsylla martialis* (Rothschild, 1903) (Siphonaptera; Ischnopsyllidae) on "*Tadarida albiventer*" [= *M. jugularis*]. This flea was also reported by Hastriter (2016: 15) and Duchemin *et al.* (2022: 1077).

Durette-Desset and Chabaud (1975: 10) described the Nematode *Molinostrongylus richardae* from a "*Mormopterus albiventer*" from Anjiro, Madagascar.

VIRUSES:
Coronaviridae
Joffrin *et al.* (2020: 5) reported an Alphacoronavirus from a bat from Madagascar.

Flaviviridae
Flavivirus
Reynes *et al.* (2011: 3) reported the isolation of Dakar bat virus from *M. jugularis*.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 13 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids. Wilkinson *et al.* (2014) tested 19 individuals in Madagascar with an RT-PCR specific for the Respiro-, Morbilli- and Henipavirus genera, two of the 19 individuals tested positive for paramyxovirus RNA.

12 out of 152 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

Rhabdoviridae
58 specimens were tested by Mélade *et al.* (2016a: 6), which laid to three seroreactive results for *Lagos bat lyssavirus* and 17 for *Duvenhage lyssavirus*.

UTILISATION:
See Goodman *et al.* (2008d).

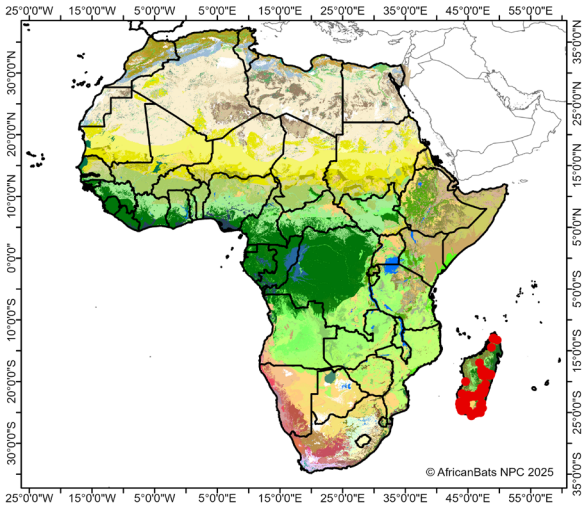

Figure 204. Distribution of *Mormopterus jugularis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Genus ***Myopterus*** E. Geoffroy St.-Hilaire, 1818

*1818. *Myopterus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 113. Publication date: 1818 [Goto Description]. - Comments: Type species: *Myopterus senegalensis* Oken, 1816 (not available) (=*Myopteris daubentonii* Desmarest, 1820). - Etymology: From the Greek "*μύς*" or "*έμυός*", meaning mouse and "*πτέρυξ*", meaning wing (see Palmer, 1904: 440). (Current Combination).
1820. *Myopteris* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 131. Publication date: 1820. - Comments: Type: *Myopteris daubentonii* Desmarest, 1820.
1837. *Myoptera* de Blainville, C. R. séances Acad. Sci., Paris, 5: 815. Publication date: 1837.
1905. *Eomops* Thomas, Ann. Mag. nat. Hist., ser 7, 16 (95): 572. Publication date: 1 November 1905 [Goto Description]. - Comments: Type species: *Mormopterus whitleyi* Scharff, 1900.

TAXONOMY:
Includes *Eomops*; see Hayman and Hill (1971: 56). Grubb *et al.* (1998: 97) indicate that *Myopterus* Oken, 1816, Lehrbuch Naturgesch. Pt 3, Zool. Sect. 2: 952, type species *Myopterus senegalensis* Oken (= *Myopteris daubentonii* Desmarest, 1820), is not available according to Opinion 417 of the ICZN.

Grubb *et al.* (1998: 97) indicate that Mahoney and Walton (1988a: 116) considered the date of Geoffroy's publication to be 1813. Gardner and Hayssen (2004: 12) mention that the correct date

should be 1818, not 1813 as mentioned on the publication itself.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Myopterus*: ***daubentonii*** Desmarest, 1820; ***whitleyi*** (Scharff, 1900).

Myopterus daubentonii Desmarest, 1820

1816. *Myopterus senegalensis* Oken, Lehrbuch Naturgeschichte, Jena, 3 (2): 952. Type locality: Senegal. Lectotype: MNHN ZM-MO-1985-1718: ad ♀, skull and alcoholic. Collected by: René Vuattoux; collection date: 10 September 1966. Paralectotype: MNHN ZM-MO-1990-53: ad ♂, skull and alcoholic. Collected by: René Vuattoux; collection date: 10 September 1966. - Comments: Not available (Opinion 417 of the ICZN) see Grubb *et al.* (1998: 97).

*1820. *Myopterus daubentonii* Desmarest, Encyclopédie Méthodique, (Zoologie, Mammalogie), 1: 132. Publication date: 1820. Type locality: Senegal: "Senegal". Holotype: [Unknown] lost. See Koopman (1993a: 238). Neotype: MNHN ZM-MO-1982-1035: ad ♂, skull and alcoholic. Collected by: René Château; collection date: 16 March 1973. Paraneotype: MNHN ZM-MO-1982-1034: ♂, skull and alcoholic. Collected by: René Château; collection date: 16 March 1973. - Comments: Type specimen lost (see Koopman, 1993a: 238). - Etymology: In honour of the French naturalist Louis-Jean-Marie d'Aubenton [=Daubenton] (1716 - 1799/1800) (see Bogdanowicz, 1994: 5; Kozhurina, 2002: 15). (Current Combination).

1915. *Myopterus albatus* Thomas, Ann. Mag. nat. Hist., ser 8, 16 (96): 469. Publication date: 1 December 1915. Type locality: Congo (Democratic Republic of the): Uele River [04 09 N 22 26 E]. [Goto Description]. Holotype: NHMUK 1919.5.9.1: Collected by: M. Hutereau; original number: 17. Congo Museum o. 2911.

? *Myopterus daubentonii albatus:* (Name Combination).

Taxonomy:
Koopman (1989a) and Simmons (2005) recognise *albatus* Thomas, 1915 as a subspecies. Allen (1939a: 110) used *Myopterus senegalensis* Oken, 1816 for this species.

Common Names:
Czech: morous krysový, spaka krysová. English: Daubenton's Winged-mouse Bat, Daubenton's Free-tailed Bat, Senegal Mastiff Bat. French: Myoptère de Daubenton, Myoptère du Sénégal. German: Daubentons Pergamentflügel-Fledermaus.

Conservation status:
Global Justification

Listed as Data Deficient (DD ver 3.1 (2001)) since, although it has been recorded over a very wide area, there are only very few records, and very little is known with certainty about its distribution, threats and habitat requirements (Mickleburgh *et al.*, 2008bc; IUCN, 2009; Mickleburgh *et al.*, 2019i).

Assessment History

Global

2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019i). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008bc; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004ca; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional

None known.

Common Names:
Czech: krysoví morousi, spaky. English: Winged-mouse Bats, African Free-tailed Bats, Winged-rat Free-tailed Bats. French: Myoptères. German: Pergamentflügel-Fledermäuse.

Major threats:
The species is generally threatened by habitat loss, especially the removal of potential roost trees (Mickleburgh *et al.*, 2008bc; IUCN, 2009; Mickleburgh *et al.*, 2019i).

Conservation actions:
Mickleburgh *et al.* (2008bc) [in IUCN (2009)] and Mickleburgh *et al.* (2019i) report that there appear to be no direct conservation measures in place, and it is not known if the species is present within any protected areas. Further studies are needed into the distribution, natural history and threats to this bat.

General distribution:
Myopterus daubentonii is patchily recorded from eight localities in West and Central Africa. It has been reported from Côte d'Ivoire, Central African Republic and northern Democratic Republic of the Congo. It is generally a lowland species but has been found up to 1,250 m asl.

Native: Central African Republic; Congo (The Democratic Republic of the); Côte d'Ivoire; Senegal.

Echolocation:
Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

Roost:
Brosset and Vuattoux (1968: 85) reported five specimens from Côte d'Ivoire (as *M. senegalensis*), that were captured in a hollow

trunk of a Borassus palm (*Borassus aethiopum*). The tree was standing in a savanna area, but only a few hundred meters from a gallery forest. The bats were roosting at an altitude of about 12 meters.

POPULATION:
Structure and Density
This appears to be a rare species, known from very few specimens (Mickleburgh *et al.*, 2008bc; IUCN, 2009; Mickleburgh *et al.*, 2019i).

Trend
2018: Unknown (Mickleburgh *et al.*, 2019i). 2008: Unknown (Mickleburgh *et al.*, 2008bc; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Senegal.

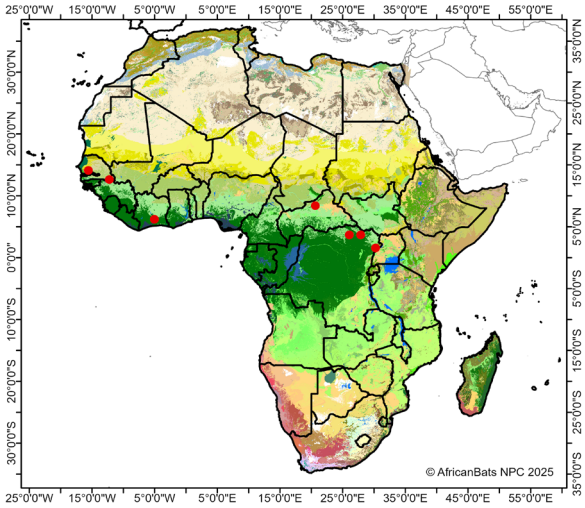

Figure 205. Distribution of *Myopterus daubentonii*.

Myopterus whitleyi (Scharff, 1900)

*1900. *Mormopterus Whitleyi* Scharff, Ann. Mag. nat. Hist., ser 7, 6 (36): 569. Publication date: 1 December 1900. Type locality: Nigeria: Mid-Western Region, Nikrowa Forest Reserve, Sapoba: Benin City [06 19 N 05 41 E]. [Goto Description]. Holotype: NHMUK 1900.10.26.1: ad ♂, skull and alcoholic.
? *Myopterus whitleyi:* (Name Combination, Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: morous západoafrický. English: Bini Winged-mouse Bat, Whitley's Winged-mouse Bat, Bini Free-tailed Bat. French: Myoptère de Whitley, Myoptère de Bini. German: Whitleys Pergamentflügel-Fledermaus, Bini Pergamentflügel-Fledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008bd; IUCN, 2009; Monadjem *et al.*, 2017ba).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ba). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008bd; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004cf; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is presumably threatened by general conversion of forest to agricultural land and logging activities (Mickleburgh *et al.*, 2008bd; IUCN, 2009; Monadjem *et al.*, 2017ba).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008bd) [in IUCN (2009)] and Monadjem *et al.* (2017ba) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the species distribution, natural history, and adaptability to habitat degradation.

GENERAL DISTRIBUTION:
Myopterus whitleyi is distributed in West and Central Africa. It has been recorded from Ghana in the west, through parts of Nigeria, Cameroon, Gabon, and the Democratic Republic of the Congo to western Uganda in the east.

Native: Cameroon; Central African Republic (Barrière *et al.*, 2002: 234); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 545); Gabon; Ghana; Nigeria; Uganda.

POPULATION:
Structure and Density
It is generally considered to be a rare species. It is found roosting singly or in small numbers (Mickleburgh *et al.*, 2008bd; IUCN, 2009; Monadjem *et al.*, 2017ba).

Trend
2016: Decreasing (Monadjem *et al.*, 2017ba).
2008: Decreasing (Mickleburgh *et al.*, 2008bd; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Gabon, Ghana, Nigeria, Uganda.

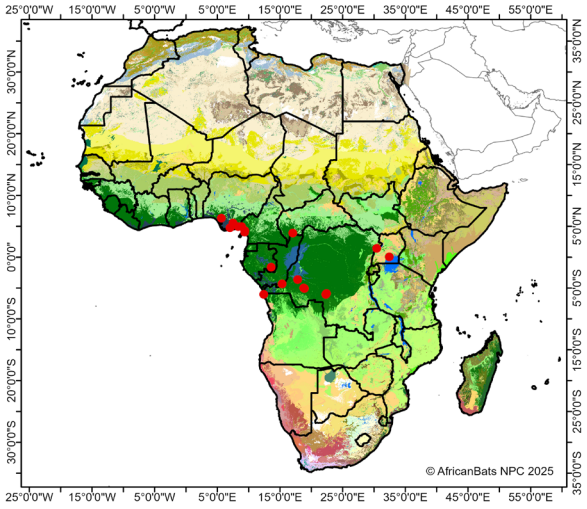

Figure 206. Distribution of *Myopterus whitleyi*.

Genus ***Otomops*** Thomas, 1913

*1913. *Otomops* Thomas, J. Bomb. nat. Hist. Soc., 22: 91. Publication date: April 1913. - Comments: Type species: *Nyctinomus wroughtoni* Thomas, 1913. - Etymology: From the Greek substantive "*οὖς*" (genitive "*ὠτός*", "*ûs*", "*ōtós*"), meaning "ear" and the masculine German substantive *Mops*, as the genus has outstandingly large ears (see Lanza *et al.*, 2015: 309). - Phonetics: oh'-toh-mops. (Current Combination).

TAXONOMY:
Richards *et al.* (2012: 910) suggest that three distinct taxa might be recognized in Africa: *Otomops madagascariensis* from Madagascar; *O. martiensseni* s.s. from southern, eastern, central, and western Africa; and an "undescribed taxon" (now identified as *O. harrisoni*) from north-east Africa and the Arabian Peninsula.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Otomops*: *formosus* Chasen, 1939 – Java (Simmons, 2005: 447); ***harrisoni*** Ralph, Richards, Taylor, Napier, and Lamb, 2015; *johnstonei* Kitchener, How and Maryanto, 1992 – Alor Isl (Indonesia) (Simmons, 2005: 447); ***madagascariensis*** Dorst, 1953; ***martiensseni*** (Matschie, 1897); *papuensis* Lawrence, 1948 – southeastern New Guinea (Simmons, 2005: 448); *secundus* Hayman, 1952 – northeastern New Guinea (Simmons, 2005: 448); *wroughtoni* (Thomas, 1913) – southern and northeastern India, Cambodia (Simmons, 2005: 448).

COMMON NAMES:
Czech: velkouší morousi. English: Big-eared Bulldog Bats, Big-eared Free-tailed Bats, Mastiff Bats. French: Molosses à grandes oreilles. German: Riesen-Bulldoggfledermäuse. Italian: Otocarlìno.

ETYMOLOGY OF COMMON NAME:
So named because they have outstanding large round-pointed ears that are attached along the nose and lie in the plane of the face (see Taylor, 2005).

BIOGEOGRAPHY:
Lamb *et al.* (2008) suggests that African and Oriental *Otomops* lineages diverged around 4.2 Myr, while Malagasy and African lineages split around 1.5 Mya.

MOLECULAR BIOLOGY:
Genetics
Patterson *et al.* (2018: 7) found the average interspecific genetic distance (uncorrected cyt-*b* p-distance) between *O. harrisoni* and *O. martiensseni* to be 2.5 %.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burundi, Kenya, Madagascar, Rwanda.

Otomops harrisoni Ralph, Richards, Taylor, Napier and Lamb, 2015

*2015. *Otomops harrisoni* Ralph, Richards, Taylor, Napier and Lamb, Zootaxa, 4057 (1): 1, 18, figs 8 - 10. Publication date: 9 December 2015. Type locality: Ethiopia: Bale district: Sof Omar Cave [06 54 N 40 48E, 1340 m]. Holotype: HZM 60.36217: ad ♂, skull and alcoholic. Collected by: Paul Jeremy James Bates, Malcolm J. Pearch and O. Nurhussein; collection date: 19 July 1998; original number: A51. Paratype: HZM 40.31315: ad ♂. Collection date: 19 July 1998. Paratype: HZM 41.31316: ad ♀. Collection date: 19 July 1998. Paratype:

HZM 42.31317: ad ♀. Collection date: 19 July 1998. Paratype: HZM 43.31318: ad ♀. Collection date: 19 July 1998. Paratype: HZM 44.31328: ad ♂. Collection date: 19 July 1998. Paratype: HZM 56.36213: ad ♀. Collection date: 19 July 1998. Paratype: HZM 57.36214: ad ♀. Collection date: 19 July 1998. Paratype: HZM 58.36215: ad ♀. Collection date: 19 July 1998. Paratype: HZM 59.36216: ad ♀. Collection date: 19 July 1998. Paratype: HZM 61.36218: ad ♀. Collection date: 19 July 1998. Paratype: HZM 62.36219: ad ♀. Collection date: 19 July 1998. Ralph *et al.* (2015: 19) mention "(also DM 14750)". Paratype: HZM 63.36220: ad ♀. Collection date: 19 July 1998. Paratype: HZM 64.36221: ad ♂. Collection date: 19 July 1998. - Etymology: In honour of Dr. David L. Harrison (1926 - 2015), who's numerous publications on Afro-Arabian Chiroptera, in particular the Molossidae, have significantly improved our knowledge of this poorly known family (Ralph *et al.* (2015: 20).

? *Otomops martiensseni:*

Common Names:

Chinese: 哈氏巨犬吻蝠. English: Harrison's large-eared giant mastiff bat. German: Harrison-Riesen-Bulldoggfledermaus

Similar Species:

Ralph *et al.* (2015: 25) report that *O. harrisoni* is in general larger than other *Otomops* species.

Conservation status:

Patterson *et al.* (2018: 11) report the status of *O. harrisoni* as Vulnerable.

General distribution:

Native: Djibouti; Eritrea (Kock and Zinner, 2004: 3 as *O. martiensseni*); Ethiopia (in a disused railway tunnel 8 km east of Asmara) for the first time (Kock and Zinner, 2004: 3 as *O. martiensseni*); Kenya (Patterson *et al.*, 2018: 1), Rwanda (Patterson *et al.*, 2018: 1) and Yemen (Hud Sawa cave, Ar-Rayadi Al-Gharbi Mountains) on the Arabian Peninsula (Al-Jumaily, 1999; Hutson *et al.*, 2001 as *O. martiensseni*).

Ralph *et al.* (2015: 27) suggest that the range might include additional localities in Uganda, northern areas of Tanzania and southern areas of Somalia.

Patterson *et al.* (2018: 1) found both O. martiensseni and *O. harrisoni* in a cave in the Musanze district, Rwanda. As they found both species in Kenya, they also caution the identifications of *Otomops* specimens from that country, especially those from Kwale, Lake Baringo, Nairobi, Naivasha, and
Wei-Wei River (p. 11).

Dental Formula:

The permanent dental formula of *O. harrisoni* is $I^1/_2$, $C^1/_1$, $PM^2/_2$, $M^3/_3$ = 30, characteristic of molossid bats (see Ralph *et al.*, 2015: 26).

Echolocation:

Ralph *et al.* (2015: 26) indicate that Taylor *et al.* (2005) reported the following values for *O. martiensseni* specimens from Bungule, Kenya: F_{peak}: 12.00 kHz, F_{min}: 10.50 kHz, F_{max}: 50 kHz, and duration of 9.00 ms. However, since this locality is equidistant from localities were either *O. martiensseni* or *O. harrisoni* was found, the taxonomic assignment of the specimens involved remains uncertain.

Patterson *et al.* (2018: Suppl.) recorded the following parameters for 10 Kenyan specimens identified as "*O.* cf. *harrisoni*: F_{max}: 13.99 ± 2.93 (9.52 - 17.95) kHz, F_{start}: 19.35 ± 3.50 (10.72 - 21.90) kHz, F_{end}: 11.58 ± 1.17 (9.63 - 13.13) kHz, duration: 10.13 ± 2.46 (7.04 - 15.16) ms. However, they also found (p. 7) differences between *O. harrisoni* populations from two localities in Kenya: Chyulu Hills: F_{peak}: 17.18 ± 0.42 (16.40 - 17.95) kHz, F_{max}: 21.67 ± 0.10 (21.48 - 21.90) kHz, F_{min}: 12.53 ± 0.29 (11.80 - 13.13) kHz and call duration: 10.72 ± 1.10 (7.57 - 12.67) ms; and Mount Suswa: F_{peak}: 11.86 ± 0.72 (9.52 - 13.80) kHz, F_{max}: 17.81 ± 1.70 (10.72 - 21.62) kHz, F_{min}: 110.94 ± 0.47 (9.63 - 12.80) kHz and call duration: 9.74 ± 1.21 (7.04 - 15.16) ms.

Molecular Biology:

Karyotype
Warner *et al.* (1974) reported 2*n* = 48, FN = 58, BA = 12, a submetacentric X chromosome and a submetacentric Y chromosome for one male *O. martiensseni* specimen from Kenya, which differed from previously reported karyotypes. It is therefore possible that this male might have been a representative of *O. harrisoni*.

Habitat:

Ralph *et al.* (2015: 27) mention that these bats are found at high altitudes (above 1,000 m) characterised by relatively drier climates (< 500 mm annual precipitation), including warm semi-arid, tropical savanna, warm desert and temperate oceanic climates (e.g., the Ethiopian highlands).

Roost:

Ralph *et al.* (2015: 27) indicate that individuals roost predominantly in mountain-associated cave systems and lava caves.

Diet:

Faecal data from Ethiopia indicate that medium (size range: 1 - 5 cm) to large (wing span size range: 2.5 - 30 cm) Lepidoptera (Noctuidae,

Geometridae and Saturniidae) form 97 % by volume of this bat's diet (see Ralph *et al.*, 2015: 26).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
At Mount Suswa (Kenya), Patterson *et al.* (2018: 10, Suppl.) found the following ectoparasites: *Brachytarsina alluaudi* (Falcoz, 1923) [Diptera, Hippoboscidae], *Hypoctenes clarus* (Jordan, 1922) [Hemiptera, Polyctenidae], *Lagaropsylla* sp. [Siphonaptera, Ischnopsyllidae], and some unidentified Argasidae and Macronyssidae.

VIRUSES:
Kamau *et al.* (2022: 5) reported coronaviruses and retroviruses from bats from a cave at Mount Suswa, Kenya.

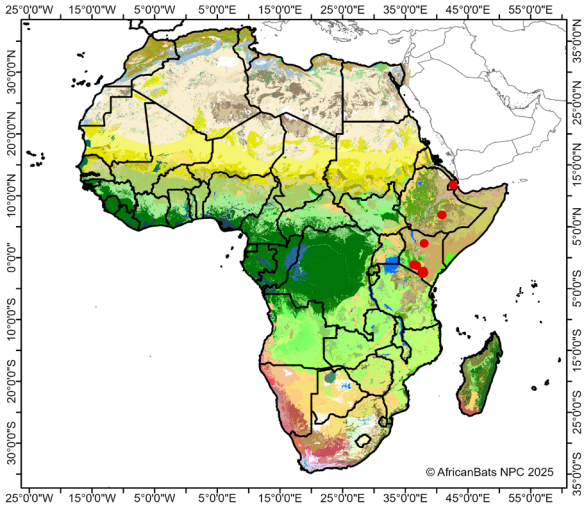

Figure 207. Distribution of *Otomops harrisoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Djibouti, Ethiopia, Kenya.

Otomops madagascariensis Dorst, 1953

*1953. *Otomops madagascariensis* Dorst, Mém. Inst. Scient. Madagascar, (A) 8: 236. Type locality: Madagascar: S of Soalala: Namoroka, Réserve Naturelle: Cave P. Saboureau, No. 8 [16 23 S 45 28 E]. Holotype: MNHN ZM-MO-1953-1: ad ♀, skull and alcoholic. Collected by: Renaud ("René") Paulian; collection date: September 1952. See Peterson *et al.* (1995: 181), Richards *et al.* (2012: 912). Paratype: MNHN ZM-MO-1985-442: ad ♀, alcoholic (skull not removed). Collected by: Renaud ("René") Paulian; collection date: September 1952. - Etymology: Referring to the island where this taxon occurs. (Current Combination).
2000. *Otomops martiensseni madagascarensis:* Horáček, Hanák and Gaisler, Bats of the Palearctic region. (Lapsus).
? *Otomops madagascariensis madagascariensis:* (Name Combination).
? *Otomops martiensseni madagascariensis:* (Name Combination).

TAXONOMY:
Previously recognised as a subspecies or synonym of *Otomops martiensseni* (Koopman, 1993a: 239). Valdivieso *et al.* (1979) listed it as a distinct species, as did Peterson *et al.* (1995: 183) and Russ *et al.* (2001). We are (yet) unable to confirm whether the original spelling is *madagascariensis* (see Koopman, 1993a: 239, Peterson *et al.*, 1995, Russ *et al.*, 2001, Simmons, 2005: 447) or *madagascarensis* (see Horáček *et al.*, 2000: 137; Fenton *et al.*, 2002: 1584).

COMMON NAMES:
Czech: morous madagaskarský. English: Madagascar Large-eared Free-tailed Bat, Madagascar Free-tailed Bat, Madagascar Giant Free-tailed bat, Madagascar Mastiff Bat. French: Molosse à grandes oreilles de Madagascar. German: Madagassische Riesen-Bulldoggfledermaus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Muldoon *et al.* (2009: 1114) report on subfossil remains from the Ankilitelo fauna (late Holocene, appr. 500 years ago).

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread but patchy distribution in Madagascar. It is not well known in Madagascar, but it is likely distributed more widely than current records suggest and it is unlikely that it is declining at a rate that would warrant listing in a higher category of threat (Andriafidison *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017cd).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cd). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008l; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The threats to this species are unclear, but more research is needed into possible disturbance at its roost sites (Andriafidison *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017cd).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008l) [in IUCN (2009)] and Monadjem *et al.* (2017cd) report that this species roosts in one cave that is locally protected by 'fady' or taboo (Andriafidison *et al.*, 2007). It has been recorded from five protected areas: Parc National du Tsingy de Bemaraha, Parc National de Namoroka, Parc National d'Isalo, Réserve Spéciale d'Ankarana and Réserve Spéciale d'Analamerana (Goodman *et al.*, 2005a). A total of nine roosting colonies are currently known: six in Réserve Spéciale d'Ankarana (Cardiff, 2006), two in Parc National du Tsingy de Bemaraha (Andriafidison *et al.*, 2007) and one in Sarodrano (Goodman *et al.*, 2005a; Andriafidison *et al.*, 2007), and all receive some form of protection. More research is needed on its roosting ecology and surveys are required in areas where this species is expected to occur.

GENERAL DISTRIBUTION:
Otomops madagascariensis is endemic to the island of Madagascar where it has a disjunct distribution from the north to the south-west of the island. It has an elevation range of 5 m to 800 m above sea level (Goodman *et al.*, 2005a), where it occurs in dry deciduous and spiny bush areas (Garbutt, 2022: 97).

O'Brien (2011: 289) reports it from the Tanzanian island of Mafia.

Native: Madagascar (Valdivieso *et al.*, 1979; Peterson *et al.*, 1995: 183; Russ *et al.*, 2001; Simmons, 2005: 447).

DETAILED MORPHOLOGY:
Baculum
The baculum of *O. madagascariensis* is an elongated rod with a notable twist to the mid-shaft. In lateral view, its proximal portion is distinctly wider than the proximal end (Rakotondramanana and Goodman, 2017: 62); length: 0.74 ± 0.057 (0.65 - 0.80) mm, width: 0.13 ± 0.028 (0.09 - 0.18) mm.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Taylor *et al.* (2012a) and Dammhahn and Goodman (2013)] mention a wing loading value of 12.9 Pa, aspect ratio 8.3 for a wingspan of 39 cm and a wing area of 183 cm^2 and a body mass of 24 g.

ECHOLOCATION:
Hending *et al.* (2023: 372) mention a F_{peak} of 17.3 ± 1.9 kHz, duration:31 ± 36 0.ms and Interpulse interval of 423 ± 148 ms.

MOLECULAR BIOLOGY:
Genetics
See Lamb *et al.* (2008).

HABITAT:
Dammhahn and Goodman (2013: 108) report that this species' foraging habitat includes open areas and the area above the forest canopy.

ROOST:
Otomops madagascariensis is an obligate cave-dweller (Betke *et al.*, 2024: 1), which roosts in limestone or sandstone (Goodman *et al.*, 2005a; Andriafidison *et al.*, 2007), where the colonies can count to 100 animals.

DIET:
This bat's diet primarily consists of moths (Lepidoptera - 43.5 %) and beetles (Coleoptera - 38.9 %), with smaller quantities of flies (Diptera), bugs (Hemiptera) and mayflies (Ephemeroptera) (Garbutt, 2022: 97; Goodman *et al.*, 2022: 1905).

PREDATORS:
O. madagascariensis is predated by Barn Owl (*Tyto alba* (Scopoli, 1769)) and Bat Hawk (*Macheiramphus alcinus* Bonaparte, 1850) (Garbutt, 2022: 97).

POPULATION:
Structure and Density
The colony of *O. madagascariensis* in a cave in the south of Parc National du Tsingy de Bemaraha consisted of between 90 and 100 individuals in 2003 (Andriafidison *et al.*, 2007). The Sarodrano roost in the south of Madagascar contained at least 67 animals in November 2003 (Andriafidison *et al.*, 2007). The maximum colony size at Réserve Spéciale d'Ankarana was 97 individuals (S. G. Cardiff *pers. comm.* [in Andriafidison *et al.* (2008l) in IUCN (2009); Monadjem *et al.*, 2017cd]).

Trend
2016: Unknown (Monadjem *et al.*, 2017cd).
2008: Unknown (Andriafidison *et al.*, 2008l; IUCN, 2009).

PARASITES:
Lagadec *et al.* (2012: 1696), Lei and Olival (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of *Leptospira* sp. bacteria in this

species, which were identified as having sequences closely related to *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

Laudisoit *et al.* (2012) describe a new species *Lagaropsylla makay* (Siphonaptera; Ischnopsyllidae), and they also mention a new parasite-host association between *Araeopsylla martialis* (Rothschild, 1903) (Siphonaptera; Ischnopsyllidae) and *O. madagascariensis* (see also Duchemin *et al.*, 2022: 1077).

Ramasindrazana *et al.* (2016: 6) report the presence of an unnamed filariod in this bat species.

VIRUSES:

Paramyxoviridae

Wilkinson *et al.* (2012: 160) tested 8 individuals from the Madagascar using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids. Wilkinson *et al.* (2014) tested 18 individuals from Anjohikinakina in Madagascar with an RT-PCR specific for the *Respiro-*, *Morbilli-* and *Henipavirus* genera, five of the 18 individuals tested positive for paramyxovirus RNA.

Seven out of 39 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

Rhabdoviridae

Mélade *et al.* (2016a: 6) examined 20 specimens for *Lagos bat lyssavirus* and got three positive results. Four out of 18 animals had a positive outcome for *Duvenhage lyssavirus*.

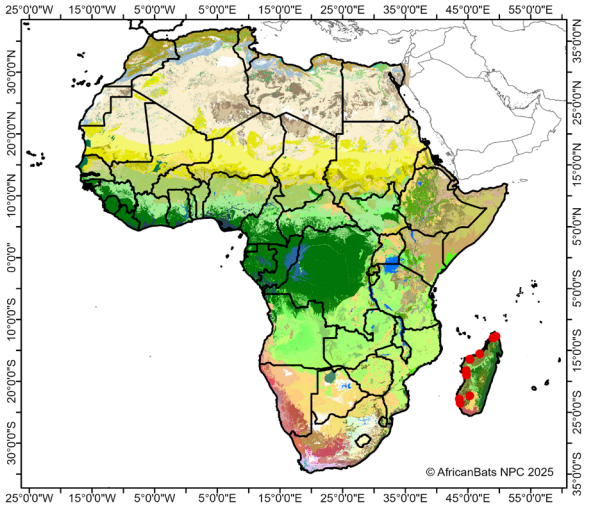

Figure 208. Distribution of *Otomops madagascariensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Otomops martiensseni (Matschie, 1897)

*1897. *Nyctinomus martiensseni* Matschie, Arch. Naturgesch. Berlin, 63 (1): 84. Publication date: October 1897. Type locality: Tanzania: 25 mi W of Tanga, SE portion of W Usambara Mts: Magrotto Plantation [05 07 S 38 45 E]. [Goto Description]. Holotype: ZMB 97523: ♂, skin and skeleton and skull. Collected by: G. Martienssen; collection date: August 1897. See Turni and Kock (2008: 71). - Comments: Horáček *et al.* (2000: 137) mention the type locality as "Usanbara Mts., W of Tanga, NE Tanzania". Grubb *et al.* (1998: 98) indicate that the locality has been defined by Swynnerton, 1945, Proc. Zool. Soc. Lond., 115: 63). - Etymology: In honour of "Herr Martienssen of the Königlich Museum für Naturkunde" who found the type specimen (see Long, 1995: 4).

1966. *Otomops maertiensseni:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: pl XX. Publication date: December 1966. (Lapsus).

2017. *O[tomops] martiensenni:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 10. Publication date: 6 April 2017. (Lapsus).

2017. *Otomops martiensenii:* Waruhiu, Ommeh, Obanda, Agwanda, Gakuya, Ge, Yang, Wu, Zohaib, Hu and Shi, Virol. Sin., 32 (2): 7. Publication date: 6 April 2017. (Lapsus).

2017. *Otomops martienssi:* Tao, Shi, Chommanard, Queen, Zhang, Markotter, Kuzmin, Holmes and Tong, J. Virol., 91 (5) e01953-16: Suppl. Publication date: 11 January 2017. (Lapsus).

? *Otomops martiensseni:* (Name Combination, Current Combination).

TAXONOMY:

Koopman (1993a: 239) included *madagascariensis*, but see Peterson *et al.* (1995: 183), Long (1995) and Simmons (2005: 447). Lamb *et al.* (2008: 30) indicate that there are two clades in *martiensseni*, of which "clade 1" (north-east Africa + Yemen) would constitute an undescribed taxon. Additionally, Lamb *et al.* (2008: 31) indicate that the population from Côte d'Ivoire may represent a distinct lineage.

Ralph *et al.* (2015) proved that the specimens from Ethiopia, Eritrea, Somalia, Djibouti and Yemen represent a different species: *O. harrisoni*, which is larger and more robust than any other *Otomops*.

Ammerman *et al.* (2012: 23) indicate that the separation between *martiensseni* and *madagascariensis* took place less than 2 million years ago.

Simmons (2005: 447) recognises one subspecies *icarus* Chubb, 1917.

COMMON NAMES:
Afrikaans: Bakoor-losstertvlermuis. Chinese: 大?犬吻?. Czech: morous Martienssenův. English: Martienssen's Big-eared Bulldog Bat, Large-eared Free-tailed Bat, Giant Mastiff Bat, Martiensen's Free-tailed Bat, Martienssen bat, Large-eared Giant Mastiff Bat. French: Grand molosse à grandes oreilles, Chauve-souris bouledogue géante. German: Großohrige Riesen-Bulldoggfledermaus. Italian: Otocarlìno di Martienssèn. Kinande (DRC): Mulima.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened (NT ver 3.1 (2001)) because this species is probably still in significant decline globally (but probably at a rate of less than 30 % over ten years), owing to the probable continued loss of the known major East African populations. Smaller populations from southern Africa may be increasing. The status of populations in Central and West Africa, where the species is still known from very few specimens, remains unclear. Almost qualifies as threatened under criterion A2c (Mickleburgh *et al.*, 2008dd; IUCN, 2009; Richards *et al.*, 2017).

Assessment History
Global
2016: NT ver 3.1 (2001) (Richards *et al.*, 2017). 2008: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2008dd; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004cq; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Richards *et al.*, 2016e). 2004: VU D2 ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

Legal Status
Richards (2017) report that it is a listed Threatened or Protected Species (ToPS) under the South African National Environmental Management (NEMBA): Biodiversity Act (No. 10 of 2004) and is protected by provincial ordinance in the KwaZulu-Natal province.

MAJOR THREATS:
The leading threat to this species appears to be roost disturbance (Ralph *et al.*, 2015). Populations in Durban (South Africa) have been found to use old buildings with attics as roosts, and it appears that the main threat to these populations is indirect poisoning through the application of toxic timber treatments (Fenton *et al.*, 2002).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dd) [in IUCN (2009)] and report that there is a need to reassess the status of all known roosts (and to locate additional localities) to ascertain numbers and status of colonies, so that key sites can be identified. While Richards *et al.* (2017) report that species has been recorded from Comoe National Park, Côte d'Ivoire (Fahr and Kalko 2011 in Richards *et al.* (2017), Garamba National Park, Democratic Republic of Congo (Verschuren, 1957), and a national park in Rwanda (Hutson *et al.*, 2001). The species occurs in several protected areas in South Africa (Adams *et al.*, 2015). An IUCN Species Action Plan has been developed for this species (Hutson *et al.*, 2001); this action plan requires revision given the reviewed species limits of *O. martiensseni* (Lamb *et al.*, 2008; Richards *et al.*, 2012) and the description of new northeast African species, *O. harrisoni* (Ralph *et al.*, 2015).

GENERAL DISTRIBUTION:
Otomops martiensseni has been widely, but patchily, recorded from much of sub-Saharan Africa. In Africa, it has been reported from Côte d'Ivoire and Ghana in West Africa, through Central Africa (recorded from Central African Republic, the Democratic Republic of the Congo, Rwanda and western Uganda) to East Africa (Kenya and Tanzania) to southern Africa (Malawi, central Angola [Chitau], Zimbabwe, Zambia and eastern South Africa). It is found at elevations from sea level to 2,900 m asl, although the highest elevations might need to be referred to *O. harrisoni*.

Records from Madagascar are now referred to *O. madagascariensis* (see Taxonomy section above).

Lamb *et al.* (2008: 30, 39) mention it from Côte d'Ivoire, Ghana, and Burundi, but also see Taxonomy paragraph. Records from Djobuti, Eritrea, Ethiopia, Somalia, Yemen are now referred to *O. harrisoni*, as might be the case for some of the records from Kenya, Tanzania and Uganda (see Taxonomy section above).

Patterson *et al.* (2018: 1) found both *O. martiensseni* and *O. harrisoni* in a cave in the Musanze district of Rwanda.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 545; Taylor *et al.*, 2018b: 63); Botswana (Adams *et al.*, 2015: 711); Central African Republic; Congo (The Democratic

Republic of the) (Ansell, 1974; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 545); Côte d'Ivoire; Ghana; Kenya (Patterson *et al.*, 2018: 5); Malawi (Monadjem *et al.*, 2010d:454); Rwanda (Patterson *et al.*, 2018: 1); South Africa (Monadjem *et al.*, 2010d:545;Adams *et al.*, 2015: 710-711); Tanzania; Uganda; Zambia Monadjem *et al.*, 2010d: 545); Zimbabwe (Lamb *et al.*, 2008; Monadjem *et al.*, 2010d: 545).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Large species, with narrowest wings of any bat for fast flying in open areas (Anonymus, 2004f: 57).

FUNCTIONAL MORPHOLOGY:
Based on the analysis of wing dimensions, Thollesson and Norberg (1991: 34) suggest that the longer hand wings and more pointed wing tips of *O. martiensseni* indicate that this is a species primarily flying in open areas at a high altitude. Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.9 Pa, aspect ratio 8.3 for a wingspan of 39 cm and a wing area of 183 cm^2 and a body mass of 24 g.

ECHOLOCATION:
From Bungule in Kenya Taylor *et al.* (2005) reported a F_{max}: 16.5 kHz. However, due to the split off of *O. harrisoni*, the taxonomic status of the specimens involved is uncertain (see Ralph *et al.*, 2015: 26).

At Sengwa in Zimbabwe, Jacobs (1996) and Fenton and Bell (1981) recorded a highest frequency of 17 kHz. Taylor (1999b) recorded F_{max}: 29.5 ± 2.4 kHz (open flight) and 14.7 ± 1.5 (emergence) from two localities in the Durban area in South Africa. Whereas, Fenton *et al.* (2004) reported a F_{max}: 14.7 ± 1.68 kHz from the Durban area in South Africa. From the same area, Schoeman and Waddington (2011: 291) mention a F_{peak}: 10.7 ± 0.4 kHz and a duration: 27 ± 1.5 ms.

Fenton (2004b: 4) states that there is evidence that, in this species, calls originally associated with echolocation may actually serve more for communication.

Adams *et al.* (2015: 709) report the following values from South Africa: F_{char}: 11.70 ± 3.61 (10.51 - 13.54) kHz; F_{high}: 13.19 ± 1.08 (11.01 - 15.67) kHz; F_{low}: 10.82 ± 0.65 (9.11 - 12.23) kHz; Band width: 2.40 ± 0.90 (0.65 - 5.64) kHz; F_{max}: 12.41 ± 0.90 (10.76 - 14.55) kHz; duration: 21.18 ± 3.61 (11.79 - 27.81) ms. Also from the RSA (Mapungubwe National Park), Parker and Bernard (2018: 57) reported on 20 calls: F_{char}: 10.74 ± 0.63 kHz, F_{max}: 11.52 ± 0.60 kHz, F_{min}: 10.28 ± 0.50 kHz, F_{knee}: 10.81 ± 0.64 kHz, duration: 22.68 ± 13.89 ms, with 3.98 ± 2.40 calls/sec.

Nine calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 13.16 ± 1.93 kHz, F_{min}: 9.75 ± 2.64 kHz, F_{knee}: 12.61 ± 1.63 kHz, F_{char}: 11.77 ± 1.02 kHz, slope: 16.52 ± 6.04 OPS, duration: 12.99 ± 5.28 ms.

For seven calls from the Aberdares Range in Kenya, Eisenring *et al.* (2016: SI 2) reported: F_{peak}: 14.8 ± 2.8 (9.9 - 17.4), Fsub max: 22.0 ± 4.2 (14.5 - 26.4), F_{min}: 9.9 ± 2.5 (5.2 - 13.2), DT: 0.1 ± 0.0 (0.1 - 0.2), DF: 12.1 ± 2.4 (9.3 - 16.0), IPI: 3.3 ± 2.0 (1.5 - 5.5).

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 9 bats: F_{max}: 12.88 ± 1.09 kHz, F_{min}: 11.83 ± 1.4 kHz, F_{knee}: 12.67 ± 0.98 kHz, F_{char}: 12.01 ± 0.83 kHz, slope: -31.73 ± 563.48 OPS, duration: 9.13 ± 5.96 ms. 17 calls recorded by Cory-Toussaint and Taylor (2022: Table S1) had a duration: 7.57 ± 2.16 ms, F_{min}: 11.54 ± 0.65 kHz, F_{max}: 12.03 ± 0.80 kHz, F_{knee}: 11.92 ± 0.82 kHz and F_{char}: 11.63 ± 0.62 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 3 *Otomops martiensseni* calls from the Kruger Park (RSA): F_{min}: 10.5 ± 1.1 (9.7 - 11.8) kHz, duration: 10.6 ± 2.0 (8.4 - 12.4) ms, F_{max}: 10.9 ± 1.2 (10.0 - 12.3) kHz, F_{knee}: 10.6 ± 1.1 (9.8 - 11.8) kHz, F_{char}: 10.6 ± 1.1 (9.8 - 11.8) kHz,

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 11.8 kHz and duration: 27 ms.

MOLECULAR BIOLOGY:
Karyotype
Đulić and Mutere (1973a) reported 2*n* = 48, FN = 56, BA = 10, a submetacentric X chromosome, and an acrocentric Y chromosome. However, Warner *et al.* (1974) reported 2*n* = 48, FN = 58, BA = 12, a submetacentric X chromosome and a submetacentric Y chromosome for one male specimen from Kenya. In view of the split off of *O. harrisoni* the Kenyan karyotype might represent the latter species rather than *O. martiensseni*.

Genetics
See Hoofer and Van Den Bussche (2003), Lamb *et al.* (2006) and Lamb *et al.* (2008).

HABITS:
O. martiensseni is probably a long-range forager, which hunts over a wide diversity of habitats, e.g., semi-arid areas and montane forests up to 2,000 m (Anonymus, 2004f: 57). Adams *et al.* (2015), referring to Fenton and Griffin (1997), indicate that foraging occurs at altitudes exceeding 600 m above ground. Actually, Fenton and Griffin (1997: 248) reported one call in the 10 - 13 kHz range (used by *O. martiensseni*) at an altitude between 500 and 550 m.

Foord *et al.* (2018: 5) indicate that open-air feeders (e.g., *O. martiensseni*) may commute over 10 km between roosts and feeding areas, but do prefer smaller feeding areas.

ROOST:
In the Durban area, Taylor *et al.* (1999: 67) found roosts on the brick surface of the inner gable apex wall within the roof space, with entrances height between 3 and 12 m. The colony size varied between one and 30. Richardson and Taylor (1995: 73) already remarked that the exit holes did not have obstructing trees in the way.

Anonymus (2004f: 57) indicates that *O. martiensseni* is generally colonial with larger colonies in underground sites (e.g., caves and lava tubes), whereas in South Africa small colonies occur in houses. Happold and Happold (2023: 115) indicate that the most common group size is up to 50 individuals, but sometimes there can be hundreds, and occasionally only singles or pairs.

POPULATION:
Structure and Density
Although *O. martiensseni* was once considered to be rare, with gaps in distribution, additional collecting has demonstrated local abundance in several areas (Long, 1995; Taylor, 1998; Fenton *et al.*, 2002; Skinner and Chimimba, 2005). For example, it is common around Durban in KwaZulu Natal Province of South Africa (Fenton *et al.*, 2002), and is fairly common in Comoe National Park, Côte d'Ivoire (Richards *et al.*, 2017).

Trend
2016: Decreasing (Richards *et al.*, 2017). 2008: Decreasing (Mickleburgh *et al.*, 2008dd; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Richardson and Taylor (1995: 73) found that males might be chased from their birth colony once they become mature.

REPRODUCTION AND ONTOGENY:
Martin and Bernard (2000: 32) indicate that the corpus luteum undergoes luteolysis in late pregnancy. Krutzsch (2000: 126) further mentions that the species exhibits classical mammalian male-female synchrony of reproductive cycles.

Richardson and Taylor (1995: 72) reported births in Durban (RSA) in early to mid-December, and that juveniles were of almost adult size by mid-January. The young could then still be distinguished by their greyer colour.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] indicated that juveniles have been recorded from October through May.

MATING:
Ober *et al.* (2016: 375) mention that *O. martiensseni* forms single male/multiple female groups.

PARASITES:
SIPHONAPTERA
Ischnopsyllidae
Beaucournu and Kock (1996) reported *Araeopsylla scitula* Rothschild, 1909 from a bat from Kenya. However, in view of the split off of *O. harrisoni*, this latter species might have been the host for this ectoparasite.

ACARI
Trombiculidae
Stekolnikov (2018a: 189) mentioned *Willmannium suswaensis* (Vercammen-Grandjean & Langston, 1976) from a bat collected at Mount Suswa (Kenya).

HEMIPTERA
Polyctenidae
Eoctenes faini Benoit, 1958 was reported from Rwanda by Szentiványi *et al.* (2022: 6).

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Otomops martiensseni*: Adenoviruses and Polyomaviruses.

Adenoviridae
Adenovirus
Two of the 19 specimens from the Suswa Cave (Kenya) by Conrardy *et al.* (2014: 259) tested positive for this virus.

Coronaviridae - Coronaviruses
SARS-CoV

Tong *et al.* (2009) tested two bats collected in Kenya during 2006 positive for the presence of coronavirus RNA in faecal samples.

28.6 % (10 out of 35) of the Kenyan *O. martiensseni* specimens were positive for CoV (Tao *et al.*, 2017: 3).

Flaviviridae
Hepacivirus (BHV)
Quan *et al.* (2013: Table S5) report that 3 of 15 Kenyan specimens were infected with clade C *Hepacivirus* (20.0 %). Shchelkanov *et al.* (2020a: 18) assigned this virus to Hepacivirus M.

Pegivirus (BPgV)
2 of the 15 specimens examined by Quan *et al.* (2013: Table S5) were also infected with clade K *Pegivirus* (13.3 %).

Paramyxoviridae
Paramyxovirus
Five of the 19 specimens from the Suswa Cave by Conrardy *et al.* (2014: 259) tested positive for this virus, and this was also the case for nine out of 40 specimens from Kenya, which were tested by Mortlock *et al.* (2015: 1481).

Polyomaviridae
Orthopolyomavirus
Initially, three novel orthopolyomaviruses were detected in 2006 from Kenya by Tao *et al.* (2012). Additional surveillance detected 6 of the 19 specimens from the Suswa Cave to be positive tested by Conrardy *et al.* (2014: 259).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Horton *et al.* (2014: Table S1) tested 16 Kenyan *O. martiensseni* specimens but failed to find neutralising antibodies to IKOV (Ikoma lyssavirus).

Remark: as most of these viruses were found on "*O. martiensseni*" specimens from Kenya, the actual host species might be *O. harrisoni*.

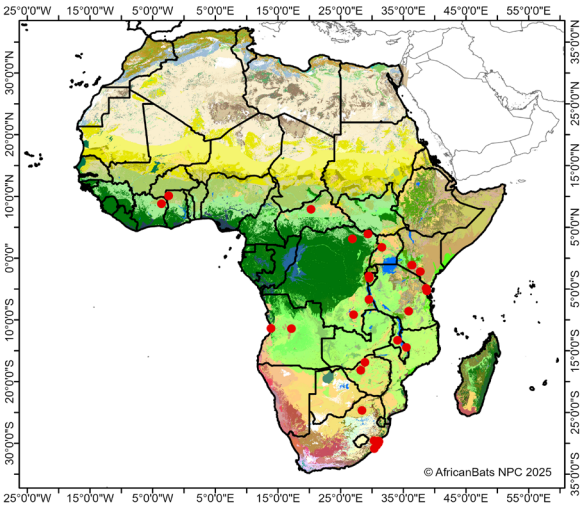

Figure 209. Distribution of *Otomops martiensseni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Kenya.

Otomops martiensseni icarus Chubb, 1917

*1917. *Otomops icarus* Chubb, Ann. Durban Mus., 1: 433, pl 21. Publication date: 21 May 1917. Type locality: South Africa: KwaZulu-Natal: Durban [29 52 S 31 00 E]. [Goto Description]. Holotype: NHMUK 1916.10.9.1: ♂. - Etymology: Named after Icarus, son of Daidalos, who fled from their prison with wings made of wax and feathers.
? *Otomops martiensseni icarus:* (Name Combination, Current Combination).

GENERAL DISTRIBUTION:
From Angola to KwaZulu-Natal, Malawi (Horáček *et al.*, 2000: 137).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Côte d'Ivoire, Ghana, South Africa, Uganda.

Otomops martiensseni martiensseni (Matschie, 1897)

*1897. *Nyctinomus martiensseni* Matschie, Arch. Naturgesch. Berlin, 63 (1): 84. Publication date: October 1897. Type locality: Tanzania: 25 mi W of Tanga, SE portion of W Usambara Mts: Magrotto Plantation [05 07 S 38 45 E]. [Goto Description]. Holotype: ZMB 97523: ♂, skin and skeleton and skull. Collected by: G. Martienssen; collection date: August 1897. See Turni and Kock (2008: 71). - Comments: Horáček *et al.* (2000: 137) mention the type locality as "Usanbara Mts., W of Tanga, NE Tanzania". Grubb *et al.* (1998: 98) indicate that the locality has been defined by Swynnerton, 1945, Proc. Zool. Soc. Lond., 115: 63). - Etymology: In honour of "Herr Martienssen of the Königlich Museum für Naturkunde" who found the type specimen (see Long, 1995: 4).
? *Otomops martiensseni martiensseni:* (Name Combination, Current Combination).

GENERAL DISTRIBUTION:
Central African Republic to Yemen and south to Zimbabwe (Horáček *et al.*, 2000: 137).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Central African Republic, Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Rwanda, South Africa, Tanzania, Zimbabwe.

Genus ***Platymops*** Thomas, 1906

*1906. *Platymops* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (101): 499. Publication date: 1 May 1906 [Goto Description]. - Comments: Type species: *Platymops Macmillani* Thomas, 1906 (=*Mormopterus setiger* Peters, 1878). - Etymology: From the Greek adjective "*πλατύς*" (platýs), meaning "flat" and the masculine German substantive *Mops*, referring to the extremely flattened skull of the genus (see Lanza *et al.*, 2015: 315). (Current Combination).
? *Mormopterus (Platymops):* (Name Combination).

TAXONOMY:
Considered a subgenus of *Mormopterus* by Koopman (1993a: 238), Czaplewski *et al.* (2003: 68), but a valid genus by Kock (1969a: 155), Simmons (2005).

Included in *Mormopterus* by Jacobs and Fenton (2002: 1).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Platymops*: ***setiger*** (Peters, 1878).

COMMON NAMES:
Czech: ploší morousi. English: East African Flat-headed Bats, Peters's flat-headed Bats. French: Tadarides à tête plate. German: Flachkopf-Bulldoggfledermäuse. Italian: Platicarlìni.

Platymops setiger (Peters, 1878)

*1878. *Mormopterus setiger* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 196, pl 1, fig 2. Type locality: Kenya: Taita district: Ndi [03 14 S 38 30 E, 2 000 m]. [Goto Description]. Syntype: ZMB 5265a: ♀, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008). Syntype: ZMB 5265b: ♀, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008). - Comments: Allen (1939a: 109) mentioned 1881; Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 483, pl., fig. 3. - Etymology: From the masculine Latin adjective *sètiger*, meaning "covered with coarse hair, bristly", referring to the coarse fur of the species Lanza *et al.*, 2015: 316).
1960. *Platymops setiger:* Harrison and Fleetwood, Durban Mus. Novit., 5 (20): 269. (Name Combination, Current Combination).

TAXONOMY:
See Freeman (1981b: 133, 161). Included in *Platymops* by Harrison and Fleetwood (1960: 277 - 278).

COMMON NAMES:
Chinese: 彼德犬吻蝠. Czech: morous plochý. English: East African Flat-headed Bat, Peters's Flat-headed Bat, Flat-headed free-tailed bat. French: Sauromys à tête plate, Tadaride à tête plate de Peters. German: Peters' Flachkopf-Bulldoggfledermaus. Italian: Carlìno setolóso.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017aj).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017aj). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008al; IUCN, 2009). 2004: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2004ay; IUCN, 2004). 1996: LR/lc [assessed as *Mormopterus setiger*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There are presumably no major threats to this species (Mickleburgh *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017aj).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008al) [in IUCN (2009)] and Monadjem *et al.* (2017aj) report that there appear to be no direct conservation measures in place. In view of the species' East African range, it seems likely that it is present within some

protected areas, although this needs to be confirmed. Further studies are needed into the distribution, natural history and potential threats to this species.

GENERAL DISTRIBUTION:
Platymops setiger is an East African species present in Kenya, southwestern Ethiopia (Glass, 1965: 179), southeastern Sudan and is possibly present in adjacent Uganda, although this needs to be confirmed. It has been recorded at elevations of up to 2,000 m asl.

Native: Ethiopia; Kenya; Sudan.

Presence uncertain: Uganda.

DETAILED MORPHOLOGY:
Vomeronasal complex (VNC)
Smith *et al.* (2024: 9) found two oval depressions just caudal to the incisive foramen on the (pre)maxillary bones.

MOLECULAR BIOLOGY:
Karyotype
Warner *et al.*, 1974) reported 2*n* = 48, FN = 54, BA = 8 and submetacentric X and acrocentric Y chromosomes.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Mickleburgh *et al.*, 2008al; IUCN, 2009; Monadjem *et al.*, 2017aj).

Trend
2016: Unknown (Monadjem *et al.*, 2017aj). 2008: Unknown (Mickleburgh *et al.*, 2008al; IUCN, 2009).

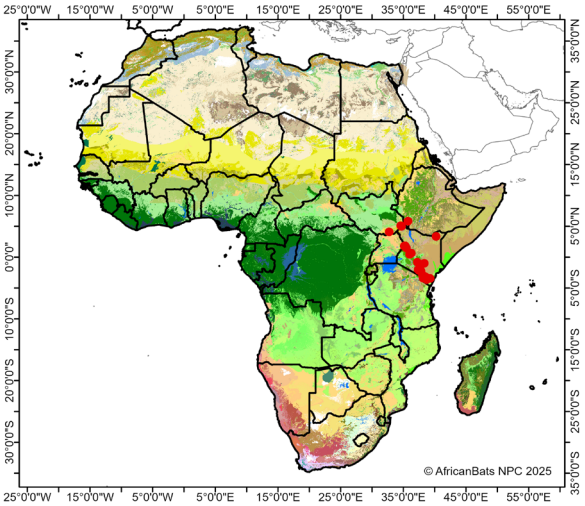

Figure 210. Distribution of *Platymops setiger*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Kenya.

Platymops setiger macmillani Thomas, 1906

*1906. *Platymops Macmillani* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (101): 500. Publication date: 1 May 1906. Type locality: Ethiopia: Between Addis Ababa and Lake Rudolf. [Goto Description]. Holotype: NHMUK 1906.11.1.10: ad ♂, skull and alcoholic. Collected by: Ph.C. Zaphiro. Presented/Donated by: W.N. McMillan Esq. 7 specimens. - Etymology: In honour of Mr. W.N. McMillan, to whose liberality science is indebted for the exploration of which it is part of the outcome (see Thomas, 1906b: 501).

1956. *Platymops barbatogularis* Harrison, Ann. Mag. nat. Hist., ser 12, 9 (104): 549. Publication date: 18 December 1956. Type locality: South Sudan: SE Sudan, Ilemi triangle: Lokomarinyang Marsh [05 02 N 35 33 E]. [Goto Description]. Holotype: NHMUK 1967.1232: ad ♂, skin and skull. Collected by: John George Williams; collection date: 10 June 1953. Formerly HZM 2.1897 (see Harrison (1956e: 549). Paratype: NHMUK 1957.258. - Comments: Evenhuis (2003: 54) indicates that ser. 12, 9 (104) is the "August 1956" issue which was published on "18 December 1956".
Jelle Zijlstra (pers. comm., 26/02/2023) pointed out that the type locality is in the "Ilemi Triangle", an area disputed between South Sudan and Kenya, and is currently under the de facto control of Kenya.

1960. *Platymops barbatogularis parkeri* Harrison and Fleetwood, Durban Mus. Novit., 5 (20): 270, figs 1 - 6. Publication date: 30 April 1960. Type locality: Kenya: Lualeni borehole: Maktau [03 24 S 38 08 E]. [Goto Description]. Holotype: NHMUK 1959.524: ad ♀, skin and skull. Collected by: Ian Parker; collection date: 12 February 1958; original number: 2.

? *Mormopterus setiger macmillani:* (Name Combination).

? *Platymops setiger macmillani:* (Name Combination, Current Combination).

TAXONOMY:
Kock (1969a: 155) considers *barbatogularis* to be a synonym of *macmillani*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Kenya, South Sudan.

Platymops setiger setiger (Peters, 1878)

*1878. *Mormopterus setiger* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 196, pl 1, fig 2. Type locality: Kenya: Taita district: Ndi [03 14 S 38 30 E, 2 000 m]. [Goto Description]. Syntype: ZMB 5265a: ♀, skull and alcoholic.

Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008). Syntype: ZMB 5265b: ♀, skull and alcoholic. Collected by: Dr. Johann Maria Hildebrandt; collection date: July 1877. See Turni and Kock (2008). - Comments: Allen (1939a: 109) mentioned 1881; Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 483, pl., fig. 3. - Etymology: From the masculine Latin adjective *sètiger*, meaning "covered with coarse hair, bristly", referring to the coarse fur of the species Lanza *et al.*, 2015: 316).

? *Mormopterus setiger setiger:* (Name Combination).

? *Platymops setiger setiger:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, South Sudan.

Genus ***Sauromys*** Roberts, 1917

1917. *Platymops* Roberts, Ann. Transv. Mus., 6(1): 5. Publication date: 28 June 1917. - Comments: Type species: *Platymops (Sauromys) petrophylus* Roberts, 1917. Not of Thomas, 1906.

*1917. *Platymops (Sauromys)* Roberts, Ann. Transv. Mus., 6(1): 5. Publication date: 28 June 1917. - Comments: Type species: *Platymops (Sauromys) haagneri* Roberts, 1917 (=*Platymops petrophilus* Roberts, 1917). As a subgenus of *Platymops* Thomas, 1906. - Etymology: From Greek "*sauros*" meaning lizard and "mys" meaning mouse (see Jacobs and Fenton, 2002: 1).

? *Mormopterus (Sauromys):* (Name Combination).

? *Sauromys:* (Current Combination).

? *Tadarida (Sauromys):* (Name Combination).

TAXONOMY:
Bronner *et al.* (2003) state that the status of *Sauromys*, described as a monotypic subgenus of the extralimital *Platymops* for the South African flat-headed free-tailed bat, remains unclear. Peterson (1965) raised it to generic rank, a treatment endorsed by many subsequent authors, and corroborated by a limited multivariate analysis of wing bone and cranial characteristics (Peterson, 1985). However, morphometric studies by Freeman (1981b) and Legendre (1984) concluded that it is a subgenus of *Mormopterus*, a position followed by Koopman (1993a, 1994), and Jacobs and Fenton (2002: 1). Simmons (2005) retains *Sauromys* as a valid genus in the 3rd Edition of Mammal Species of the World, a treatment we favour because of the unique ecology and morphology of *S. petrophilus*. Analysis of the Rag2 data confirmed the split between *Mormopterus* and *Sauromys* (see Ammerman *et al.*, 2013: 309).

Meester *et al.* (1986) also state that originally described as a subgenus, this genus was regarded as a synonym of *Platymops* by Shortridge (1942), Roberts (1951) and Ellerman *et al.* (1953). Harrison (1962) retains it as a subgenus, while Peterson (1965) raises it to generic rank, in which he is followed by Hayman and Hill (1971), Smithers (1971), Corbet and Hill (1980) and Rautenbach (1982). However, Freeman (1981b), followed by Koopman (1982) and Legendre (1984), conclude that both *Sauromys* and *Platymops* are subgenera of *Mormopterus*. We take the view that both *Platymops* and *Sauromys* are valid genera.

Generic and species classification of African flat-headed molossids is unclear. Roberts (1917c) originally described *Sauromys* as a subgenus of *Platymops*. Later Roberts (1951, 1954) dropped *Sauromys* as a subgenus, as Shortridge (1942) reported that a minute upper premolar was found on the type *Platymops macmillani* Thomas, 1906. Peterson (1965) indicates that the minute premolar on the type *P. macmillani* is probably a milk premolar and that normal adult dental formula should be considered as having only one upper premolar. For this reason and others (e.g., glands not on wings) Peterson (1965) raises *Sauromys* to generic status. Koopman (1975) indicates that *Sauromys* is a subgenus within *Tadarida*, however Freeman (1981b) found that all the so-called flat-headed bats; *Sauromys*, *Platymops*, and *Neoplatymops*, are phenotypically related to *Mormopterus*. While the phenogram in Freeman (1981b) also indicates that *Tadarida aegyptiaca* (E. Geoffroy 1818) and *T. brasiliensis* (I. Geoffroy St.-Hilaire 1824) are phenetically similar to *Mormopterus*, this grouping is explained due to convergence of shape due to similar life styles (Freeman, 1981b). Meester *et al.* (1986) did not follow Freeman (1981b) and rather followed Peterson (1965) recognizing *Sauromys*, *Mormopterus* and *Platymops* as valid genera. While Koopman (1993a) followed Freeman (1981b) in classifying *Sauromys* and *Platymops* as subgenera in the genus *Mormopterus*, Simmons (2005) recognizes *Sauromys* as a distinct genus.

Peterson (1965) suggests that a detailed comparison between *Sauromys* and *Tadarida* needs to be performed, including an investigation into the specific status and geographic variation. Ammerman *et al.* (2012: 21) suggest that *Sauromys* is more appropriately recognized as a member of the genus *Tadarida*, which split off

from *T. aegyptiaca* some 6.5 million years ago. However, based on their morphological data, Gregorin and Cirranello (2015: 10) still find it premature to transfer *Sauromys* into *Tadarida*.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Sauromys*: ***petrophilus*** (Roberts, 1917).

COMMON NAMES:
Czech: ještěří morousi. French: Sauromys. German: Flachkopf-Bulldoggfledermäuse.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery (2007: 619) reported on the presence of *Sauromys* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa.

Sauromys petrophilus (Roberts, 1917)

*1917.	*Platymops (Sauromys) petrophilus:* Roberts, Ann. Transv. Mus., 6(1): 5. Publication date: 28 June 1917.
1917.	*Platymops petrophilus* Roberts, Ann. Transv. Mus., 6(1): 5. Publication date: 28 June 1917. Type locality: South Africa: Western Transvaal: near Rustenburg: Bleskop. [Goto Description]. Holotype: TM X835: ♂. Collected by: G.P. Van Dam; collection date: 2 February 1917; original number: 16. - Etymology: From the Greek "*petros*" meaning rock and "*philos*" meaning loving. (Name Combination).
?	*Mormopterus petrophilus petrophilus:* (Name Combination).
?	*Mormopterus petrophilus:* (Name Combination).
?	*Platymops haagneri haagneri:*
?	*Sauromys petrophilus:* (Name Combination, Current Combination).

TAXONOMY:



Figure 211. *Sauromys petrophilus umbratus* from Kliphuis, Cederberg, Western Cape South Africa.

Roberts (1951, 1954) recognised two species and five subspecies of flat-headed bats in southern Africa: *Platymops haagneri* Roberts, 1917 (*haagneri*, *umbratus* Shortridge and Carter, 1938) and *Platymops petrophilus* Roberts, 1917 (*petrophilus*, *erongensis* Roberts, 1946, *fitsimonsi* Roberts, 1946). Ellerman *et al.* (1953) suggested that the two species are conspecific, and rather recognized five subspecies of *Platymops petrophilus* (*petrophilus*, *haagneri*, *umbratus*, *erongensis* and *fitzsimonsi*). Meester *et al.* (1986) also recognized the five subspecies suggested by Ellerman *et al.* (1953) for *petrophilus* but within the genus *Sauromys*, following Peterson (1965: 12). Freeman (1981b) indicates that *erongensis* (Roberts, 1946) may be a synonym of *haagneri* (Roberts, 1917) and *fitzsimonsi* (Roberts, 1946) is possibly a synonym of *umbratus* (Shortridge and Carter, 1938). Included in *Mormopterus* by Jacobs and Fenton (2002: 1). Jacobs and Fenton (2002: 1) considered *M. petrophilus* to be monotypic.

COMMON NAMES:
Afrikaans: Platkop-losstertvlermuis. Czech: morous ještěří. English: Rock-loving Flat-headed Bat, Rock-dwelling Flat-headed Bat, Roberts' Flat-headed Bat, Roberts's Flat-headed Bat, Flat-headed Free-tailed Bat. French: Sauromys de Roberts. German: Roberts' Flachkopf-Bulldoggfledermaus. Portuguese: Morcego de cabeca curta.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
No fossils are known (Jacobs and Fenton, 2002: 1).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008an; IUCN, 2009; Monadjem *et al.*, 2017bh).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bh). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008an; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bc; IUCN, 2004). 1996: LR/lc [assessed as *Mormopterus petrophilus*] (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Jacobs *et al.*, 2016f). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species. In parts of its range it is believed to be threatened by considerable habitat change resulting from deforestation (Mickleburgh *et al.*, 2008an; IUCN, 2009; Monadjem *et al.*, 2017bh).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008an) [in IUCN (2009)] and Monadjem *et al.* (2017bh) report that this species is present in several protected areas in Namibia and Angola. In South Africa it has been reported from the protected Algeria forestry station. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Sauromys petrophilus is found in southern Africa, ranging along the west coast from the Angola and Namibia border area, south into southern South Africa, and from here into northeastern South Africa, Zimbabwe, and western Mozambique. It is found between 100 m and 2,000 m asl. In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 915,652 km^2.

The Ghanaian specimen which should be in the USNM (see Meester *et al.*, 1986), could not be located in the collection (see Jacobs and Fenton, 2002: 2).

Native: Angola; Botswana (Monadjem *et al.*, 2010d: 545); Mozambique (Monadjem *et al.*, 2010d: 545; Monadjem *et al.*, 2010c: 382); Namibia (Monadjem *et al.*, 2010d: 545); South Africa (Seamark and Kearney, 2007; Monadjem *et al.*, 2010d: 545)); Zimbabwe (Monadjem *et al.*, 2010d: 545).

Presence uncertain: Ghana.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Jacobs and Fenton (2002).

Schoeman and Jacobs (2002: 157) mention the following wing parameters for 51 specimens from the Algeria Forestry Station (RSA): Fa: 39.0 ± 1.0 mm, Wing area: 93.1 ± 11 cm^2, Wing span: 26.3 ± 1.9 cm, Wing loading: 11.2 ± 1.1 N/m^2, and aspect ratio: 7.4 ± 0.6.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
As indicated by Rautenbach and Nel (1980: 112), the extremely flattened skull is an adaptation to roosting in the narrowest of rock crevices.
For further details, see Jacobs and Fenton (2002).

DETAILED MORPHOLOGY:
Other
For a description of the crania, ears and tragus, and wingshape and aspect ratio, see Jacobs and Fenton (2002).

Curtis and Simmons (2018: 1390) found a relatively large, anteroposteriorly elongated, single, mineralized midline element positioned anterior to the dorsal margin of the nasal aperture in the cupular cartilages. Their CT-microscans showed a variation in the grayscale, suggesting porosity or trabeculae, which in turn might suggest a bony structure.

FUNCTIONAL MORPHOLOGY:
Toussaint and McKechnie (2012: 1138) found that the rapid increases in Evaporate Water Loss at high ambient temperatures in *S. petrophilus* may imply that, notwithstanding having a comparatively heat tolerance, this species may also be most vulnerable to lethal dehydration during future heat waves.

Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 10.8 Pa, aspect ratio 7.6 for a wingspan of 26 cm and a wing area of 89 cm^2 and a body mass of 10 g.

ECHOLOCATION:
See Jacobs and Fenton (2002).

From Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the type of calls to be low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 29.2 ± 1.8 kHz.

Two calls by bats from the Kalahari Desert had the following characteristics: F_{char}: 24.0 ± 0.2 kHz, F_{max}: 30.3 ± 3.2 kHz, F_{min}: 23.7 ± 0.1 kHz, duration: 4.3 ± 0.7 ms (Adams and Kwiecinski, 2018: 4).

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 103 calls of 5 bats: F_{max}: 41.46 ± 6.35 kHz, F_{min}: 29.31 ± 2.95 kHz, F_{knee}: 31.89 ± 3.62 kHz, F_{char}: 29.85 ± 1.74 kHz, slope: 117.33 ± 1045.12 OPS, duration: 6.35 ± 2.42 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor

(2022: Table S1) had a duration: 7.06 ± 1.11 ms, F_{min}: 28.70 ± 0.44 kHz, F_{max}: 29.37 ± 0.52 kHz, F_{knee}: 29.19 ± 0.47 Khz and F_{char}: 28.85 ± 0.44 kHz.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported $2n$ = 48, FN = 62, BA = 16, a submetacentric X chromosome, and an acrocentric Y chromosome for specimens from Namibia and South Africa. However, this did not include specimens from the Western Cape that Rautenbach *et al.* (1993) included with *Chaerephon pumilus*, but have subsequently been reidentified as *S. petrophilus* (Jacobs and Fenton, 2001).

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *S. petrophilus* activity was significantly and positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *S. petrophilus* favoured open habitats surrounding wetlands (Sirami *et al.*, 2013: 35) .

HABITS:
See Jacobs and Fenton, 2002).

ROOST:
See Jacobs and Fenton (2002).

DIET:
See Jacobs and Fenton (2002).

From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 464 faecal pellets from 51 bats (in volume percent): Diptera (37.8 ± 31.2), Hemiptera (32.9 ± 23.7), Coleoptera (19.5 ± 23.1), Hymenoptera (7.9 ± 16.2), Neuroptera (0.6 ± 3.0), Trichoptera (0.4 ± 2.9), Lepidoptera (0.3 ± 2.2), and unknown (1.0 ± 3.3).

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention *S. petrophilus* as possible prey of Lanner falcon (*Falco biarmicus* Temminck, 1825) and Peregrine falcon (*Falco peregrinus* Tunstall, 1771),

POPULATION:
Structure and Density
This is a locally common species. It is generally found in small numbers, with colonies thought to be tens of animals rather than hundreds (Jacobs and Fenton, 2002).

Trend
2016: Stable (Monadjem *et al.*, 2017bh). 2008: Stable (Mickleburgh *et al.*, 2008an; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
See Jacobs and Fenton, 2002).

REPRODUCTION AND ONTOGENY:
See Jacobs and Fenton (2002).

VIRUSES:
Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 12 individuals from Riemvasmaak, Northern Cape, South Africa using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) tested 12 individuals from Riemvasmaak, Northern Cape, South Africa by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

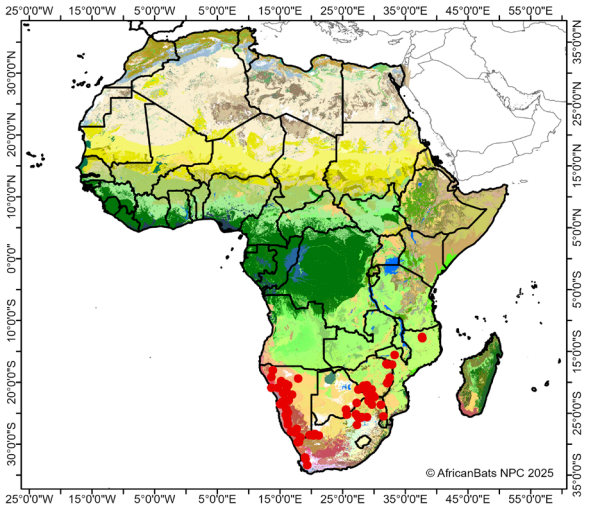

Figure 212. Distribution of *Sauromys petrophilus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Namibia, South Africa.

Sauromys petrophilus erongensis (Roberts, 1946)

*1946. *Platymops petrophilus erongensis* Roberts, Ann. Transv. Mus., 20 (4): 308. Type locality: Namibia: Damaraland: Omaruru district: Eronga Mountains: Ombu Farm [21 35 S 15 43 E]. [Goto Description]. Holotype: TM 9494: ♂. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 19 September 1941; original number: 112 (14). Holotype: TM 9570: ♂. Collected by: Austin Roberts; collection

date: 22 September 1941; original number: 128. Paratype: TM 9495: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 14 September 1941; original number: 77. Paratype: TM 9496: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 17 September 1941; original number: 93. Paratype: TM 9497: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 17 September 1941; original number: 95. Paratype: TM 9497a: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 14 September 1941. Paratype: TM 9498: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 18 September 1941; original number: 105. Paratype: TM 9499: ♂. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 18 September 1941; original number: 106. Paratype: TM 9500: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 18 September 1941; original number: 108. Paratype: TM 9501: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 18 September 1941; original number: 107. Paratype: TM 9502: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 19 September 1941; original number: 113. Paratype: TM 9503: ♀. Collected by: The Barlow TM-Expedition and Austin Roberts; collection date: 19 September 1941; original number: 115. Paratype: TM 9504: ♂. Collected by: Austin Roberts; collection date: 19 September 1941; original number: 116. Paratype: TM 9505: ♂. Collected by: Austin Roberts; collection date: 19 September 1941; original number: 117. Paratype: TM 9506: ♂. Collected by: Austin Roberts; collection date: 19 September 1941; original number: 118. Paratype: TM 9507: ♀. Collected by: Austin Roberts; collection date: 20 September 1941; original number: 124. Paratype: TM 9508: ♂. Collected by: Austin Roberts; collection date: 20 September 1941; original number: 125. Paratype: TM 9511: ♂. Collected by: Austin Roberts; collection date: 22 September 1941; original number: 129. Paratype: TM 9512: ♀. Collected by: Austin Roberts; collection date: 22 September 1941; original number: 129. - Etymology: Referring to the Eronga mountains, where the type specimen was collected.

? *Mormopterus petrophilus erongensis:* (Name Combination).

? *Sauromys petrophilus erongensis:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Namibia.

Sauromys petrophilus haagneri (Roberts, 1917)

1917. *Platymops (Sauromys) haagneri:* Roberts, Ann. Transv. Mus., 6 (1): 5. Publication date: 28 June 1917. (Name Combination).

*1917. *Platymops haagneri* Roberts, Ann. Transv. Mus., 6 (1): 5. Publication date: 28 June 1917. Type locality: Namibia: Great Namaqualand: Keetmanshoop [26 35 00 S 18 08 00 E, 984 m]. [Goto Description]. Holotype: TM X472: ad ♂. Collected by: Mr. Sigmund Haagner. Presented/Donated by: Mr. Sigmund Haagner.

2025. *Sauromys petrophillus:* Conenna, Muñoz-Garcia and Korine, Mammal Rev., xxx (e70005): 2. Publication date: 7 May 2025. (Lapsus).

? *Sauromys haagneri:* (Name Combination).

? *Sauromys petrophilus haagneri:* (Name Combination, Current Combination).

COMMON NAMES:
Afrikaans: Haagnerse Platkopvlermuis. English: Haagner's Flat-headed Bat.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Namibia, South Africa.

Sauromys petrophilus petrophilus (Roberts, 1917)

*1917. *Platymops (Sauromys) petrophilus:* Roberts, Ann. Transv. Mus., 6(1): 5. Publication date: 28 June 1917.

? *Sauromys petrophilus petrophilus:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Mozambique, South Africa, Zimbabwe.

Sauromys petrophilus umbratus (Shortridge & Carter, 1938)

*1938. *Platymops haagneri umbratus* Shortridge and Carter, Ann. S. Afr. Mus., 32 (4): 282. Publication date: July 1938. Type locality: South Africa: Western Cape province: 11 mi [=18 km] NE Clanwilliam, Pakhuis Pass: Kliphuis [32 08 S 19 00 E]. [Goto Description]. Holotype: KM 2827.

1946. *Platymops petrophilus fitzsimonsi* Roberts, Ann. Transv. Mus., 20 (4): 308. Type locality: South Africa: SW Cape province: near Ceres: Mitchell's Pass. [Goto Description]. Holotype: TM 8968: ♀. Collected by: Austin Roberts; collection date: 7 November 1940; original number: 63. Paratype: TM 8969: ♀. Collected by: Austin Roberts; collection date: 7 November 1940.

? *Sauromys petrophilus umbratus:* (Name Combination, Current Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS: South Africa.

Genus ***Tadarida*** Rafinesque, 1814

*1814. *Tadarida* Rafinesque, Précis des découvertes et travaux somiologiques, 55. Publication date: 3 June 1814. - Comments: Type species: *Cephalotes teniotis* Rafinesque, 1814. - Etymology: Meaning unknown (Flannery, 1990: 366). Possibly from the Greek "data" or Latin "taeda" and "nukterida" (see Kozhurina, 2002: 18). Braun and Mares (1995: 182) refer to Gotsch (1979), who states this is a word created by C.S. Rafinesque. Lanza *et al.* (2015: 317 - 318) gives the following explanation: "From the feminine Greek substantive "*νυκτερίς*" (nykterís) [genitive "*νυκτερίδος*" (nikterídos)], meaning "bat"; by aphaeresis] and dialectal deformation, the above genitive turned into "tadarida" in southern Italy. Some examples of similar dialect deformations are according to Forsyth Major (1893): tagddariti (Naples); taddarita, taddarida and taddarito (Calabria), tardaritòla and tardarira (Sicily)". See also Riccucci (2015a: 77; 2015b: 61) for some additional (although unlikely) suggestions. - Phonetics: tad-a-rid-a, tah-dah-reed′-ah. (Current Combination).

1818. *Nyctinomus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 114, pl 2. Publication date: 1818 [Goto Description]. - Comments: Type species: *Nyctinomus aegyptiacus* E. Geoffroy St. Hillaire, 1818.
In the original description, Geoffroy Saint-Hilaire (1818) mentions three species: *Nyctinomus Ægyptiacus* [=*Tadarida aegyptiaca*, *Vesp. acetabulosus* Hermann [=*Mormopterus acetabulosus*] and *Vesp. plicatus* Buchanan [=*Chaerephon plicatus*], which would make *Nyctinomus* a partial synonym of these three genera. - Etymology: From the Greek "*νύξ*" or "*νυκτός*", meaning night and "*νομός*", meaning habitation (see Palmer, 1904: 466). - Phonetics: nik-tee-noh′-mus.

1821. *Nyctimones* J. E. Gray, London Med. Repos., 15: 299. Publication date: 1 April 1821. - Comments: Generally, the name is reported as *Nyctinomes*, but Gray (1821: 299) actually mentioned *Nyctimones*, with one species *Vesp. acetabulosus*.

1821. *Nyctinoma* Bowdich, Analysis of the Natural Classification of Mammalia, p 28.

1822. *Nyctinomia* Fleming, The Philosophy of Zoology, 2: 178 [Goto Description].

1825. *Dinops* Savi, Nuov. Giorn. Letter. Pisa, Sci., 10: 229. - Comments: Type species: *Dinops cestoni* Savi, 1824 (=*Cephalotes teniotis* Rafinesque, 1814). - Etymology: From the Greek "*δεινός*", meaning terrible and "*ώψ*", meaning face or aspect, probably referring to the deeply grooved or wrinkled face (see Palmer, 1904: 234).

1830-1831. *Dysopes* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 69. Publication date: 1830-1831. - Comments: Not of Illiger, 1811. The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831".

1973. *Tatarida:* Eisentraut, Bonn. zool. Monogr., 3: 113. (Lapsus).

1984. *Rhizomops* Legendre, Rev. suisse Zool., 91 (2): 427. Publication date: June 1984. - Comments: Type species: *Rhizomops brasiliensis* (I. Geoffroy Saint-Hilaire, 1824). - Etymology: From the Greek "*riza*" meaning root (see Legendre, 1984: 427).

1995. *Dynops:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: ???. (Lapsus).

? *Tadarida sp.:*

TAXONOMY:
Formerly included *Chaerephon*, *Mops*, *Mormopterus*, and *Nyctinomops*; see Freeman (1981b: 133). Includes *Rhizomops*, but see Legendre (1984); see also Owen *et al.* (1990). Mahoney and Walton (1988c) regarded *Nyctinomus* as the prior name for this genus.

Based on their analysis of molecular data, Lamb *et al.* (2011: 9) suggest that the genus *Tadarida* - as currently recognized - is not a natural group. *Tadarida teniotis* - the type species of the genus - forms a separate clade from *T. aegyptiaca* - the type species of *Nyctinomus* - and "*C. jobimena*". They suggest that the two latter species - together with other species - might be placed in a separate genus: *Nyctinomus*, but they await further taxonomic sampling and resolution of the phylogeny of other African taxa before making this formal.

Currently (Simmons and Cirranello, 2024a) recognized species within the genus *Tadarida*: ***aegyptiaca*** (E. Geoffroy Saint-Hilaire, 1818); *brasiliensis* (I. Geoffroy Saint-Hilaire, 1824) – southern Brazil, Bolivia, Argentina and Chile to Oregon, south Nebraska and Ohio (USA), Greater and Lesser Antilles (Simmons, 2005: 450); ***fulminans*** (Thomas, 1903); *insignis* (Blyth, 1862) – Japan, Taiwan, Korea, southern China (Simmons, 2005: 450); *latouchei* Thomas, 1920 – northern China, Thailand, Laos, Japan (Simmons, 2005: 450); ***lobata*** (Thomas, 1891); ***teniotis*** (Rafinesque, 1814); ***ventralis*** (Heuglin, 1861).

COMMON NAMES:
Czech: širokouší morousi, hroznohledové, netopýři morousovití. English: Guano Bats, Free-tailed Bats, Tadarine Bats. French: Tadarides. German: Gewöhnliche Bulldoggfledermäuse. Italian: Tadarìde. Ukrainian: Тадарида [= Tadaryda].

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery (2007: 619) reported on the presence of *Tadarida* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa.

PARASITES:
Barbosa *et al.* (2016: 215) reported *Trypanosoma erneyi* from a *Tadarida* sp. from Mozambique.

ACARI
Myobiidae
Fain (1994: 1280) reports one species of *Schizomyobia*, living on Old World *Tadarida*.

Trombiculidae
Zajkowska *et al.* (2018: 118) reported *Microtrombicula intranasalis* Vercammen-Grandjean, 1965 from a Rwandese bat originally identified as "*Nyctinomus* sp.".

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Congo (Democratic Republic of the), Egypt, Ghana, Kenya, Madagascar, Namibia, Niger, Somalia, South Africa, South Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia.

Tadarida aegyptiaca (E. Geoffroy St.-Hilaire, 1818)

*1818. *Nyctinomus ægyptiacus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 128, pl 2, No 2. Publication date: 1818. Type locality: Egypt: Giza province: Giza [30 01 N 31 13 E]. Holotype: MNHN ZM-MO-1986-1084: ad ♂, skull and alcoholic. Collected by: Etienne Geoffroy-Saint-Hilaire. Rode (1941: 251) mentions numbers "228" and "A.467". - Comments: Type locality restricted from "Egypt" to Giza by Koopman (1975: 422): see Qumsiyeh (1985: 73), Meester *et al.* (1986: 70). - Etymology: From the scientific Latin feminine adjective *aegyptiacus*, meaning "Egyptian", as the species was decribed from an Egyptian specimen (see Lanza *et al.*, 2015: 319).
1855. *D[ysopes] aegyptiacus:* Giebel, Die Säugethiere, 957. (Name Combination).
1923. *Nyctinomus tongaensis:* Thomas and Hinton, Proc. zool. Soc. Lond., 1923, II: 251. Publication date: 6 July 1923. (Name Combination, Current Spelling).
2012. *Nyctinomus aegyptiacus:* Benda, Faizolâhi, Andreas, Obuch, Reiter, Ševčík, Uhrin, Vallo and Ashraf, Acta Soc. Zool. Bohem., 76: 163, 516. Publication date: 27 December 2012. (Alternate Spelling).
2018. *Tadarida aegyptica:* Lazzeroni, Burbrink and Simmons, Ecol. Evol., 8 (24): 12584. Publication date: 28 November 2018. (Lapsus).
? *Tadarida (Tadarida) aegyptiaca:* (Name Combination).
? *Tadarida aegyptiaca:* (Name Combination, Current Combination).

TAXONOMY:
Benda *et al.* (2012a: 516) place this taxon in the genus *Nyctinomus*, a view followed by a.o. Bendjeddou *et al.* (2016b: 23).

Based on morphometrics, Reddy *et al.* (2019: 273) suggest that two distinct groupings occur across southern Africa: an eastern characterised by larger, angular crania, and a central-western one characterised by smaller, more rounded crania, which correspond to previously described taxa. Both also have different bacula. Whether the two taxa differ on (sub)specific level still needs to be determined.

COMMON NAMES:
Afrikaans: Egiptiese losstertvlermuis. Bengali: Lomba-leji Chamchika. Chinese: 北非犬吻. Czech: morous egyptský, přišerec egipecký, tadarida jižní, morous jižní. Dutch: Egyptischte bulvleermuis. English: Egyptian Free-tailed Bat, Egyptian Guano Bat, Egyptian Nyctinome. French: Tadaride d'Egypte, Molosse d'Egypte. German: Ägyptische Bulldoggfledermaus. Italian: Tadarìda egiziàna. Portuguese: Morcego de cauda livre do egipto. Tamil: எகிப்தி ய வாலற்ற வௌவால், Ekiptiya Vāarra Veḷavā.

ETYMOLOGY OF COMMON NAME:
The original specimens were collected in Egypt during the Napoleonic wars by E. Geoffroy Saint-Hilaire, who at that time served under Napoleon (see Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery and Avery (2011: 18) report on Holocene and Pleistocene remains from Wonderwerk (Northern Cape province, South Africa).

CONSERVATION STATUS:
Global Justification
Broadly distributed and locally common, hence is listed as Least Concern (LC ver 3.1 (2001)) (Mickleburgh *et al.*, 2008ar; IUCN, 2009; Monadjem *et al.*, 2017bi).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bi). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008ar; IUCN, 2009). 2004: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2004bb; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (MacEwan *et al.*, 2016a). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
No serious threats other than roost disturbance from human interference is noted for this species (Molur *et al.*, 2002). Pesticides used against locusts are a threat as for all bat species found in the Saharan belt (Mickleburgh *et al.*, 2008ar; IUCN, 2009; Monadjem *et al.*, 2017bi). Furthermore, Doty and Martin (2012: 75) report

on fatalities due to wind turbines in the Eastern Cape, South Africa. Aronson (2022: 225) found that this species accounts for the majority of carcasses (45 %) found near wind turbine facilities in the RSA, and that most of the fatalaties occurred between February and April.

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008ar) [in IUCN (2009)] and Monadjem *et al.* (2017bi) report that the species is protected by national legislation in some of the Mediterranean range states as well as in South Africa. It is likely to be found in protected areas. A survey using bat detectors should be undertaken to help clarify the distribution limits and population size of this species as it is probably more widespread than current records indicate. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
Tadarida aegyptiaca is found throughout Africa, and in the Arabian Peninsula through to India, Sri Lanka and Bangladesh. In the Mediterranean region there are isolated records from southern Morocco and western Algeria, but it is more widely distributed in Egypt along the Nile River valley eastwards to the Red Sea coast and south to the Sudanese border. The species is thought to be more widely distributed than is currently known and may well occur elsewhere in the region. In South Asia, this widely distributed species is presently known from Afghanistan (Kabul Province) (Habibi, 2003), Bangladesh (no exact location) (Khan, 2001; Srinivasulu and Srinivasulu, 2005), India (Andhra Pradesh, Gujarat, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Rajasthan, Tamil Nadu and West Bengal), Pakistan (Punjab and Sind) and Sri Lanka (Central and Uva Provinces) (Molur *et al.*, 2002). Elevation: sea level up to 2,100 m asl.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,214,127 km^2. In the RSA, the species' distribution is linked with land use/land cover (Babiker Salata, 2012: 50).

Native: Afghanistan; Algeria; Angola (Crawford-Cabral, 1989; Hayman, 1963; Monadjem *et al.*, 2010d: 545; Taylor *et al.*, 2018b: 63); Bangladesh; Botswana (Monadjem *et al.*, 2010d: 545); Congo (The Democratic Republic of the); Egypt; Eritrea (Lavrenchenko *et al.*, 2004b: 132); Eswatini (Monadjem *et al.*, 2010d: 546, Monadjem *et al.* (2021: 5); Ethiopia; India; Iran, Islamic Republic of; Kenya; Lesotho (Lynch, 1994: 197; Monadjem *et al.*, 2010d: 545); Mauritania; Morocco (Benda *et al.*, 2004d; El Ibrahimi and Rguibi Idrissi, 2015: 365; Dbiba *et al.*, 2025: 7); Mozambique (Monadjem *et al.*, 2010d: 545; Monadjem *et al.*, 2010c: 382); Namibia (Monadjem *et al.*, 2010d: 545); Nigeria; Oman; Pakistan; Saudi Arabia; South Africa (Seamark and Kearney, 2007; Monadjem *et al.*, 2010d: 546); Sri Lanka; Sudan; Tanzania; Tunisia (Bendjeddou *et al.*, 2016b: 23); Uganda; Yemen (Benda *et al.*, 2011b: 45); Zambia (Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 546); Zimbabwe (Monadjem *et al.*, 2010d: 546).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Schoeman and Jacobs (2002: 157) reported the following parameters for 43 specimens from the Algeria Forestry Station (RSA): Fa: 45.1 ± 1.2 mm, Wing area: 115.2 ± 8.4 cm^2, Wing span: 30.8 ± 1.0 cm, Wing loading: 13.1 ± 1.6 N/m^2, and aspect ratio: 8.3 ± 0.6.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.0 Pa, aspect ratio 9.7 for a wingspan of 35 cm and a wing area of 130 cm^2 and a body mass of 16 g.

In their study on rewarming along an altitudinal gradient in the RSA, Marsden *et al.* (2022: 5) found that the body mass of these bats increased with increasing altitude. Their mass-specific rewarming rate was negatively correlated with altitude.

ECHOLOCATION:
From Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the type of calls to be low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 22.8 ± 1.9 kHz.

Schoeman and Waddington (2011: 291) mention a peak frequency of 21.8 ± 1.7 kHz and a duration of 12.8 ± 0.7 ms for specimens from Durban, South Africa.

From Waterberg, South Africa, Taylor *et al.* (2013b: 18) recorded the following parameters for 8 calls: F_{max}: 28.3 ± 3.36 (24.8 - 34.1) kHz, F_{min}: 21.6 ± 2.73 (17.2 - 24.0) kHz, F_{knee}: 24.2 ± 1.47 (21.9 - 26.1) kHz, F_{char}: 22.8 ± 1.39 (20.5 - 24.5) kHz, duration: 7.2 ± 3.10 (3.3 - 10.9) ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 24 (22 - 26) kHz.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg range (RSA): F_{min}:17 - 24 kHz, F_{char}: 20 - 24 kHz, F_{knee}: 22 - 26

kHz, slope: 65 - 221 OPS, duration: 3 - 11 ms. In the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded 20 calls with the following characteristics: F_{char}: 23.68 ± 1.51 kHz, F_{max}: 29.23 ± 5.77 kHz, F_{min}: 22.47 ± 1.74 kHz, F_{knee}: 25.72 ± 2.92 kHz, duration: 9.87 ± 3.93 ms, with 4.10 ± 2.72 calls/sec.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 23.68 ± 1.51 kHz, F_{max}: 29.23 ± 5.77 kHz, F_{min}: 22.47 ± 1.74 kHz.

Moores and Brown (2017: 612) recorded the following parameters for 25 calls from southern Morocco: F_{start}: 26.0 ± 2.6 (22.2 - 30.4) kHz, F_{max}: 19.6 ± 1.6 (17.4 - 22.3) kHz, F_{end}: 18.4 ± 0.8 (17.2 - 19.5) kHz, duration: 9.4 ± 1.4 (8.1 - 12.2) ms, interpulse interval: 373 ± 153 (220 - 780) ms.

Adams and Kwiecinski (2018: 4) reported the following values for 5 calls from the Kalahari Desert: F_{char}: 21.6 ± 1.2 kHz, F_{max}: 25.2 ± 1.1 kHz, F_{min}: 21.2 ± 1.1 kHz, duration: 4.9 ± 0.6 ms.

Weier *et al.* (2020: Suppl.) reported on 16 calls from the Okavango River Basin with the following characteristics: F_{max}: 21.69 ± 1.48 kHz, F_{min}: 19.83 ± 3.23 kHz, F_{knee}: 21.25 ± 0.89 kHz, F_{char}: 20.65 ± 0.71 kHz, slope: 8.58 ± 9.28 OPS, duration: 6.07 ± 2.83 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 99 calls of 8 bats: F_{max}: 26.82 ± 2.55 kHz, F_{min}: 23.4 ± 0.89 kHz, F_{knee}: 25.19 ± 1.28 kHz, F_{char}: 23.52 ± 0.97 kHz, slope: 92.93 ± 90.54 OPS, duration: 6.49 ± 2.74 ms. 15 calls recorded by Cory-Toussaint and Taylor (2022: Table S1) had a duration: 6.70 ± 1.94 ms, F_{min}: 21.28 ± 0.77 kHz, F_{max}: 23.88 ± 1.81 kHz, F_{knee}: 22.84 ± 1.19 kHz and F_{char}: 21.34 ± 0.77 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 16 *Tadarida aegyptiaca* calls from the Kruger Park (RSA): F_{min}: 21.3 ± 2.2 (16.3 - 25.2) kHz, duration: 7.9 ± 3.0 (3.5 - 11.2) ms, F_{max}: 26.6 ± 3.9 (22.3 - 35.2) kHz, F_{knee}: 23.5 ± 1.9 (21.3 - 27.0) kHz, F_{char}: 22.6 ± 1.3 (21.0 - 25.3) kHz,

Luo *et al.* (2019a: Supp.) reported the following data (bats leaving their roost): F_{peak}: 19.44 kHz, F_{start}: 24.44 kHz, F_{end}: 16.67 kHz, Band width: 7.77 kHz, and duration: 15.5 ms.

54 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 17 - 24 kHz, F_{max}: 25 - 34 kHz, F_{char}: 21 - 25 kHz, F_{knee}: 22 - 26 kHz and duration 3 - 11 ms.

Based on 217 passes, Parker (2022: 20) reported the following data from the Mountain Zebra National Park (RSA): F_{min}: 22.26 ± 2.56 kHz, F_{char}: 23.70 ± 3.33 kHz and F_{max}: 26.33 ± 8.31.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 23.68 ± 1.51 kHz, F_{max}: 29.23 ± 5.77 kHz and F_{min}: 22.47 ± 1.74 kHz.

Molecular Biology:

Karyotype

Both Nagorsen *et al.* (1976: 10) and Rautenbach *et al.* (1993) reported $2n$ = 48 and an actrocentric Y chromosome. While Nagorsen *et al.* (1976: 10) reported FN = 54 [2 pairs of rnetacentrics, 2 pairs of submetacentrics and a graded series of 19 pairs·of acrocentrics], BA = 8, and a submetacentric X chromosome, Rautenbach *et al.* (1993) reported FN = 68, BA = 22, and a metacentric X chromosome, for specimens from Namibia and South Africa. Nagorsen *et al.* (1976: 10) do remark that (some of) the acrocentric chromosomes might actually be subtelocentric, which might explain the different FN.

Habitat:

Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *T. aegyptiaca* activity was significantly and positively influenced by wetland size, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *T. aegyptiaca* favoured open habitats surrounding wetlands (Sirami *et al.*, 2013: 35).

Habits:

Rautenbach and Nel (1980: 112) indicate that this is fast flying bat which follows a relatively straight flight path.

Thomas and Jacobs (2013: 129) report that, at De Hoop Nature Reserve, South Africa, bats feeding on Diptera (such as *T. aegyptiaca*) emerged later than bats feeding on Lepidoptera (e.g., *Rhinolophus capensis* and *Nycteris thebaica*).

Roost:

In the Durban area (RSA), Taylor *et al.* (1999: 68) found these bats roosting in high-rise buildings of the Central Business District, and the colony sizes varied between 30 and an estimated 300.

Toussaint *et al.* (2010) examined roost temperature in Pretoria, South Africa, and in the same country, Czenze *et al.* (2021: 3) found

these bats inhabiting roosts where the temperature approached the bat's normothermic body temperature.

DIET:
In Zimbabwe, Fenton and Thomas (1980: 86) report that the diet of *T. aegyptiaca* consists of Lepidoptera and Coleoptera.

From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 314 faecal pellets from 43 bats (in volume percent): Diptera (34.6 ± 33.4), Coleoptera (25.5 ± 30.7), Hemiptera (19.2 ± 24.6), Hymenoptera (8.4 ± 22.2), Lepidoptera (5.4 ± 13.4), Ephemeroptera (2.7 ± 7.7), Neuroptera (1.5 ± 6.5), Orthoptera (0.6 ± 3.4), and unknown (1.4 ± 7.1).

For Saudi-Arabia, Benda *et al.* (2012a: 524) indicate that some diet samples were dominated by Lepidoptera, whereas others were dominated by Coleoptera and Hymenoptera or by Heteroptera and Brachycera. In Iran, three digestive tracts were analysed: One tract was empty, one contained Lepidoptera (30 % of volume), Coleoptera (Scarabaeidae) (30 %), Neuroptera (Myrmeleontidae) (10 %), and Orthoptera (Ensifera) (30 %), and the third tract contained Coleoptera (Elateridae, Carabidae) (60 %) and Orthoptera (Ensifera) (40 %).

PREDATORS:
Avery *et al.* (2005: 1054) found this species to be present in pellets from *Tyto alba* (Scopoli, 1769) in South Africa.

Mikula *et al.* (2016: Supplemental data) and Malan *et al.* (2022: 167) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
This species is widespread and common in its South Asian range, where its population seems to be stable (Molur *et al.*, 2002).

Trend
2016: Unknown (Monadjem *et al.*, 2017bi). 2008: Unknown (Mickleburgh *et al.*, 2008ar; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Toussaint *et al.* (2010) examined heterothermy in *T. aegyptiaca* in Pretoria, South Africa.

REPRODUCTION AND ONTOGENY:
In Pretoria (South Africa), Tsita (1993), Bernard and Tsita (1995: 18) and le Grange *et al.* (2011: 170 - 171) found spermatogenesis occurring in January, and spermatozoa were first found in the epididymis in May, where they were stored until the end of September. In females, follicular development was already taking place in January. Copulation, ovulation and fertilization took place in August to early September; and births took place in December. Their conclusion was that *T. aegyptiaca* is a monoestrous, monotocous seasonal breeder. le Grange *et al.* (2011: 173) also indicate that, at 33° S, spermatogenesis only started in February, and that follicular development only started in April, but copulation, ovulation, and fertilization also occurred at the end of August.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births in November or December.

PARASITES:
Copeland *et al.* (2011: 363) reported the rediscovery of the "terrible hairy fly" (*Mormotomyia hirsuta* (after 62 years) in guano produced by *C.* cf. *bivittatus* and *T. aegyptiaca* at Ukasi Hill, Kenya.

From Algeria, the following ectoparasites were reported by Bendjeddou *et al.* (2017: 15): Nycteribiidae: *Nycteribia (Nycteribia) pedicularia* Latreille, 1805 and *Phthiridium biarticulatum* Hermann, 1804; Streblidae: *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851: and Arachnida: *Spinturnix myoti* (Kolenati, 1856) and *Eyndhovenia euryalis* (G. Canestrini, 1885). Mechouk *et al.* (2022: 4) furthermore, mentioned *Argas vespertilionis* Latreille, 1796.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species as having been found on "*Nyctinomus aegyptiacus*": Argasidae: *Carios vespertilionis* Latreille, 1802; Ischnopsyllidae: *Araeopsylla gestroi* (Rothschild, 1906); and Streblidae: *Raymondia huberi huberi* Frauenfeld, 1856;

Orlova *et al.* (2020b: 1) reported the first case of an infection by *Parasteatonyssus nyctinomi* in Namibia (Macronyssidae, Arachnida).

Sándor *et al.* (2021a: 4) mentioned the following Argasidae: *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933), *Chiropterargas confusus* (Hoogstraal, 1955), and *Carios vespertilionis* Latreille, 1802.

VIRUSES:
Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV) - Oelofsen and Van der Ryst (1999) tested 24 individuals from two localities in the Free State Province, South Africa for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 55 individuals from four localities using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) tested 89 individual brains, from 9 localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

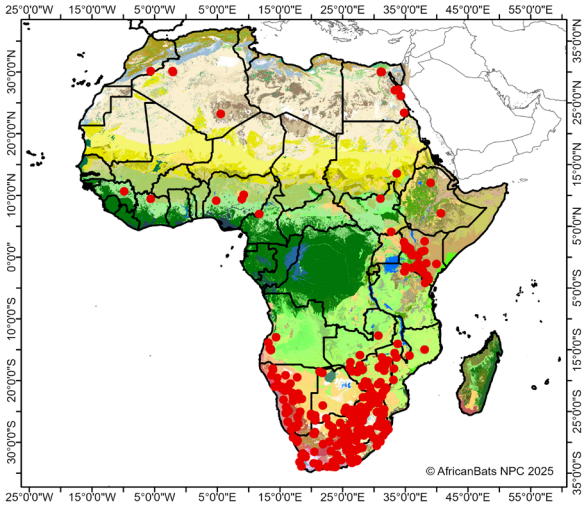

Figure 213. Distribution of *Tadarida aegyptiaca*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Namibia, Niger, Nigeria, South Africa, Zambia.

Tadarida aegyptiaca aegyptiaca (E. Geoffroy St.-Hilaire, 1818)

*1818. *Nyctinomus ægyptiacus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 128, pl 2, No 2. Publication date: 1818. Type locality: Egypt: Giza province: Giza [30 01 N 31 13 E]. - Comments: Type locality restricted from "Egypt" to Giza by Koopman (1975: 422): see Qumsiyeh (1985: 73), Meester *et al.* (1986: 70). - Etymology: From the scientific Latin feminine adjective *aegyptiacus*, meaning "Egyptian", as the species was decribed from an Egyptian specimen (see Lanza *et al.*, 2015: 319).
1826. *Dysopes geoffroyi* Temminck, Monogr. Mamm, 1 (6): 226, pls 19, 23. Publication date: 1826. - Comments: Allen (1939a: 110), Qumsiyeh (1985: 73) mentioned 1827 as year of publication. Kock (1969a: 137), Meester *et al.* (1986: 70) mention 1826. Substitute for *aegyptiacus* E. Geoffroy St. Hilaire (see Ellerman and Morrison-Scott, 1951: 135; Harrison, 1964a: 109; Kock, 1969a: 137; Qumsiyeh, 1985: 73; Meester *et al.*, 1986: 70).
1877. *Dysopes talpinus* Heuglin, Reise in Nordost Afrika, 2: 28. Publication date: 1877. Type locality: South Sudan: Bahr-el-Ghazal province: Kidj district: Bahr el Jebel, West bank: "Kidj district" [ca. 07 06 N 30 46 E].
1916. *Nyctinomus (Nyctinomus) tongaënsis* Wettstein, Anz. kais. Akad. Wiss., Wien, 53: 192. Publication date: 1916. Type locality: South Sudan: Upper White Nile: Tonga [09 29 13 N 31 02 16 E, 360 m]. [Goto Description]. Syntype: NMW 8406: ♂, alcoholic (skull not removed). Collected by: Prof. Dr. Franz Werner; collection date: 16 April 1916. Presented/Donated by: Otto Ritter von Westersheim Wettstein. See Benda *et al.* (2012a: 582). Syntype: NMW 8407: ♂, skull and alcoholic. Collected by: Prof. Dr. Franz Werner; collection date: 16 April 1916. Presented/Donated by: Otto Ritter von Westersheim Wettstein. See Benda *et al.* (2012a: 582). - Comments: Wettstein (1916: 189, 192) mentions two male type specimens, collected by Prof. Dr. Franz Werner on 16 April 1914.
1938. *[Nyctinomus] tongaënsis:* Frechkop, Exploration du Parc National Albert, 54. (Name Combination).
1971. *tongaensis:* Hayman and Hill, Order Chiroptera: Smithsonian Institution Press - Washington, D.C.: 65. (Current Spelling).
? *Tadarida aegyptiaca aegyptiaca:* (Name Combination, Current Combination).

GENERAL DISTRIBUTION:
Arabia, N Africa (Horáček *et al.*, 2000: 136).

PARASITES:
SIPHONAPTERA
Ischnopsyllidae
Araeopsylla scitula (Rothschild 1909) found in southern Africa from Cape, Natal, Transvaal Provinces of South Africa, Lesotho and Botswana (Haeselbarth *et al.*, 1966: 189).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Cameroon, Côte d'Ivoire, Egypt, Ethiopia, Guinea, Kenya, Morocco, Nigeria, South Africa, South Sudan, Sudan, Tanzania, Uganda.

Tadarida aegyptiaca bocagei (Seabra, 1900)

1900. *Nyctinomus Anchietæ* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 82. Publication date: August 1900. Type locality: Angola: W Angola: Quibula. [Goto Description].
*1900. *Nyctinomus Bocagei* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 84. Publication date: August 1900. Type locality: Angola: Benguela district: East of Hanha: Galanga [12 04 S 15 09 E]. [Goto Description].

1900. *Nyctinomus brunneus* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 83. Publication date: August 1900. Type locality: Angola: NE of Benguela: Quissange [12 30 S 14 05 E]. [Goto Description].
1941. *Tadarida bocagei:* Hill and Carter, Bull. Am. Mus. Nat. Hist., 78 (1): 55. Publication date: 25 July 1941. (Name Combination).
? *Tadarida (Tadarida) aegyptiaca bocagei:* (Name Combination).
? *Tadarida aegyptiaca bocagei:* (Name Combination, Current Combination).

TAXONOMY:
If page precedence is to be taken into account, *anchietae* might be the senior synonym for this form.

COMMON NAMES:
Afrikaans: Bocagese Losstertvlermuis. English: Bocage's Free-tailed Bat. Kimbundu (Angola): Olondiriri.

GENERAL DISTRIBUTION:
Angola and Zambia to South Africa (Horáček *et al.*, 2000: 136).

PREDATORS:
Dean (1975: 218) reports on remains being found in barn owl (*Tyto alba*) pellets in South Africa.

PARASITES:
HEMIPTERA
Cimicidae
Stricticimex transverses Ferris and Usinger, 1957 from Kanye, Botswana (Haeselbarth *et al.*, 1966: 15).

SIPHONAPTERA
Ischnopsyllidae
Araeopsylla scitula (Rothschild, 1909) found in southern Africa from Cape, Natal, Transvaal Provinces of South Africa, Lesotho and Botswana (Haeselbarth *et al.*, 1966: 189).

ACARI
Trombiculidae
Microtrombicula kanyei Vercammen-Grandjean, 1965 was reported by Stekolnikov (2018a: 155) from bats from Kanye, Botswana.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Eswatini, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe.

†*Tadarida engesseri* Rachl, 1983

*1983. *Tadarida engesseri* Rachl, Die Chiroptera (Mammalia) aus den mittelmiozänen Kalken des Nordlinger Rieses (Suddeutschland). Thesis Doct, Ludwig-Maximilians. Universität München. Type locality: Germany: Steinberg (Ries).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Middle Miocene (Astaracanian).

GENERAL DISTRIBUTION:
Native: Europe; Morocco Hugueney *et al.* (2015: 472).

Tadarida fulminans (Thomas, 1903)

*1903. *Nyctinomus fulminans* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (71): 501. Publication date: 1 November 1903. Type locality: Madagascar: Eastern Betsileo: Fianarantsoa [21 36 S 47 05 E, 1 130 m]. [Goto Description]. Holotype: NHMUK 1882.3.1.34: ♂, skull and alcoholic. Collected by: Rev. W. Deans Cowan; original number: 4. - Etymology: From the Latin "*fulminate*" meaning strike with lightning.
1946. *Nyctinomus mastersoni* Roberts, Ann. Transv. Mus., 20 (4): 306. Type locality: Zimbabwe: Bindura district: Masembura Nature Reserve: Chikupu caves [17 24 S 31 20 E]. [Goto Description]. Holotype: TM 9976: ad ♂, skin and skull. Collected by: H.B. Masterson; collection date: 10 July 1945. Topotype: ROM 64580: ad ♂, skin and skull. Collected by: Randolph Lee Peterson and G.E. Turner; collection date: 11 May 1972.
2004. *Tadarida fulmilans:* Goodman and Cardiff, Acta Chiropt., 6 (2): 227. (Lapsus).
? *Tadarida fulminans mastersoni:* (Name Combination).
? *Tadarida fulminans:* (Name Combination, Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Afrikaans: Madagaskarse grootlosstertvlermuis. Chinese: 岛犬吻蝠. Czech: morous východoafrický. English: Large Free-tailed Bat, Lightning Guano Bat, Large Guano Bat, Madagascan Large Guano Bat, Madagascan Large Free-tailed Bat, Madagascan Free-tailed Bat, Madagascar Large Free-tailed Bat, Malagasy Free-tailed Bat, Malagasy Large Free-tailed Bat.

French: Tadaride de Thomas, Grande Tadaride de Madagascar, Molosse de Madagascar. German: Madagassische Bulldoggfledermaus.

ETYMOLOGY OF COMMON NAME:
The colloquial name refers to the island where the species occurs.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide range across east and southern Africa. Although it is not a common species and can be patchily distributed, it is not thought to be facing any major threats (Cotterill *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bu).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bu). 2008: LC ver 3.1 (2001) (Cotterill *et al.*, 2008; IUCN, 2009). 2004: LC ver 3.1 (2001) (Cotterill, 2004b; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016z). 2004: Considered a vagrant. Not assessed, due to known form a single locality (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species (Cotterill *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bu).

CONSERVATION ACTIONS:
Cotterill *et al.* (2008) [in IUCN (2009)] and Monadjem *et al.* (2017bu) report that it has been recorded from one protected area in Madagascar and is presumed to exist in many protected areas within its range in eastern and southern Africa, however, there appear to be no active conservation measures in place. Further studies are needed into the distribution and taxonomic status of bats allocated to *Tadarida fulminans*.

GENERAL DISTRIBUTION:
Tadarida fulminans ranges through East Africa, southern Africa and a few localities on the island of Madagascar. Populations have been recorded through eastern and southeastern Africa, from around the border of Kenya and Uganda as far south as the border between Zimbabwe and South Africa. The most westerly record is from eastern Democratic Republic of the Congo. In Madagascar, it is only known from a few records, mostly from the central-south region near to Fianarantsoa and Isalo National Park, and from records at Tolagnaro near the southeast coast (Jenkins *et al.*, 2007a). Further surveys are needed within Madagascar (Goodman and Cardiff, 2004). It ranges from about sea level (at Fort Dauphin in Madagascar) to close to 2,000 m asl (Albertine Rift).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 541,523 km^2.

Native: Congo (The Democratic Republic of the); Kenya; Madagascar; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 546); Mozambique (Monadjem *et al.*, 2010d: 546; Monadjem *et al.*, 2010c: 382); Rwanda; South Africa (Monadjem *et al.*, 2010d: 546); Tanzania; Zambia (Ansell, 1957; Ansell, 1967; Monadjem *et al.*, 2010d: 547); Zimbabwe (Monadjem *et al.*, 2010d: 547).

ECHOLOCATION:
See Taylor (1999b).

MOLECULAR BIOLOGY:
Karyotype
Peterson and Nagorsen (1975) reported 2*n* = 48, FN = 54, BA = 8, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from Zimbabwe. However, Rautenbach *et al.* (1993) reported 2*n* =48, FN =66, BA =20, a metacentric X chromosome and an acrocentric Y chromosome for specimens from South Africa.

HABITAT:
Thomas (1901d: 7) indicate that *T. fulminans* is the only molossid bat that is absent from urban areas, which is probably linked to its high wing loading coupled with high roost specificity.

ROOST:
Happold and Happold (2023: 122) indicate that *T. fulminans* roosts in groups of about 20 individuals (although not all of the animals were possibly captured at that time). Garbutt (2022: 97) mentions that colony sizes on Madagascar can contain 20-50 animals, but always less than 100.

POPULATION:
Structure and Density
Locally common, but patchily distributed in Africa. On Madagascar this bat is an uncommon, patchily distributed species. Colonies of this species may consist of dozens of individuals (although always fewer than 100 animals) (Cotterill *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bu).

Trend
2016: Stable (Monadjem *et al.*, 2017bu). 2008: Stable (Cotterill *et al.*, 2008; IUCN, 2009).

PARASITES:
Polyctenidae
Hypoctenes fani Benoit 1958, a single female collected from Rwanda (Haeselbarth *et al.*, 1966: 18; Szentiványi *et al.*, 2022: 6).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Kenya, Madagascar, Malawi, Mozambique, Namibia, Rwanda, South Africa, Tanzania, Zambia, Zimbabwe.

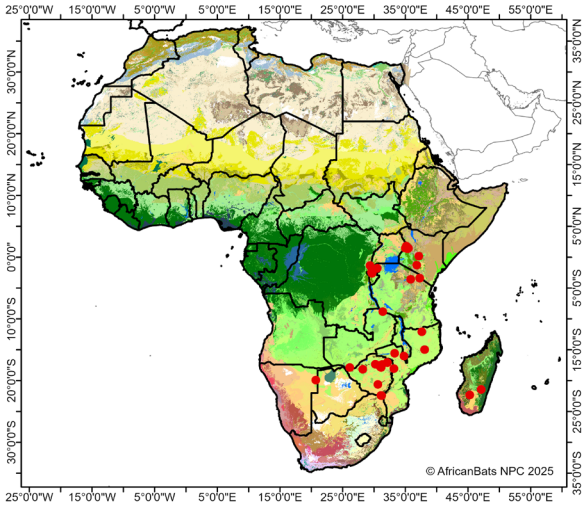

Figure 214. Distribution of *Tadarida fulminans*.

Tadarida lobata (Thomas, 1891)

*1891. *Nyctinomus lobatus* Thomas, Ann. Mag. nat. Hist., ser 6, 7 (39): 303. Publication date: 1 March 1891. Type locality: Kenya: West Pokot: upper reaches of Turkwell: Turkwell Gorge, at or near [ca. 01 52 N 35 22 E]. [Goto Description]. Holotype: NHMUK 1893.2.3.7: ♂, skull and alcoholic. Collected by: Sir Frederick John Jackson. Peterson and Harrison (1970: 1) indicate that this specimen is probably a male, although they could not find any trace of scrotal development. - Etymology: From "*lobata*" meaning lobed.
? *Tadarida (Chaerephon) pumila limbata:*
? *Tadarida lobata:* (Name Combination, Current Combination, Current Spelling).
? *Tadarida pumila limbata:*

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Afrikaans: Grootoor-losstervlermuis. Chinese: 大耳犬吻蝠. Czech: morous širokouchý. English: Big-eared Guano Bat, Big-eared Kenyan Guano Bat, Kenyan Big-eared Free-tailed Bat, Big-eared Free-tailed Bat, Big-eared Kenya Free-tailed Bat, Eastern Africa Free-tailed Bat. French: Tadaride du Kenya, Tadaride de l'Afrique orientale, Molosse à grandes oreilles. German: Großohr-Bulldoggfledermaus.

ETYMOLOGY OF COMMON NAME:
The colloquial name perhaps refers to the country from which the species was originally described (see Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) because it is associated with rocky areas in dry savanna habitat, and is unlikely to be declining fast enough to qualify for listing in a more threatened category (Cotterill, 2008e; IUCN, 2009; Monadjem and Cotterill, 2017).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Cotterill, 2017). 2008: LC ver 3.1 (2001) (Cotterill, 2008e; IUCN, 2009). 2004: DD ver 3.1 (2001) (Cotterill, 2004e; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no identifiable threats to this species (Cotterill, 2008e; IUCN, 2009; Monadjem and Cotterill, 2017).

CONSERVATION ACTIONS:
Cotterill (2008e) [in IUCN (2009)] and Monadjem and Cotterill (2017) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further surveys are needed to better determine the range of this species, and to understand whether it is restricted to rocky areas or can persist in modified habitats.

GENERAL DISTRIBUTION:
Tadarida lobata has only been recorded from four localities in Kenya and four localities in Zimbabwe

(Skinner and Chimimba, 2005). It is found between 600 and 2,000 m asl.

Native: Kenya; Zimbabwe (Monadjem *et al.*, 2010d: 547).

POPULATION:
Structure and Density
It appears to be a rare species found in small colonies (Cotterill, 2008e; IUCN, 2009; Monadjem and Cotterill, 2017). The apparent rarity might be attributed to their high-flying habits and inaccessible daylight roosts (Cotterill, 1996b).

Trend
2016: Unknown (Monadjem and Cotterill, 2017).
2008: Unknown (Cotterill, 2008e; IUCN, 2009).

PARASITES:
Duszynski (2002: 20) indicates that *T. lobata* might be a host for *Eimeria dukei* Lavier, 1927, but as Pellérdy (1974) mentioned the bat as "*Tadarida limbata*" this might not be correct.

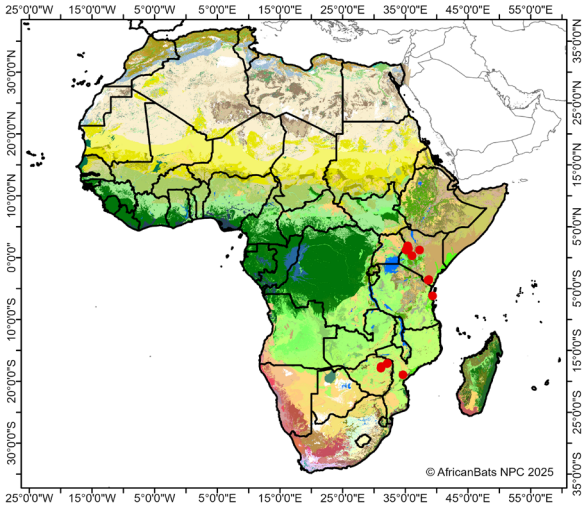

Figure 215. Distribution of *Tadarida lobata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Mozambique, Tanzania, Zimbabwe.

Tadarida teniotis (Rafinesque, 1814)

*1814. *Cephalotes teniotis* Rafinesque, Précis des découvertes et travaux somiologiques, 12, 55. Publication date: 3 June 1814. Type locality: Italy: Sicily. [Goto Description]. - Etymology: From the Greek "*teniotis*" meaning striped, banded.

1825. *Dinops Cestonii* Savi, Nuov. Giorn. Letter. Pisa, Sci., 10: 230. Type locality: Italy: Tuscany: Pisa [43 43 N 10 24 E]. Syntype: ZFMK MAM-1983.0173: ♂, alcoholic (skull not removed). Collected by: Prof. Paulo Savi; collection date: 1846. On label: "*Nyctinomus cestonii* (Savi) Dobson (In der Sammlg. Von Berthold als *Dysops Savii* angegeben) Toscana"; ex Göttingen Museun 1978: see Hutterer (1984: 32).

1826. *Dysopes rupelii* Temminck, Monogr. Mamm, 1 (6): 224, pl 18. Publication date: 1826. Type locality: Egypt: Cairo [30 03 N 31 15 E]. Lectotype: SMF 12380: skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: prior to 1823. Locality: Egypt. Original number: II.K.1.b. Paralectotype: RMNH MAM.35946: ad, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell. Paralectotype: RMNH MAM.35947: ad. Collected by: Wilhem Peter Edward Simon Rüppell. Paralectotype: RMNH MAM.35948: ad, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell. Paralectotype: RMNH MAM.35953: ad, alcoholic (skull not removed). Collected by: Wilhem Peter Edward Simon Rüppell. Paralectotype: SMF 12379: skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: prior to 1823. Locality: Egypt. Old catalog number: II.K.1.a. - Comments: Type locality restricted from "Egypt" to Cairo by Qumsiyeh (1985: 71). Incorrect original spelling (*rüpelii*) corrected by Qumsiyeh (1985: 71) as *rueppellii*.

1840. *Dysopes Savii* Schinz, Europäische Fauna oder Verzeichniss der Wirbelthiere Europa's, 1: 138. - Comments: Substitute for *cestoni* (see Ellerman and Morrison-Scott, 1951: 134; Harrison, 1964a: 106). - Etymology: In honour of Gaetano Savi (1769 - 1844) (see Kozhurina, 2002: 17).

1855. *D[ysopes] Rüppelli:* Giebel, Die Säugethiere, 957. (Name Combination).

1855. *Dysopes cestonii:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen, Suppl 5: 702.

1876. *Nyctinomus cestonii:* Dobson, Monograph of the Asiatic Chiroptera and catalogue of the species of bats in the collection of the Indian Museum Calcutta, 180.

1877. *Dysopes rüppellii:* Dobson, Proc. zool. Soc. Lond., 1876, IV: 719. Publication date: April 1877. - Comments: Correction of Temminck's *Dysopes rüpelii*.

1891. *Nyctinomus taeniotis:* Thomas, Proc. zool. Soc. Lond., 1891, II: 182. (Lapsus).

1897. *midas* Schulze, Helios, Berlin, 14: 95. - Comments: Preoccupied by *midas* Sundevall, 1843 (See Pavlinov *et al.*, 1995: 91).

1914. *Cephalotes tæniotis:* Cabrera, Fauna Ibérica, 145. (Lapsus).

1985. *rueppellii* Qumsiyeh, Spec. Publ. Mus. Texas Tech. Univ., 23: 71. - Comments: Emendation of *rüpelii* Temminck, 1827. (Emendation).

1988. *Tadarida taeniotis:* Estrada-Peña and Sánchez, Rev. Ibér. Parasitol., 48 (3): 310. (Lapsus).

2018. *Tadarida tenioti:* Lazzeroni, Burbrink and Simmons, Ecol. Evol., 8 (24): 12584. Publication date: 28 November 2018. (Lapsus).

? *Tadarida (Tadarida) teniotis rueppelli:* (Name Combination).

? *Tadarida (Tadarida) teniotis:* (Name Combination).

? *Tadarida teniotis rueppelli:* (Name Combination, Alternate Spelling).

? *Tadarida teniotis rueppellii:* (Name Combination).

? *Tadarida teniotis:* (Name Combination, Current Combination).

TAXONOMY:
Revised by Aellen (1966a) and Kock and Nader (1984).

Amorim *et al.* (2023: 706) indicate that two subspecies are often recognized: *Tadarida teniotis teniotis* (Europe) and *Tadarida teniotis rueppelli* (Africa and Middle East), but the validity of these is questionable.

Populations in Japan, Taiwan and Korea are now treated as a separate species, *T. insignis* (Simmons, 2005).

COMMON NAMES:
Albanian: Lakuriq nate bishtlirë, Lakuriq nate bisht-lire. Arabian: Khaffash. Armenian: Լայնականջ ծալքաշուրթ չղջիկ. Azerbaijani: Bükükdodaq enliqulaq. Basque: Saguzar buztanluze europar, Saguzar buztanluzea. Belarusian: Тадарыда еўрапейская. Bosnian: Golorepi šišmiš. Breton: Molos Cestoni. Bulgarian: Булдогов прилеп. Castilian (Spain): Murciélago rabudo. Catalan (Spain): Ratpenat cuallarg, Rat penat cuallarg. Croatian: Sredozemni slobodnorepac. Czech: Tadarida evropská, Morous evropský, Hroznohled pyskatý, Psohubec myšový, Netopýr vrásopyskatý. Danish: Europæisk bulldogflagermus. Dutch: Zuideuropese bulvleermuis, Bulveermuis, Europese bulvleermuis. English: European Free-tailed Bat, European Guano Bat, Striped or Banded Guano Bat, Wrinkle-lipped Bat, Eurasian Free-tailed Bat. Estonian: Euroopa kurdmokk. Finnish: Doggilepakko. French: Molosse de Cestoni, Tadaride d'Europe, Molosse d'Europe, Tadaride de Cestoni. Frisian: Muskusbulflearmûs. Galician (Spain): Morcego rabudo. Georgian: ევროპული ტადარიდა. German: Bulldoggfledermaus, Europäische Bulldoggfledermaus. Greek: Νυχτονόμος. Hebrew: Pashaf Matsui. Hungarian: Európai szabadfarkú-denevér, Nycteris i urophoros. Irish Gaelic: Ialtóg earrshaor Eorpach. Italian: Molosso del Cestoni. Latvian: Brīvastes sikspārnis. Lithuanian: Europinis raukšlėtalūpis. Luxembourgish: Europäesch Bulldogfliedermaus. Macedonian: Опашест лилјак [= Opashest Liljak]. Maltese: Tadarida. Montenegrin: Dugorepi slijepi miš. Norwegian: Middelhavsfrihale. Polish: Molos europejski. Portuguese: Morcego-rabudo. Rhaeto-Romance: Moloss buldoc. Romanian: Lilacul cu coadă liberă europeană. Russian: Складчатогуб широкоухий. Serbian: Средоземни репаш [= Sredozemni repaš], Широкоухий складчатогуб. Scottish Gaelic: Ialtag eàrr-shaor Eòrpach. Slovak: Tadarida buldogovitá. Slovenian: Dolgorepi netopir. Swedish: Veckläppad fladdermus. Turkish: Avrupa Serbest Kuyruklu Yarasası. Ukrainian: Тадарида європейська [= Tadaryda yevropeys'ka]. Welsh: Ystlum cynffonog.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Amorim *et al.* (2013: 7) indicate that palaeodistribution models predict that during the Last Glacial Maximum (LGM: 23,000 - 18,000 YBP) the climatic conditions for *T. teniotis* were favorable in southern Europe and northern Africa.

CONSERVATION STATUS:
Global Justification
The species is widely distributed over a large extent of occurrence. It occurs in urban areas and forages in other modified habitats. Population trends are not known but are not believed to approach the threshold for the population decline criterion of the IUCN Red List. Consequently, it is assessed as Least Concern (LC ver 3.1 (2001)) (Aulagnier *et al.*, 2008e; IUCN, 2009; Benda and Piraccini, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Benda and Piraccini, 2016). 2008: LC ver 3.1 (2001) (Aulagnier *et al.*, 2008e; IUCN, 2009). 1996: LR: lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is negatively affected by disturbance and loss of roosts in buildings, and by use of pesticides. It is also potentially threatened by wind farms (GMA Europe Workshop, 2006), and deforestation affects the species in some parts of its range (Z. Amr *pers. comm.,* 2005 [in Aulagnier *et al.* (2008e in IUCN, 2009]). However, none of these are considered to be major threats at present (Aulagnier *et al.*, 2008e; IUCN, 2009; Benda and Piraccini, 2016).

Sherwin *et al.* (2012: 174) report aerial hawking and long-distance dispersal to be risk factors related with climatic change.

CONSERVATION ACTIONS:
Aulagnier *et al.* (2008e) [in IUCN (2009)] and Benda and Piraccini (2016) report that it is protected by national legislation in a number of range states and receives international legal protection through the Bonn Convention (Appendix II and Eurobats Agreement) and Bern Convention in parts of its range where these

apply. It occurs in several protected areas across its range.

GENERAL DISTRIBUTION:
Tadarida teniotis is mainly a Palaearctic species, although the south-eastern edge of its range extends into the Indomalayan region. It is well known in the Mediterranean basin, occurring from Portugal, Spain eastwards through southern Europe to the Balkans, Turkey, Israel, Palestine and Jordan. In North Africa it has been recorded from Morocco, Algeria, Tunisia, Libya and Egypt. It is possibly present on Madeira (to Portugal) as there was a supposed old record, but it has not been recorded from there again. It occurs on all the Canary Islands (to Spain) except for Fuerteventura and Lanzarote. It is also recorded from a number of Mediterranean islands (Hutson, 1999; Simmons, 2005). It occurs from sea level to 3,100 m.

Populations in Japan, Taiwan and Korea are now considered to be a separate species, *T. insignis* (Simmons, 2005).

Native: Afghanistan; Albania; Algeria (Kock and Nader, 1984: 129: Horáček *et al.*, 2000: 136); Andorra; Armenia; Azerbaijan; Bangladesh; Bhutan; Bosnia and Herzegovina; Bulgaria; Croatia; Cyprus; Egypt; France [Corse]; Georgia; Gibraltar; Greece [Kriti]; Holy See (Vatican City State); India; Iran, Islamic Republic of; Iraq; Israel; Italy [Sardinia, Sicily]; Jordan; Kazakhstan; Kyrgyzstan; Lebanon; Libyan Arab Jamahiriya (Horáček *et al.*, 2000: 136); Macedonia, the former Yugoslav Republic of; Malta; Monaco; Montenegro; Morocco (Benda *et al.*, 2010a: 161; El Ibrahimi and Rguibi Idrissi, 2015: 364; Dbiba *et al.*, 2025: 7); Myanmar; Nepal; Portugal; Russian Federation; San Marino; Saudi Arabia; Serbia; Spain [Baleares, Canary Is.]; Switzerland; Syrian Arab Republic; Tajikistan; Tunisia (Kock and Nader, 1984: 131; Horáček *et al.*, 2000: 136; Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26; 2023: 4); Turkey; Turkmenistan; Uzbekistan.
Presence uncertain: China.

FUNCTIONAL MORPHOLOGY:
Maniakas and Youlatos (2012: 574) studied the external and muscular forelimb features that could be associated with high-speed flight in open air. They found (p. 576) that the mass of the muscles responsible for the downstroke represented 59.3 % of the total forelimb musculature, and that more than half of these muscles are formed by the M. pectoralis. The muscles responsible for the upstroke are comparatively small, which might indicate that the upstroke in this bat is less important than for other bat groups (p.580). All these features result in a fast, steady enduring flight with relatively limited manoeuvrability.

Amador *et al.* (2019: Suppl.) [referring to Marques *et al.* (2004)] mention a wing loading value of 19.2 Pa, aspect ratio 9.8 and tip shape index of 0.84 for a wingspan of 41 cm and a wing area of 200 cm^2 and a body mass of 30 g.

SEXUAL DIMORPHISM:
Bats from Libya Amorim *et al.* (2023: 709 [referring to Benda *et al.* (2014c)]) display some sexual dimorphism, with males weighting between 24.70 and 35.00 g and a forearm between 53.40 and 58.80 mm and females weighting between 27.50 and 34.20 g and a forearm between 56.70 and 60.70 mm.

ECHOLOCATION:
For 10 Greek specimens, Papadatou *et al.* (2008b: 133) report a start frequency of 15.4 ± 3.28 kHz, a terminating frequency of 11.1 ± 1.34 kHz, a peak frequency of 13.2 ± 1.18 kHz, and a bandwidth of 5.3 ± 1.49 kHz. The duration of the call is 18.4 ± 4.74 ms, and the interpulse interval is 764.6 ± 259.37 ms. Walters *et al.* (2012: suppl.) report the following figures for 35 calls from bats from France, Greece, Italy and Switzerland: duration: 15.03 ± 3.47 ms, F_{max}: 14.61 ± 4.95 kHz, F_{min}: 10.64 ± 1.51 kHz, bandwidth: 3.97 ± 3.76 kHz, F_{peak}: 11.76 ± 2.28 kHz.

In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for seven calls: F_{start}: 15.7 ± 3.8 (12.4 - 22.6) kHz, F_{end}: 9.8 ± 0.4 (9.4 - 10.5) kHz, F_{peak}: 11.7 ± 0.4 (11.1 - 12.6) kHz, duration: 16.3 ± 2.2 (13.1 - 19.3) ms, and interpulse duration: 571.8 ± 254.6 (163.0 - 800.0) ms.

14 calls from Iranian specimens were reported by Benda *et al.* (2012a: 183): F_{start}:19.0 ± 2.6 (14.1 - 22.2) kHz, F_{end}: 11.8 ± 2.2 (8.9 - 14.2) kHz, F_{peak}: 14.5 ± 1.3 (10.6 - 15.9) kHz, duration: 10.6 ± 0.8 (9.5 - 11.8) ms, and interpulse interval: 368.7 ± 89.8 (266.0 - 484.0) ms.

Hackett *et al.* (2016: 223) recorded 44 calls in Israel with the following values: Pulse duration: 12.17 ± 3.34 ms, F_{start}: 22.73 ± 5.02 (17.5 - 29.2) kHz, F_{end}: 15.90 ± 1.44 (13.1 - 17.5) kHz, F_{peak}: 18.49 ± 1.57 (15.1 - 21.4) kHz.

Disca *et al.* (2014: 226) indicate that in Morocco the type of call is FM-QFC, with the following parameters: F_{start}: 22.3 ± 4.2 kHz, F_{end}: 13.3 ± 0.7 kHz, F_{peak}: 14.4 ± 0.8 kHz, bandwidth: 9.0 ± 3.9 kHz, duration: 18.7 ± 2.7 ms.

In Tunisia, Dalhoumi *et al.* (2023: 5) reported F_{start}: 13.2 ± 1.76 (11.4 - 16.7) kHz, F_{end}: 11.71 ± 0.70 (11.1 - 12.8) kHz, F_{max}: 12.16 ± 0.81 (11.3 - 13.0) kHz, duration: 14.25 ± 2.06 (10.7 - 17.3) ms and Interpulse interval: 772.13 ± 179.48 (634.9 - 1095.0) ms.

Ait-Abdesselam *et al.* (2025: 40) reported an F_{max} of 12.83 ± 1.14 kHz for Algerian bats.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats; 2 calls): F_{peak}: 13.2, 13 kHz, F_{start}: 15.4, 17 kHz, F_{end}: 11.1, 12.1 kHz, Band width: 4.3, 4.9 kHz, and duration: 18.4, 16.6 ms.

Molecular Biology:

Karyotype

Đulić and Mrakovcic (1980) reported 2*n* = 48, FN = 76, BA = 30, a submetacentric X chromosome and a subtelocentric Y chromosome for one male from Croatia. Arroyo Nombela *et al.* (1986), however, reported 2*n* = 48, FN = 78, BA = 32 , a submetacentric X and an acrocentric Y for specimens from Spain. Volleth and Eick (2012: 167) mention 2*n* = 48 and a segment number of 25. The autosomal complement consists of five meta- and submetacentrics, and 19 subtelocentric and acrocentric pairs, of which the smallest is dot-like (Arslan and Zima, 2014: 14). These authors also indicate that the X chromosome was found to be subtelocentric in some studies.

Volleth *et al.* (2023b: 7) reported 2*n* = 48 and Fna = 60 (provisionally) and a metacentric X chromosome.

Genetics

Combining mtDNA fragments, 14 microsatellites and ecological modelling tools, Amorim *et al.* (2017: 38) found three main haplogroups in Mediterranean *T. teniotis*: one restricted to the eastern Mediterranean and two that are widespread across the Iberian Peninsula and Morocco. The nuclear data indicated that the bats from the Canary Islands showed the lowest signs of gene flow with the continental populations. Furthermore, they found that gene flow between Morocco and the central Mediterranean area is higher than that between the Iberian Peninsula and the central Mediterranean. Amorim *et al.* (2019: 1) confirmed that the nuclear DNA of bats from the Canary Islands is highly differentiated and isolated from that the two other genetic populations they distinguished: one from Morocco, Iberia and France, and the other from Italy eastwards to Anatolia and the Middle East.

Mata *et al.* (2017: 152) reported the mitogenome to be 16,869 bp long, containing 13 protein-coding genes, 2 ribosomal RNA genes, 22 transfer RNA genes, and 1 control region (d-loop). All protein-coding genes start with the ATG start codon, except for ND2, ND3, and ND5 which begin with ATA or ATT. Eleven protein-coding genes terminated in a canonical stop codon, TAA or TAG, two contain incomplete stop codons, T or TA. Cytochrome b terminates in the mitochondria-specific stop codon AGA.

Habitat:

In her study on the summer foraging habitats of bats in the Mediterranean region of the Iberian Peninsula, Rainho (2007: 176) found that *T. teniotis* showed low activity over fresh-water habitats, and primarily seemed to use pine-tree woodlands and Mediterranean shrublands. For southern Portugal, Marques *et al.* (2004: 99) reported that *T. teniotis* foraged preferentially over forested areas, particularly pine and cork oak woodlands. They used both alluvial plains and the valleys of a mountainous area, but not its ridges. In northern Algeria, Ait-Abdesselam *et al.* (2025: 45) recorded this species mainly from urban and suburban areas.

Habits:

In southern Portugal, Marques *et al.* (2004: 99) found that *T. teniotis* is a late emerger, leaving its roost about one hour after sunset. They also found that these bats have only one foraging bout, which lasted on average 6 hours and 39 minutes. Its flight speed can reach over 50 km/h, and flying can be maintained for over 10 hours.

Ancillotto and Russo (2014: 221) found that that *T. teniotis* can discriminate between familiar and stranger individuals. They also found that the animals show higher rates of aggressive behaviours towards the strangers. Females show less aggressiveness than males, especially towards other females, and both sexes behave less aggressive towards juveniles.

Roost:

In Libya, Benda *et al.* (2014c: 119) found a roosting colony in a fissure in the ceiling in the portal of a large, but shallow cave.

Diet:

Rydell and Arlettaz (1994: 175) suggest that the intense narrowband echolocation calls with low frequency (11 - 12 kHz) without strong harmonics emitted by *T. teniotis* seems to be a specialization for long-range detection of large, tympanate insects such as Lepidoptera and Neuroptera, which are less well represented in the diet of

most other aerial-hawking bats. Based on faecal analyses, they found the following volume percents: southeastern France: Lepidoptera (68.3 %), Neuroptera (24.3 %), others (4.3 %), Acari (0.5 %), and unidentified (2.6 %); Kirghizstan: Lepidoptera (86.8 %), others (12.8 %), unidentified (0.4 %).

Benda *et al.* (2014c: 124) examined four sets of faecal pellets from Libya. Ten pellets from Wadi an Nazrat contained only large moths (Lepidoptera) as did one pellet from the quarry at Wadi al Kuf. Twenty pellets from another location at Wadi al Kuf contained 97 % by volume medium-sized moths and 3 % beetles (Coleoptera). Eight pellets from one animal from Wadi Darnah contained 56 % by volume medium-sized moths and 44 % lacewings (Neuroptera: Chrysopidae).

Benda *et al.* (2012a: 515) indicate that Orthoptera formed the largest contributing group in the diet of *T. teniotis* in Turkey and Jordan. On Rhodes, Coleoptera (especially Curculionidae) formed the most important group. In Iran, Lepidoptera were the most important diet item and Coleoptera, Orthoptera (Ensifera) and Heteroptera also contributed substantially to the diet. Neuroptera (Chrysopidae) and Auchenorrhyncha were almost negligible.

In northeastern Portugal, Mata *et al.* (2016: 1, 2) found significant dietary differences between males and females, where females ate more larger moths and more moths with migratory behaviour (* in below listing). In guano pellets of 69 females and 74 males, Lepidoptera were present in 98.6 % of the females pellets and in 100 % of the males pellets. Split over the various families and species (which all occur in northern African too), they found (wingspan; % in females, % in males): Crambidae: *Nomophila noctuella** (Denis and Schiffermüller, 1775) (rush veneer) (26 - 32 mm; 7.2, 14.9), other Crambidae 6 5.8 9.5; Gelechiidae: *Mirificarma mulinella* (Zeller, 1839) (5.5 - 7.5 mm; 7.2, 14.9), other Gelechiidae (0.0, 2.7); Geometridae: *Aspitates ochrearia* (Rossi, 1794) (yellow belle) (25 - 34 mm; 4.3, 10.8), *Rhodometra sacraria** (Linnaeus, 1767) (vestal) (22 - 28 mm; 14.5, 36.5), other Geometridae (20.3, 13.5); Noctuidae: *Agrotis ipsilon** (Hufnagel, 1766) (dark sword-grass) (40 - 45 mm; 21.7, 4.1), *Agrotis puta* (Hübner, 1803) (shuttle-shaped dart) (30 - 32 mm; 13.0, 18.9), *Agrotis segetum* (Denis & Schiffermüller, 1775) / *Agrotis trux* (Hübner, [1824]) (turnip/crescent dart) (32 - 42 mm; 37.7, 36.5), *Autographa gamma** (Linnaeus, 1758) (silver y) (30 - 45 mm; 43.5, 23.0), *Hoplodrina ambigua* (Denis & Schiffermüller, 1775) (vine's rustic) (32 - 34 mm; 18.8, 35.1), *Mythimna albipuncta* (Denis & Schiffermüller, 1775) (white-point) (30 - 35 mm; 5.8, 9.5), *Mythimna vitellina* (Hübner, 1808) (delicate) (36 - 43 mm; 24.6, 28.4), *Noctua pronuba* (Linnaeus, 1758) / *Noctua janthe* Borkhausen, 1792 (large/lesser broad-bordered yellow underwing) (50 - 60 mm / 30 - 40 mm; 14.5, 13.5), *Peridroma saucia** (Hübner, 1808) (pearly underwing) (43 - 50 mm; 24.6, 12.2), *Phlogophora meticulosa** (Linnaeus, 1758) (angle shades) (45 - 52 mm; 18.8, 8.1), other Noctuidae (31.9, 36.5); Tortricidae: *Tortrix viridana* Linnaeus, 1758 (European oak leafroller) (18 - 23 mm; 5.8, 13.5), other Tortricidae (2.9 5.4); other Lepidoptera (17.4, 21.6); unidentifiedLepidoptera (13.0, 23.0). Other orders present in the pellets were: Coleoptera (1.4, 1.4); Diptera (10.1, 12.2), Hemiptera (2.9, 8.1), Neuroptera (7.2, 12.2), unidentified Insecta (1.4, 1.4), and also some unidentified Arthropoda (7.2, 5.4).

PREDATORS:
In Israel, Reuven (1991: 79) observed *T. teniotis* being preyed upon by a Lanner Falcon (*Falco biarmicus* Temminck, 1825). Balmori (2012: 9) furthermore reports bats being taken by Peregrine Falcon (*Falco peregrinus* Tunstall, 1771) and Common Kestrel (*Falco tinnunculus* Linnaeus, 1758) as well as by Barn Owl (*Tyto alba* (Scopoli, 1769)) and Tawny Owl (*Strix aluco* Linnaeus, 1758), but also by a Garden Dormouse (*Eliomys quercinus* (Linnaeus, 1766)).
Mikula *et al.* (2016: Supplemental data) mention the following diurnal avian predators: Lanner falcon (*Falco biarmicus* Temminck, 1825), Peregrine falcon (*Falco peregrinus* Tunstall, 1771) and Eurasian hobby (*Falco subbuteo* Linnaeus, 1758),

POPULATION:
Structure and Density
It is a common species in suitable habitats. Summer and winter colonies typically number 5 - 100 individuals, although colonies of up to 300 - 400 animals have been recorded. It is probably sedentary, although seasonal in some areas (e.g., Malta). It is not abundant in the Caucasus, nor is it highly gregarious - large colonies are not known in this region (K. Tsytsulina *pers. comm.,* 2005 in Aulagnier *et al.*, 2008e [in IUCN, 2009) and Benda and Piraccini (2016)]). There are only six records for Iran, however, there have not been extensive survey efforts there (M. Sharifi *pers. comm.,* in Aulagnier *et al.*, 2008e [in IUCN, 2009] and Benda and Piraccini (2016)).

Trend
2016: Unknown (Aulagnier *et al.*, 2008e). 2008: Unknown (Aulagnier *et al.*, 2008e; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 13 years.

REPRODUCTION AND ONTOGENY:
In Spain, Balmori (2003: 37) reported births taking place from the end of June to the beginning of July.

In Portugal, Amorim *et al.* (2015: 228) found that drought had a severe negative influence on the reproduction of *T. teniotis*. This drought probably resulted in reduced food resources early in the pre-breeding season, which limited the ability to restore the bat's body condition after the winter and before the breeding season.

MATING:
In a colony in Valladolid, Spain, Balmori (2003: 37; 2017: 460) found that *T. teniotis* bats were organized in 'harems' made up by a dominant male together with a variable number of females, in which the male defends the refuge ("resource defence polygyny"). The males were emitting mating calls to attract passing-by females. These harems were formed between August and October. When competitors were present, the males reacted by noisy and fast chasing-flights and the releasing of a strong scent, probably used to mark their territory.

Balmori (2017: 465) found two peaks of sexual activity: one in spring (April - June) and another in summer/autumn (August - October), but also indicated that each female might only enter heat once a year.

PARASITES:
In Italy, Voyron *et al.* (2011: 193) reported the following fungal entities from live *T. teniois* specimens: *Aspergillus fumigatus var. fumigatus* and *Trichosporon chiropterorum*.

Benda *et al.* (2010b: 315) only found the mite *Parasteatonyssus hoogstraali* Keegan, 1956 parasiting on *Tadarida teniotis* in Jordan. They do report on other ectoparasites found previously: the bat fly *Nycteribia pedicularia* Latreille, 1805 found in Palestine, bat fleas *Araeopsylla wassifi* Traub, 1954 in Turkey and Egypt, *A. gestroi* (Rotschild, 1906) in Lebanon, and a tick *Argas vespertilionis* (Latreille, 1802) in Egypt. Geldenhuys *et al.* (2021: 21) reported the presence of *Argas (Chiropterargas) boueti* Roubaud and Colas-Belcour, 1933 on bats from northern Africa. Balmori (2012: 9) also mentioned *Steatonyssus periblepharus* Kolenati, 1858, *Ewingana baekelandae* Estrada-Peña, 1992, and unidentified Trombiculidae, as well as the bat bug *Cimex pipistrelli* Jenyns, 1839 and the flea *Araeopsylla gestroi* (Rothschild, 1906).

Parasteatonyssus hoogstraali Keegan, 1956 was already reported by Estrada-Peña and Sanchez (1988: 310) from *T. teniotis* on Frontera, Canary Islands.

The following enteroparasites were reported by Balmori (2012: 9): Trematodes *Plagiorchis vespertilionis* (Müller, 1784), *Prosthodendrium ascidia* (Van Beneden, 1873) and *Lecithodendrium linstowi* Dollfus, 1931; Nematodes: *Molinostrongylus alatus* (Ortlepp, 1932), *Pseudophysaloptera formosana* (Yokogawa, 1922), *Rictularia bovieri* Blanchard, 1886, *Litomosa aelleni* Tibayrenc, Bain & Ramachandran 1979, and further unidentified *Litomosa* sp. Amorim *et al.* (2020: 21) also reported on unidentified *Physaloptera* Rudolphi, 1819, *Rictularia* Froelich, 1802 and *Spirura* Blanchard, 1849.

Benda *et al.* (2014c: 124) reported the following ectoparasites from Libya: Ischnopsyllidae: *Araeopsylla gestroi* (Rothschild, 1906); Macronyssidae: *Parasteatonyssus hoogstraali* (Keegan, 1956) [1st record from Libya]; Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856).

From Algeria, Bendjeddou *et al.* (2017: 15) reported one ectoparasite: Arachnida: *Ixodes ricinus* (Linnaeus, 1758).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Araeopsylla gestroi* (Rothschild, 1906); Ixodidae: *Ixodes ricinus* (Linnaeus, 1758); Macronyssidae: *Parasteatonyssus hoogstraali* (Keegan, 1956); Pulicidae: *Synosternus cleopatrae pyramidis* (Rothschild, 1903); and Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856).

Sándor *et al.* (2021a: 4) mentioned the argasid mites *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) and *Carios vespertilionis* Latreille, 1802. Orlova *et al.* (2024: 155) reported the latter mite as *Argas vespertilionis*.

VIRUSES:
Herpesviridae
Cytomegalovirus
Nieto-Rabiela *et al.* (2019: Suppl.) mentioned this virus.

Reoviridae
Orthoreovirus
This virus was reported by Kohl and Kurth (2014: 3113) from Italian bats.

Rhabdoviridae
Lyssavirus - Rabies related viruses
European bat lyssavirus 1
Was reported by Luis *et al.* (2013: Suppl.), Willoughby *et al.* (2017: Suppl.).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Egypt, Libya, Morocco, Sudan.

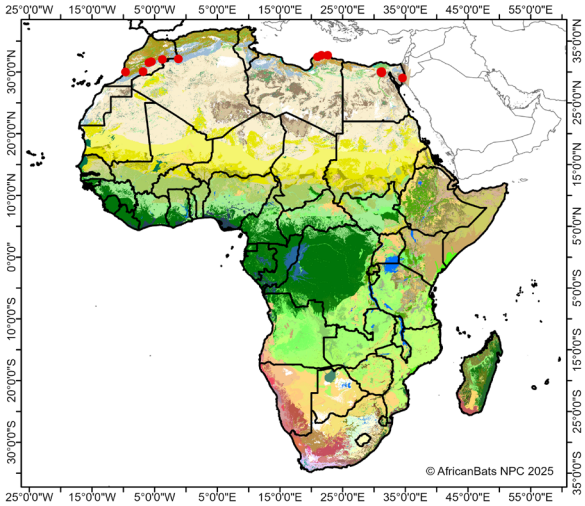

Figure 216. Distribution of *Tadarida teniotis*.

Tadarida ventralis (Heuglin, 1861)

*1861. *Nyctinomus (Dysopes) ventralis* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 4, 11. Publication date: 1861. Type locality: Eritrea: Kérén [ca. 15 45 N 38 20 E]. [Goto Description]. Lectotype: SMNS 982: ad ♀, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294), who confirm that the Lectotype status of this specimen was designated by Kock (1975: 6). - Etymology: From the scientific Latin feminine adjective *ventràlis*, meaning "ventral", referring to the presence of a wide, median, prominent orange ventral stripe (see Lanza *et al.*, 2015: 324).
1862. *Nyctinomus ventralis:* Heuglin, Peterm. Geographische Mittheilungen, 8: 26. (Name Combination).
1876. *Nyctinomus africanus* Dobson, Ann. Mag. nat. Hist., ser 4, 17 (101): 348. Publication date: 1 May 1876. Type locality: South Africa: Transvaal. [Goto Description]. Holotype: NHMUK 1875.11.19.1: ad ♂, skull and alcoholic. Presented/Donated by: Richard Browdler Sharp[e].
1877. *Dysopes ventralis:* Heuglin, Reise in Nordost Afrika, 2: 26. (Name Combination).
1877. *Nyctinomus [(Nyctinomus)] cestoni* Dobson, Proc. zool. Soc. Lond., 1876, IV: 719. Publication date: April 1877. - Comments: Not of Savi, 1825. In part (see Kock, 1975: 6).
1891. *N(yctinomus) taeniotis* Thomas, Proc. zool. Soc. Lond., 1891, II: 183. Publication date: August 1891. - Comments: Not of Rafinesque, 1814. See Kock (1975: 7).
1901. *N(yctinomus) midas* de Winton, Ann. Mag. nat. Hist., ser 7, 7 (37): 42. Publication date: 1 January 1901. - Comments: Not of Sundeval. In part. See Kock (1975: 7).
1928. *Mops ventralis:* Thomas, Ann. Mag. nat. Hist., ser 10, 1 (2): 302. Publication date: 2 February 1928. (Name Combination).
1939. *Mops rüppellii* Allen, Bull. Mus. comp. Zool., 83: 108. - Comments: Not of Temminck, 1827. In part. See Kock (1975: 7).
1951. *Tadarida africana:* Roberts, Mammals of Southern Africa, 101.
1953. *Tadarida (Tadarida) africana:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 66.
1974. *Tadarida (Tadarida) ventralis:* Largen, Kock and Yalden, Mon. Zool. ital., (NS) 16 (Suppl 5): 253. (Name Combination).
2015. *Nyctinomus taeniatus:* Lanza, Funaioli and Riccucci, The bats of Somalia and neighbouring areas, 323. (Lapsus).
? *Tadarida ventralis africana:* (Name Combination).
? *Tadarida ventralis:* (Name Combination, Current Combination).

TAXONOMY:
For use of this name in place of *africana*, see Kock (1975).

COMMON NAMES:
Afrikaans: Transvaalse losstertvlermuis, Reuse losstertvlermuis. Chinese: 非洲大犬吻蝠. Czech: morous africký, tadarida africká. English: Giant Guano Bat, Giant African Guano Bat, African Giant Free-tailed Bat, Giant African Free-tailed Bat, Transvaal Free-tailed Bat, Giant Free-tailed Bat. French: Tadaride géante d'Afrique, Grande tadaride africaine, Molosse géant. German: Große Bulldoggfledermaus, rothbraune Doggengrämler. Italian: Tadarìda ventràle. Portuguese: Morcego gigante de cauda livre.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Mickleburgh *et al.*, 2008aj; IUCN, 2009; Mickleburgh *et al.*, 2019d).

Assessment History

Global

2018: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2019d). 2008: DD ver 3.1 (2001) (Mickleburgh *et al.*, 2008aj; IUCN, 2009). 2004: NT ver 3.1 (2001) (Mickleburgh *et al.*, 2004ao; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: VU D2 ver 3.1 (2001) (Taylor *et al.*, 2016d). 2004: Considered a vagrant. Not assessed, known from a single locality (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:

The threats to this species are poorly known. It may be threatened through the conversion of suitable habitat to agricultural land and the use of pesticides in these modified areas (Mickleburgh *et al.*, 2008aj; IUCN, 2009; Mickleburgh *et al.*, 2019d).

CONSERVATION ACTIONS:

Mickleburgh *et al.* (2008aj) [in IUCN (2009)] and Mickleburgh *et al.* (2019d) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the distribution, natural history, and threats to this little-known species.

GENERAL DISTRIBUTION:

Tadarida ventralis is widely distributed in East and Southern Africa. It ranges from Eritrea in the north to Zimbabwe, and northern South Africa, in the south. The westernmost record is from the eastern Democratic Republic of the Congo, close to the border area with Uganda. Most records are from high altitude (1,500 m upwards to 2,500 m asl).

Native: Congo (The Democratic Republic of the); Eritrea; Ethiopia; Kenya; Malawi (Ansell and Dowsett, 1988: 46; Monadjem *et al.*, 2010d: 547); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 547); South Africa (Taylor *et al.*, 2015: 50); Sudan; Tanzania; Zambia (Ansell, 1986; Monadjem *et al.*, 2010d: 547); Zimbabwe (Cotterill, 2004a: 260; Monadjem *et al.*, 2010d: 547).

ECHOLOCATION:

See Taylor *et al.* (2005).

POPULATION:

Structure and Density

It has been rarely recorded and is largely known from single dead individuals (Mickleburgh *et al.*, 2008aj; IUCN, 2009; Mickleburgh *et al.*, 2019d).

Trend

2018: Unknown (Mickleburgh *et al.*, 2019d). 2008: Unknown (Mickleburgh *et al.*, 2008aj; IUCN, 2009).

REPRODUCTION AND ONTOGENY:

In Malawi, young were born at the beginning of the wet season (Happold and Happold, 1990b: 568). In E Zambia, a pregnant female was collected in November (Happold and Happold, 2023: 129).

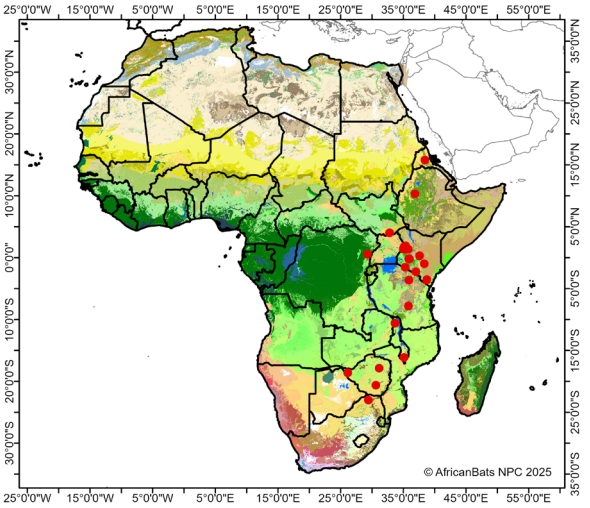

Figure 217. Distribution of *Tadarida ventralis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Congo (Democratic Republic of the), Eritrea, Ethiopia, Kenya, Malawi, South Africa, South Sudan, Tanzania, Zambia, Zimbabwe.

Superfamily VESPERTILIONOIDEA J. E. Gray, 1821

*1821. *Vespertilionoidea* J. E. Gray, London Med. Repos., 15: 299. Publication date: 1 April 1821. (Current Combination).

1928. *Vespertilionoidea:* Weber, Die Säugetiere, 24. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Introduced as tribe (but actually similar to superfamily) and originally included the families Vespertilionidae J. Gray, 1821, Natalidae J. Gray, 1866, Myzopodidae Thomas, 1904 and Molossidae Gervais, 1855 (see Jackson and Groves, 2015: 265).

2025. *Vespertilionidea:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: 1. Publication date: 18 July 2025. (Lapsus).

TAXONOMY:
Currently recognized families within the Superfamily VESPERTILIONOIDEA within Africa: **CISTUGONIDAE** Van Cakenberghe and Seamark, 2011; **MINIOPTERIDAE** Dobson, 1875; **VESPERTILIONIDAE** Gray, 1821.

COMMON NAMES:
Czech: netopýrov ci.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Ravel *et al.* (2011: 402) suggest that affinities such as the closure of the protofossa, the slender lophes, and a tiny metaconule on the upper molars (in the fossil genus *Dizzya* and an unnamed "Eochiropteran" from the El Kohol Formation in Algeria) could support an African endemic radiation of modern Vespertilionoidea.

Guan *et al.* (2025: 7) estimate that the split between the Vespertionidae and the Miniopteridae occurred some 48.18 mya, with the first Vespertilionidae appearing at 40.32 mya.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Morocco, South Sudan.

Family CISTUGONIDAE Lack, Roehrs, Stanley, Ruedi and Van den Bussche, 2010

2008. *Cistugoinae:* Van Cakenberghe and Seamark, African Chiroptera Report, 213. Publication date: 1 July 2008. - Comments: Spelling used for subfamily. (Name Combination).
*2010. *Cistugidae:* Lack, Roehrs, Stanley, Ruedi and Van den Bussche, J. Mamm., 91(4): 980. (Alternate Spelling).
2010. *Cistugonidae:* Benda, Vespertilio, 18-19: 271. - Comments: Type genus: Cistugo Thomas, 1912. (Current Combination, Current Spelling).

TAXONOMY:
Stadelmann *et al.* (2004b) showed that the genus *Cistugo* was not placed with the genus *Myotis*, but was basal to the vespertilioid radiation, which is also supported by Horáček *et al.* (2006). For this reason, the ACR (2008, 2009, 2010) recognized representatives of the genus *Cistugo* as a separate distinct subfamily within the Vespertilionidae.

Taylor *et al.* (2024: 9) reported this family's stem age at 42.7 (38.91 - 46.45) Mya, which is much earlier than the crown diversification, which dates from 1.42 (0.72 - 2.48) Mya,

Lack *et al.* (2010: 980) recognized that taxa within this group should be recognized at a family level and suggested the name “Cistugidae”. Benda (2010: 271) and ACR (2011) used a corrected form of the family (or subfamily) name: Cistugonidae (- goninae) - according to the code (genitive from *Cistugo* is *Cistugonis*, thus Cistugonidae).

Simmons and Cirranello (2020) refer to article 29.3.3 of the ICZN code to retain the usage of "Cistugidae" as family name, as this would indicate that "the stem for the formation of the family-group name is chosen by the author of the family level name". The article, however, explicitly mentions the "**entire** generic name", which would support the usage of "Cistugonidae". We therefore keep on using this name.

Currently (Simmons and Cirranello, 2024a) recognized genus within the family Cistugonidae: ***Cistugo*** Thomas, 1912.

COMMON NAMES:
Czech: žlázokřídlecovití.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The study by Amador *et al.* (2016: 26) supports the long-time separation from the Vespertilionidae, which probably occurred in the early middle Eocene (crown age 43 MYA).

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) mention the karyotype as 2*n* = 50

Genus ***Cistugo*** Thomas, 1912

*1912. *Cistugo* Thomas, Ann. Mag. nat. Hist., ser 8, 10 (56): 205. Publication date: 1 August 1912 [Goto Description]. - Comments: Type species: *Cistugo seabræ* Thomas, 1912.

TAXONOMY:
Meester *et al.* (1986) included *Cistugo* as a subgenus of *Myotis*. Baker *et al.* (1974) recorded the karyotype of *Myotis* as 2*n* = 44, AA = 50, but Dippenaar *et al.* (1983) gave it as 2*n* = 50, AA = 48 in both *seabrai* and *lesueuri*.

Hayman and Hill (1971) doubt the validity of *lesueuri* and Corbet and Hill (1980) include it in *seabrai*, while Koopman (1982) retain it as a separate species. It is possible, particularly in view of their allopatric distribution, that *lesueuri* may best be treated as a subspecies of *seabrai*.

Included as subgenus in *Myotis* by Koopman (1993a: 207), but considered a valid genus by Thomas (1915), Roberts (1919), Rautenbach *et al.* (1993), Bickham *et al.* (2004: 333), Stadelmann *et al.* (2004b: 185) and Simmons (2005). Stadelmann *et al.* (2004b: 185) state that it might be possible that the two genera share closer phylogenetic relationships with other families of bats than with the Vespertilionidae.

Lack *et al.* (2010: 980) erected a new family: Cistugoidae (see family account above for information about corrected spelling of family name), containing only the genus *Cistugo* Thomas, 1912, which they separate from the Vespertilionidae by the presence of 2 to 4 glands in the wing membrane immediately behind the forearm (see also Seamark and Kearney, 2006), which are lacking in all other vespertilionoid bats.

Taylor *et al.* (2024: 7) mention a crown date of 1.42 (0.72 - 2.48) Mya for *Cistugo*.

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Cistugo*: ***lesueuri*** Thomas, 1912; ***seabrae*** Thomas 1912.

COMMON NAMES:
Czech: žlázokřídlecové. English: Wing-gland Bats. German: Mausohren.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery (2007: 619) reported on the presence of *Cistugo* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa.

GENERAL DISTRIBUTION:
Seamark *et al.* (2012: 116-117) indicate that the ranges of the two species (*C. seabrae* and *C. lesueuri*) might not be allopatric as previously assumed but might be overlapping.

HABITAT:
Marsden *et al.* (2023: 7) indicate that bats of the genus *Cistugo* are generally urban avoiders. This can probably be attributed to their roost specificity and the rarity of these species.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Uganda.

Cistugo lesueuri Roberts, 1919

*1919. *Cistugo lesueuri* Roberts, Ann. Transv. Mus., 6(3): 112-113. Type locality: South Africa: SW Cape province: Paarl district: near Paarl, Franschhoek [=Frenchhoek] valley: L'Ormarins [=Lormarins] [33 44 S 18 58 E]. [Goto Description]. Holotype: TM 2286: ad ♂, skin and skull. Collected by: J.S. Le Sueur Esq. Collection date: 15 September 1917; original number: 154. - Comments: For details on the type locality, see Meester *et al.*, 1986: 49). - Etymology: Named after J.S. le Sueur of L'Ormarins in the Paarl district, Western Cape, who recovered the original specimen from his cat (see Smithers, 1983: 92; Taylor, 2005). (Current Combination).
? *Myotis (Cistugo) lesueuri:* (Name Combination).
? *Myotis lesueuri:* (Name Combination).

TAXONOMY:



Figure 218. A female *Cistugo lesueuri* (TM 48190) caught at the Farm Schaapplaats, Free State, South Africa.

Hayman and Hill (1971) doubt the validity of *lesueuri* and Corbet and Hill (1980) include it in *seabrae*, while Koopman (1982) retain it as a separate species. It is possible, particularly in view of their allopatric distribution, that *lesueuri* may best be treated as a subspecies of *seabrae*.

COMMON NAMES:
Afrikaans: Lesueur se langhaarvlermuis, Lesueur-langhaarvlermuis, Lesueurse Vlerkkliervlermuis. Czech: žlázokřídlec Lesueurův. English: Lesueur's Wing-gland Bat, Lesueur's Hairy Bat, Lesueur's Myotis, Wing-gland bat. French: Murin de Lesueur. German: Leseuers Mausohr.

CONSERVATION STATUS:
Global Justification
Monadjem *et al.* (2017cg) report that this species is restricted to South Africa and Lesotho in areas with suitable rock crevices and water sources. It has a large range, with an estimated extent of occurrence of over 400,000 km^2 and there are more than 20 known locations. This species is highly likely to be under collected and many more subpopulations are suspected to occur, especially within the Nama and Succulent Karoo regions of South Africa. Wind farms represent an emerging threat, as its preferred habitat coincides with suitable wind farm sites. Although declines have been recorded these are not suspected to be at levels high enough to qualify the species for listing under a threat category. However, systematic long-term monitoring should be used to estimate rates of decline across its range, as this species may require reassessing in a threatened category (Jacobs, 2008b; IUCN, 2009; Monadjem *et al.*, 2017cg).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cg). 2008: LC ver 3.1 (2001) (Jacobs, 2008b; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Jacobs, 2004b; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Avenant *et al.*, 2016b). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate, assessed as *Myotis lesueuri* (Smithers, 1986).

MAJOR THREATS:
The species is locally threatened, in parts of its range, by conversion of land to agricultural use (Jacobs, 2008b; IUCN, 2009; Driver *et al.*, 2012). However, as this species occurs mostly in high-altitude areas, this is not a severe threat. The growing trend of developing wind farms in the eastern parts of South Africa and in Lesotho is starting to pose a threat to this species. The degree of impact and levels of decline to the population are currently unknown and should be monitored (Monadjem *et al.*, 2017cg).

CONSERVATION ACTIONS:
Monadjem *et al.* (2017cg) report that in the Western Cape, the species is recorded from the three protected areas, Cedarberg Wilderness Area, Gamkaberg Nature Reserve and Karoo National Park; in the Free State the species was recorded in the Golden Gate National Park; in Lesotho it is found in Sehlabathebe National Park, as well as in the Maloti-Drakensberg Transfrontier Conservation Area. No specific interventions are currently necessary, but conservation planning and engagement with the wind energy industry will be needed in future to mitigate subpopulation loss with wind farm construction (Monadjem *et al.*, 2017cg).

GENERAL DISTRIBUTION:
This species is restricted to South Africa and Lesotho, where its distribution is best predicted by geology (Babiker Salata, 2012: 50). Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 673,792 km^2.

Native: Lesotho (Lynch and Watson, 1990; Lynch, 1994: 192; Monadjem *et al.*, 2010d: 562); South Africa (Free State - Watson, 1998; Monadjem *et al.*, 2010d: 562; KwaZulu Natal - Monadjem *et al.*, 2010d: 562; Western Cape - Herselman and Norton, 1985; Rautenbach *et al.*, 1993; Seamark and Brand, 2005; Monadjem *et al.*, 2010d: 562).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
For 4 specimens from the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) mention the following parameters: Fa: 36.0 ± 0.4 mm, Wing area: 93.3 ± 1.6 cm^2, Wing span: 23.8

± 1.1 cm, Wing loading: 7.5 ± 1.4 N/m^2, and aspect ratio: 6.1 ± 0.7.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 219. Clockwise from top lateral, ventral and dorsal skull images of TM 2286, holotype of *Cistugo lesueuri* Roberts, 1919.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 7.1 Pa, aspect ratio 6.2 for a wingspan of 24 cm and a wing area of 93 cm^2 and a body mass of 7 g.

ECHOLOCATION:
From Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the type of calls to be low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 36.8 ± 0.9 kHz.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 50, FN = 48, BA = 0, a submetacentric X chromosome, and an acrocentric Y chromosome, these results were the same as those obtained for *C. seabrae* from Namibia (Rautenbach *et al.*, 1993) .

HABITAT:
In the Free State Province of South Africa collected from broken country (e.g., koppies and cliffs), invariably away from human habitation and constructions, but close to open water (dams and streams). While in the Western Cape it inhabits fynbos and possibly the succulent karoo (Jacobs, 2008b; IUCN, 2009).

Cooper-Bohannon *et al.* (2016: Table S2) mention its occurrence in the following habitat types: Afromontane (43 %), High veld (29 %), SW Cape (13 %) and SW arid (11 %).

HABITS:
In the Free State Province of South Africa specimens were netted in the early evening, between 18:30 and 20:00, with only two specimens being caught after 21:15 (Watson, 1998: 128). When disturbed in their day roost they flew to another roost 50 meters away (Watson, 1998: 128).

ROOST:
Found in a crevice roughly four meters from the ground, on a west-facing dolorite rock face next to a river in the Free State Province of South Africa (Watson, 1998: 127).

Czenze *et al.* (2021: 3) classified this species as cool-roosting as they preferred roost sites with temperatures well below 30*C and where the maximum temperature was at least 10*C lower than outside.

DIET:
From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 39 faecal pellets from 4 bats (in volume percent): Diptera (47.3 ± 37.3), Hemiptera (32.5 ± 22.8), Hymenoptera (6.8 ± 13.5), Coleoptera (6.3 ± 4.9), Trichoptera (2.5 ± 5.0), Ephemenoptera (1.5 ± 3.0), and unknown (3.3 ± 6.5).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 75 minutes, and the digestibility rate about 80.3 %.

POPULATION:
Structure and Density
Although endemic, the species has a wide distribution within the assessment region, despite not being common and very rarely recorded (Monadjem *et al.*, 2017cg. In the Free State Province of South Africa, a group of approximately 40 individuals was located in a day roost (Watson, 1998: 127). Seamark and Brand (2005) showed that this species made up only 4.6% of the overall catch in the Cederberg, Western Cape. In inland Western Cape, near the border with the Northern Cape, a group of approximately 30 individuals was located in a day roost (T. Morgan *unpubl. data* in Monadjem *et al.* (2017cg)). Systematic long-term monitoring

should be used to estimate rates of decline across its range, as this species may be increasingly threatened by wind farm expansion (Monadjem *et al.*, 2017cg).

Trend
2016: Decreasing (Monadjem *et al.*, 2017cg).
2008: Decreasing (Jacobs, 2008b; IUCN, 2009).
2004: Decreasing (Jacobs, 2004b; IUCN, 2004).

VIRUSES:
Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)
Oelofsen and Van der Ryst (1999) tested a single individual from one locality in Lesotho for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 15 individual brains, from four localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

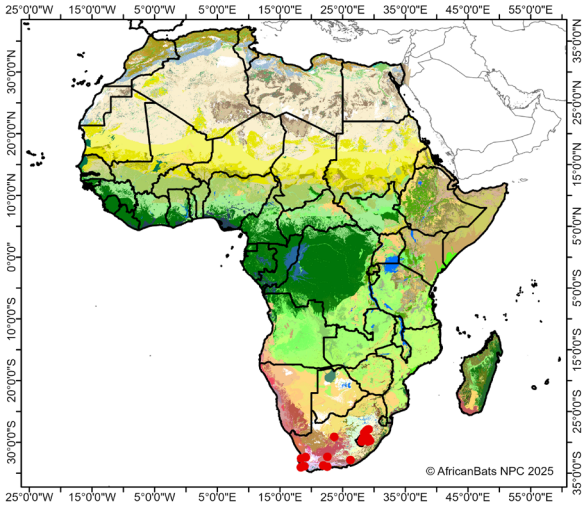

Figure 220. Distribution of *Cistugo lesueuri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Lesotho, South Africa.

Cistugo seabrae Thomas, 1912

*1912. *Cistugo seabræ* Thomas, Ann. Mag. nat. Hist., ser 8, 10 (56): 205. Publication date: 1 August 1912. Type locality: Angola: Mossamedes [=Moçamedes] [ca. 15 56 S 12 10 E]. [Goto Description]. Holotype: NHMUK 1906.1.3.3: ad ♀, skull and alcoholic. Presented by the Lisbon Museum. (Current Combination).
2004. *Myotis (Cistugo) sebrai:* Bickham, Patton, Schlitter, Rautenbach and Honeycutt, Mol. Phylogenet. Evol., 33 (2): 333. (Name Combination, Lapsus).
? *Cistugo seabrae:* (Current Combination, Current Spelling).
? *Cistugo seabrai:* (Name Combination, Alternate Spelling).
? *Myotis (Cistugo) seabrai:* (Name Combination).
? *Myotis seabrae:* (Name Combination).
? *Myotis seabrai:* (Name Combination).

TAXONOMY:



Figure 221. A male *Cistugo seabrae* (TM 47582) caught at Khamkirri, Northern Cape, South Africa. Note the gland on the wing.

See Simmons (2005).

COMMON NAMES:
Afrikaans: Angola-langhaarvlermuis, Angolase Vlerkkliervlermuis. Czech: žlázokřídlec Seabrův. English: Seabra's Wing-gland Bat, Angolan Wing-gland Bat, Angolan Hairy Bat. French: Murin d'Angola. German: Angola-Mausohr.

ETYMOLOGY OF COMMON NAME:
The colloquial name is derived from the fact that the original specimen originated from Moçâmedes on the south-western coast of Angola (Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because there are no threats, making it unlikely to be declining fast enough to qualify for listing in a more threatened category (Griffin and Jacobs, 2008; IUCN, 2009; Monadjem *et al.*, 2017bj).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bj). 2008: LC ver 3.1 (2001) (Griffin and Jacobs, 2008; IUCN, 2009). 2004: NT ver 3.1 (2001), assessed as *Cistugo seabrai* (Jacobs, 2004a; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: NT D1+D2 ver 3.1 (2001) (Jacobs *et al.*, 2016e). 2004: VU D2 ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate, assessed as *Myotis seabrai* (Smithers, 1986).

MAJOR THREATS:

There are no major threats to this species. It may be locally threatened by mining operations in a small part of its range (Griffin and Jacobs, 2008; IUCN, 2009; Monadjem *et al.*, 2017bj).

CONSERVATION ACTIONS:

Griffin and Jacobs (2008) [in IUCN (2009)] report that it is not known if there are any direct conservation measures in place for this species, and it is unclear if it occurs within any protected areas. Further studies are needed into the distribution and natural history of this little-known species.

GENERAL DISTRIBUTION:

This southern African species ranges from the type locality of Moçâmedes in southwestern Angola, southwards through western Namibia to the Northern Cape of South Africa.

Native: Angola (Crawford-Cabral, 1989; Thomas, 1912c; Monadjem *et al.*, 2010d: 562); Namibia (Thomas and Hinton, 1925; Shortridge, 1934; Rautenbach *et al.*, 1993; Kearney and Van Schalkwyk, 2009; Monadjem *et al.*, 2010d: 562); South Africa (Herselman and Norton, 1985; Stadelmann *et al.*, 2004b; Seamark and Kearney, 2006; Kearney and Van Schalkwyk, 2009; Monadjem *et al.*, 2010d: 562).

MOLECULAR BIOLOGY:

Karyotype

Rautenbach *et al.* (1993) reported 2*n* = 50, FN = 48, BA = 0, a submetacentric X chromosome, and an acrocentric Y chromosome, these results were the same as those obtained for *C. lesueuri* from South Africa (Rautenbach *et al.*, 1993).

Genetics

Stadelmann *et al.* (2004b).

HABITAT:

Little is known about the natural history of this species. All of the localities from which they have been collected are arid with a mean annual rainfall of less than 100 mm (Skinner and Chimimba, 2005).

HABITS:

Specimens have usually been caught close to open water and have been observed gleaning insects from orange trees (Roberts, 1951; Taylor, 2000; Skinner and Chimimba, 2005).

DIET:

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 80 minutes, and the digestibility rate about 79.5 %.

POPULATION:

Structure and Density

It appears to be a rarely recorded species (Griffin and Jacobs, 2008; IUCN, 2009; Monadjem *et al.*, 2017bj).

Trend

2016: Unknown (Monadjem *et al.*, 2017bj). 2008: Unknown (Griffin and Jacobs, 2008; IUCN, 2009). 2004: Decreasing (as *Cistugo seabrai*) (Jacobs, 2004a; IUCN, 2004).

PARASITES:

ACARI

Macronyssidae

Orlova *et al.* (2020c: 951) reported the presence of *Steatonyssus afer* Radovsky and Yunker, 1963 on two *Cistugo seabrae* bats from Namibia.

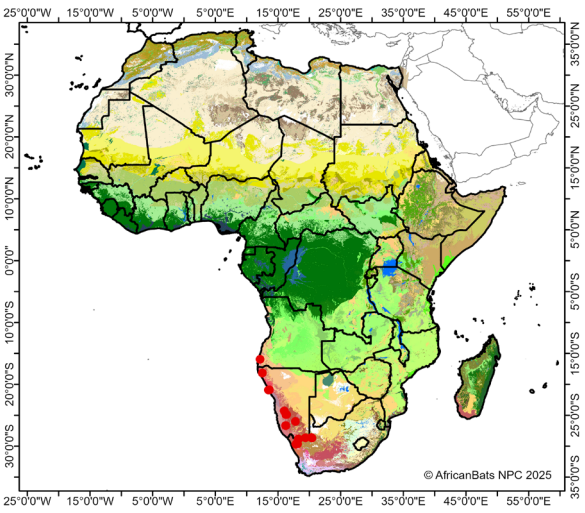

Figure 222. Distribution of *Cistugo seabrae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

"Africa", Angola, Namibia, South Africa.

†Family INDETERMINATE

†Genus ***Chambinycteris*** Ravel, 2016

*2016. *Chambinycteris* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 402. Publication date: 30 September 2016. - Etymology: Refers to Chambi, the locality where the specimens were collected (see Ravel *et al.*, 2016: 402).

TAXONOMY:
Ravel *et al.* (2016: 358) indicate that this genus has a basal position within the Emballonuridae.

Jones *et al.* (2024: 16) could not place *Chambinycteris* within a specific (super)family, but found it fell within the crown Chiroptera.

†***Chambinycteris pusilli*** Ravel, 2016

*2016. *Chambinycteris pusilli* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 403. Publication date: 30 September 2016. - Etymology: From the Latin "*pusilli*" meaning puny or sickly, referring to the small size and fragility of the species (see Ravel et al., 2016: 403). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:

Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

†Genus ***Drakonycteris*** Ravel, 2016

*2016. *Drakonycteris* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 399. Publication date: 30 September 2016. - Etymology: From the Greek "*δράκων*" meaning dragon and "*νυκτερισ*" meaning bat (see Ravel *et al.*, 2016: 399).

†***Drakonycteris glibzegdouensis*** Ravel, 2016

*2016. *Drakonycteris glibzegdouensis* Ravel, in: Ravel et al., Geodiversitas, 38 (3): 356, 399, figs 23, 24. Publication date: 30 September 2016. Type locality: Algeria: Béchar province: Gour Lazib: Sahara, Hammada du Dra: Glib Zegdou [29 42 49 N 05 45 58 W]. - Etymology: Referring to the type locality of Glib Zegbou (see Ravel *et al.*, 2016: 399). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:

Late lower Eocene (Ypresian - Brown *et al.*, 2019: Suppl.) to early middle Eocene.

Family MINIOPTERIDAE Dobson, 1875

1875. *Miniopteri* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (95): 349. Publication date: 1 November 1875.
*1875. *Miniopteridae* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (95): 348. Publication date: 1 November 1875. - Comments: Type genus: *Miniopterus* Bonaparte, 1837. Originally included the genera *Natalus* J. Gray, 1838; *Thyroptera* Spix, 1823 and *Miniopterus* Bonaparte, 1837. (Current Combination).
1878. *Miniopterææ* Trouessart, Rev. Mag. Zool., (3) 6: 253. - Comments: See Taylor (1934).
.
1897. *Minioptereae* Trouessart, Catalogus Mammalium tam viventium quam fossilium, p 134. (Alternate Spelling).
1907. *Miniopterinae:* Miller, Bull. U.S. natl. Mus., 57: xi, 227. Publication date: 29 June 1907. - Comments: Type genus: *Miniopterus* Bonapart, 1837.
1977. *Miniopteridae:* Mein and Tupinier, Mammalia, 41 (2): 207, 209. - Comments: Type genus: *Miniopterus* Bonaparte, 1837.

† indeterminate

TAXONOMY:
Bannikova *et al.* (2002: 722) indicate that the Miniopterinae do not deserve the rank of independent family (as did Koopman, 1984c, 1993a, 1994; Yoshiyuki, 1989; Corbet and Hill (1992; McKenna and Bell, 1997), but see Hoofer and Van Den Bussche (2003: 13) who make a strong case for attributing family rank. They follow Mein and Tupinier (1977), Groombridge (1994), Gopalakrishna and Chari (1983), Tiunov (1989), Pierson (1986). See also Hawkins *et al.* (2019: 11355).

In their study on rolling-circle transposons (*Helitrons*), Thomas *et al.* (2010: 55) found none of these in the Miniopteridae. They also indicated that these *Helitrons* colonized the Vespertilionidae some 30 - 36 mya, which is much later than the split between Vespertilionidae and Miniopteridae, which occurred some 43 million years ago. Patterson and Webala (2012: 32) indicate that the split between Vespertilionidae and *Miniopterus* occurred between 38 and 47 million years ago. Demos *et al.* (2019c: "6") indicate that the Miniopteridae diverged from the Vespertilionidae and Cistugidae some 48 mya.

Herkt *et al.* (2017: Appendix 4S), investigating the IUCN distribution maps and species distribution models, left out the Miniopteridae because of their exceptionally high cryptic diversity and level of phenetic similarity, which leads to unreliably identification of large amounts of published records.

Using UCE (ultraconserved elements) data, Demos *et al.* (2023: xxx) found that the continental African *Miniopterus* clade is monophyletic, with the exception of M. inflatus. This species is sister to the continental African + Malagasy clades

Currently (Simmons and Cirranello, 2024b) recognized genera of the family MINIOPTERIDAE: ***Miniopterus*** Bonaparte, 1837.

COMMON NAMES:
Czech: létavcovití, netopýři dlouhorucí. Dutch: Langvleugelvleermuizen. English: Long-fingered Bats. French: Minioptéridés. German: Langflügelfledermäuse. Italian: Miniottèridi, Minioptèridi. Russian: Длиннокрыловые. Ukrainian: Довгокрили [= Dovhokryly]. Vietnamese: Họ dơi cánh.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Amador *et al.* (2016: 26) estimated the split from the Vespertilionidae at c. 48 MYA, and a stem age at 13 MYA. Demos *et al.* (2023) situate the crown age of African Miniopteridae in the late Miocene (10.4 MYA), which also seems to be the timeframe in which the Afrotropic and Madagascar sister lineages diversified (at about 9.06 MYA). The crown age of the Malagay clade is estimated at 7.78 MYA and that of the Afrortropical clade at 8.4 MYA. They also indicate that the continental radiation originated in the Zambezian and Somalian/Ethiopian biogeographic regions, although it might be possible that a recolonisation from Madagascar might have happened.

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) indicate that the karyotype for all 25 species in the family has a 2*n* value of 46.

Based on the analysis of the karyotypes (more specifically the common derived condition of the MMY22 homolog), Volleth *et al.* (2023b: 1) state that the Miniopteridae are more closely related to the Vespertilionidae than to the Molossidae.

Genetics
Capanna *et al.* (1968: 240) already pointed out that there was a cytotaxonomic difference between the Vespertilioninae and the Miniopterinae, especially in the average length of the aploid female set.

Platt *et al.* (2016: 9) analysed the genome data for *M. natalensis* and compared it with that of several other vesper bats and they concluded that *Helitrons* and hATs were introduced into the genome of the Vespertilionidae after their divergence from *Miniopterus*.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 63 % of the species belonging to this family are confirmed viral carriers.

Three of the 15 bats collected in the dry season and examined by Kumakamba *et al.* (2021: 7) were positive for coronaviruses. One additional bat collected in the wet season was not.

Genus ***Miniopterus*** Bonaparte, 1837

*1837. *Miniopterus* Bonaparte, Iconografia Fauna italiana, 1, fasc 20 [Goto Description]. - Comments: Type species: *Vespertilio ursinii* Bonapate, 1837 (=*Vespertilio schreibersii* Kuhl, 1817). - Etymology: From the Greek "*μινύς*"

or "*μινός*", meaning small and "*πτέρυξ*", meaning wing, referring to the very short first phalanx of the third and longest finger (see Palmer, 1904: 426; Flannery, 1995a: 374; Kozhurina, 2002: 16). Lanza *et al.* (2015: 328) mention the following: "According to Bonaparte (1837) who described the genus and Lanza (2012), *Miniopterus* is a scientific masculine Latin substantive made up of the proper feminine Latin noun *Minyèias* 'Minyad', i. e. a daughter of Minyas, king of Orchomenus, turned into a bat, and of the Greek neuter substantive *πτερόν*" (pteròn) 'wing', meaning 'flying Minyad'. The etymology proposed by Kozhurina (2002), meaning 'with small (narrow) wings', is incorrect, even if formally logical. Also partially erroneous is the etymology given by some Italian dictionaries, such as Battaglia (1978) and Devoto & Oli (1997), who interpret 'minio' as 'minimum, red-lead', the red colouring agent, which obviously has nothing to do with the greyish brown colour of Miniopterus' wings". - Phonetics: min-ee-op′-ter-us. (Current Combination).

1846. *Minyopterus:* Agassiz, Nomenclator. Zool., Mamm, 235. - Comments: Variant spelling (Meester *et al.*, 1986: 45) or unjustified emendation (Jackson and Groves, 2015: 263). (Lapsus, Emendation).

1858. *Miniopteris:* Tomes, Proc. zool. Soc. Lond., 1858, XXVI (cccliv): 115. Publication date: 13 May 1858. - Comments: Variant spelling (Meester *et al.*, 1986: 45) or unjustified emendation (Jackson and Groves, 2015: 262). Not *Miniopteris* J. Gray, 1849 (Mammalia, Chiroptera, Vespertilionidae) (used as genus name for *Myotis macrotarsus* (Waterhouse, 1845) (see Jackson and Groves, 2015: 263). (Alternate Spelling).

1900. *Minneopterus:* Lampe, Jb. nass. Ver. Naturkde, 53: Cat Säugeth-Sammlung, p 12. Publication date: 1900. - Comments: Cat. Säugeth.-Sammlung, p. 12. Lapsus (see Allen, 1939a: 102; Meester *et al.*, 1986: 45). Jackson and Groves (2015: 263) indicate it appeart to be a *nomen nudum* or an unjustified emendation. (Lapsus, Emendation).

1920. *Mineopterus:* Haagner, South African Mammals, 22. (Lapsus).

1980. *Minioterus:* Bernard, Ann. Transv. Mus., 32 (3): 55. Publication date: January 1980. (Lapsus).

1986. *Mimopteris:* Castiblanco de V., Jaramillo and Muñoz A., Actual Biol., 15 (56): 27. Publication date: April-June 1986. (Lapsus).

2014. *Mineropterus:* Kohl and Kurth, Viruses, 6 (8): 3112. Publication date: 13 August 2014. (Lapsus).

2015. *Minioptera:* Golden and Comaroff, Ecol. Soc., 20 (2): 42: 5. (Lapsus).

2019. *Minioptreus:* Zeghbib, Herczeg, Kemenesi, Zana, Kurucz, Urbán, Madai, Földes, Papp, Somogyi and Jakab, Sci. Reps., 9 (15706): 1. Publication date: 31 October 2019. (Lapsus).

2024. *Minipteros:* Munjita, Mubemba, Changula, Tembo, Hamoonga, Bates, Chitanga, Munsaka and Simulundu, Front. Public Health, 12 (1471452): 3. Publication date: 20 November 2020. (Lapsus).

? *Miniopterus sp.*

? *Miniopterus sp. IVK-2011*

General Comments:

Given the rather recent taxonomic changes in *Miniopterus* from Madagascar, Goodman *et al.* (2022: 1908) indicate that it is not clear which literature data should be linked with which taxon.

Taxonomy:

Reviewed (in part) by Peterson (1981). See Goodwin (1979: 119), Maeda (1982), and Hill (1983). All have come to very different conclusions. Molecular systematics and biogeography is discussed by Appleton *et al.* (2004); their DNA data (p. 437) suggest that the number of species currently recognized (11 or 13) is a gross underestimate. Phylogenetic analyses performed by Christidis *et al.* (2014: 1) indicate that 18 clades are present within Malagasy *Miniopterus* of which only 11 have Latin binominals.

Šrámek *et al.* (2012: 165) investigated the taxonomic status of the bent-winged bats in the western Palaearctic and distinguished four species: *M. schreibersii* (s.str.) from Europe, coastal Anatolia, Levant, Cyprus, western Transcaucasia, and North Africa; *M. pallidus* from inland Anatolia, Jordan, eastern Transcaucasia, Turkmenistan, Iran and southern Afghanistan (Kandahar); a *Miniopterus* sp., recorded from Nangarhar province in eastern Afghanistan, which was tentatively assigned to *M.* cf. *fuliginosus*; and another *Miniopterus* sp. With Afro-tropic affinities confirmed from south-western Arabia and Ethiopia, which tentatively named *M.* cf. *arenarius*. They also indicate that a possible new taxon (subspecies) within *M. schreibersii* exists in the Atlas Mountains of Morocco. Bilgin *et al.* (2013: 21) indicate that this Maghrebian form possibly even represents a new species, which they tentatively call: *M. maghrebensis*.

See Taylor *et al.* (2019a: 318) for a discussion on the recent increase in Afro-Madagascan species. Demos *et al.* (2019c: "1") analysed cyt-*b* and nuclear data from sub-Saharan *Miniopterus* specimens and found evidence for five undescribed species. Their data (p. "9") confirmed the species status of *fraterculus, mossambicus, natalensis* and *newtoni* and tentatively for *africanus, arenarius, inflatus* and *minor*. *M. inflatus, minor* and *natalensis* are probably paraphyletic.

The 18 Malagasy clades recovered by Christidis *et al.* (2014) in their phylogenetic analysis were divided in into five primary lineages (representing sister species): (1) *M. griveaudi*; (2) *M. mahafaliensis, M. sororculus* and X3; (3) *M. majori, M. gleni* and *M. griffithsi*; (4) *M. brachytragos; M. aelleni* A, and *M. aelleni* B, and (5) *M. manavi* and *M. petersoni*. These are in turn linked to a group comprising *M. egeri* and five genetically distinct populations referred to as P3, P4, P5, P6 and P7.

Derouiche *et al.* (2024: 32) also distinguished five lineages in the Malagasy *Miniopterus* species, but they replaced *M. brachytragos* with *M. ambohitrensis*. On the African continent, they distinguished two groups: Group C (containing *M. inflatus* only) and group D, which is further subdivided in three subgroups: D2: *M. fraterculus* and *M. minor*; D3: *M. maghrebensis, M. natalensis* and extralimital *M. schreibersii*; D4: *M. africanus, M. mossambicus* and *M. newtoni.*

Currently (Simmons and Cirranello, 2024b) recognized species of the genus *Miniopterus*: ***aelleni*** Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi and Appleton, 2009; ***africanus*** Sanborn, 1936; ***ambohitrensis*** Goodman, Ramasindrazana, Naughton and Appleton, 2015; ***arenarius*** Heller, 1912; *australis* Tomes, 1858 – Philippines, Borneo, Java, Timor, Moluccas, southeast to Vanuatu and eastern Australia (Simmons, 2005: 519); ***brachytragos*** Goodman, Maminirina, Bradman, Christidis and Appleton, 2011; ***egeri*** Goodman, Ramasindrazana, Maminirina, Schoeman and Appleton, 2011; *eschscholtzii* G.R. Waterhouse, 1845 – Philippines; ***fraterculus*** Thomas and Schwann, 1906; *fuliginosus* (Hodgson, 1835) – Afghanistan to Myanmar; Japan; Vietnam; Korea; *fuscus* Bonhote, 1902 – Ryuku Isls (Japan) (Simmons, 2005: 519); ***gleni*** Peterson, Eger and Mitchell, 1995; ***griffithsii*** Goodman, Maminirina, Bradman, Christidis and Appleton, 2009; ***griveaudi*** Harrison, 1959; ***inflatus*** Thomas, 1903; *macrocneme* Revilliod, 1914 – New Guinea to Vanuatu and New Caledonia (Simmons, 2005: 520); ***maghrebensis*** Puechmaille, Allegrini, Benda, Bilgin, Ibáñez and Juste, 2014; *magnater* Sanborn, 1931 – northeastern India, southeastern China, Burma, Thailand, Laos and Vietnam to Malaysia, Sumatra, Java, Timor (Indonesia), Borneo, Moluccas and New Guinea including the Bismarck Arch. (Simmons, 2005: 520); ***mahafaliensis*** Goodman, Bradman, Christides and Appleton, 2009; ***majori*** Thomas, 1906; ***manavi*** Thomas, 1906; *medius* Thomas and Wroughton,1909 – southeastern China, Thailand, western Malaysia, Borneo, Java, Sulawesi, Philippines, New Guinea (Simmons, 2005: 520); ***minor*** Peters, 1867; ***mossambicus*** Monadjem, Goodman, Stanley and Appleton, 2013; ***natalensis*** (A. Smith, 1834); ***newtoni*** Bocage, 1889; ***nimbae*** Monadjem, Shapiro, Richards, Karabulut, Crawley, Nielsen, Hansen, Bohmann and Mourier, 2020; *orianae* Thomas, 1922 – Australia; *pallidus* Thomas, 1907 – N Arabia; Asian part of Turkey; Afghanistan; *paululus* Hollister, 1913 – Majuyod, Negros and Guimarás Island (Philippines), Borneo, Selaru (Simmons, 2005: 521); ***petersoni*** Goodman, Bradman, Maminirina, Ryan, Christidis and Appleton, 2008; *phillipsi* Kusuminda, Mannakkara, Ukuwela, Kruskop, Amarasinghe, Saikia, Venugopal, Karunarathna, Gamage, Ruedi, Csorba, Yapa and Patterson, 2020 – Sri Lanka; *pusillus* Dobson, 1876 – India, Nepal and Burma to Sumatra and Timor (Indonesia), Philippines and Moluccas (Simmons, 2005: 520); *robustior* Revilliod, 1914 – Loyalty Islands (east of New Caledonia) (Simmons, 2005: 521); ***schreibersii*** (Kuhl, 1817); *shortridgei* Laurie and Hill, 1957 – Java, Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Seralu, Timor, Semau, Roti and Savu Isls (Indonesia) (Simmons, 2005: 522); ***sororculus*** Goodman, Ryan, Maminirina, Fahr, Christidis and Appleton, 2007; *srinii* B. Srinivasulu and A. Srinivasulu, 2023 – India (Western Ghats); *tristis* (Waterhouse, 1845) – Philippines, Sulawesi, Sanan Isl, New Guinea, Bismarck Arch., Solomon Isls, New Hebrides (Simmons, 2005: 522); ***villiersii*** Aellen, 1956: ***wilsoni*** Monadjem, Guyton, Naskrecki, Richards, Kropff and Dalton, 2020.

Furthermore there is also the extinct African †***horaceki*** Gunnell, Eiting, and Geraads, 1837.

COMMON NAMES:
Czech: létavci, netopýři dlouhorucí. English: Long-fingered Bats, Bent-winged Bats. French: Minioptères. German: Langflügelfledermäuse, Sackfledermaus. Ukrainian: Довгокрил [= Dovhokryl].

ETYMOLOGY OF COMMON NAME:
The very long second phalanx of the third finger led to the name "long-fingered bats". The feature also allows these bats to fold or bent their wings back, hence "bent-winged bats" (see Demos *et al.*, 2019c: "2").

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
The oldest fossil remains for *Miniopterus* date from some 13.65 million years ago (see Shi and Rabosky, 2015: 1532).

Butler (1978) refers to African material of this genus, found from the early Pleistocene at Olduvai, and Avery (2007: 619) reported on the presence of *Miniopterus* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa. Geraads *et al.* (2010: 279) reported *Miniopterus* in Late Cenozoic (ca. 2.5 MYA) deposits in Ahl al Oughlam, Morocco.

Weyeneth (2010) suggested that Malagasy *Miniopterus* colonized the Comoros during the Pleistocene, favored by prevailing winds.

GENERAL DISTRIBUTION:
Due to major changes in the taxonomy of this genus over the past few years, quite an amount of identifications of Madagascan bats became uncertain and require review.

BIOGEOGRAPHY:
Weyeneth *et al.* (2008) suggest that the Comoros were colonized independently at least two or three times by ancestors from Madagascar.

DETAILED MORPHOLOGY:
Brain
Maseko and Manger (2007) describe the nuclear parcellation and neuronal morphology of the cholinergic, catecholaminergic and serotonergic systems within the brain of six adult female *Miniopterus schreibersii* [possibly *M. natalensis* or *M. fraterculus*, not *Miniopterus schreibersii*], captured from caves in northwest region of Gauteng Province, South Africa.

SEXUAL DIMORPHISM:
Goodman and Maminirina (2007) found no notable evidence for sexual dimorphism in Malagasy *Miniopterus* spp.

ECHOLOCATION:
Bioacoustic data of 11 Malagasy (Madagascar and the Comoros) has been collected and investigated by Ramasindrazana *et al.* (2011).

Taylor-Boyd *et al.* (2025: 116) report the following values for 12 calls from Zambian *Miniopterus* sp.: Interpulse interval: 63.8 ± 14.1 (35.2 - 90.7) ms; F_{max}: 59.5 ± 2.3 (54.1 - 63.0) kHz; Start slope: -24.0 ± 5.8 (-13.1 - -38.2) kHz/ms; End slope: -8.8 ± 4.0 (-10.1 - -5.6) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.3 - 0.7) ms.

HABITS:
Rainho *et al.* (2023: 7) assigned the *Miniopterus* bats in Meru county (Kenya) to a medium-to-high-flying guild flying at altitudes between 2 and 10 m.

PREDATORS:
Goodman *et al.* (2022: 1908) mention that a white-browed owl (*Athene superciliaris* (Vieillot, 1817) [= *Ninox superciliaris* (Vieillot, 1817)]) was seen feeding on small *Miniopterus* bats at Ankaranana (Madagascar).

PARASITES:
BACTERIA
Bartonellae
Bartonella
Kosoy *et al.* (2010: 1877) reported a prevalence of *Bartonella* spp. in *Miniopterus* sp. from Kenya of 22/105 (21.0 %) cultured from blood samples. Fifty-one *Bartonella* spp. *gltA* sequences were obtained from 3 identified species of *Miniopterus* (*africanus, minor, natalensis*), were 24 unique *gltA* genotypes representing at least 3 genogroups (Kosoy *et al.*, 2010: 1878). See also Kosoy (2010: 719) for further information.

HAEMOSPORIDA
Rasoanoro *et al.* (2021: 2) report that *Polychromophilus melanipherus* (Dionisi, 1899) is the only representative of this genus that infects Malagasy *Miniopterus* species.

ACARI
Myobiidae
Fain (1994: 1280) reported the genus *Calcarmyobia* to occur only on bats of the genus *Miniopterus* with 18 species and 8 subspecies.

Spinturnicidae
Szubert-Kruszyńska *et al.* (2018: 760) mentioned the presence of *Spinturnix psi* (Kolenati, 1856) on *Miniopterus* sp. grom Madagascar.

Trombiculidae
Trombigastia (Trombigastia) cadei (Vercammen-Grandjean and Brennan, 1957) was reported by Vercammen-Grandjean and Fain (1958: 26) and Stekolnikov (2018a: 118) on *Miniopterus* sp. specimens from N'Gong, S Kenya.

Uchikawa (1985c: 110) reported the presence of *Pteracarus miniopteri* Uchikawa, 1978 from *Miniopterus* sp. specimens from Madagascar, Central Africa, Cameroon, Kenya (Mombasa), South Africa (Transvaal).

DIPTERA
Streblidae
Raymondiodes leleupi Jobling, 1954 described form a poorly identified bat (*Hipposideros caffer* or *Miniopterus* sp.) from Thysville, Congo (Haeselbarth *et al.*, 1966: 104). *Nycteribosca kollari* Frauenfeld, 1855 was reported by Vermeil (1960) from Tunisia.

Nycteribiidae
Nycteribia tecta Theodor, 1957 (Haeselbarth *et al.*, 1966: 110). Duron *et al.* (2014: 2108) mention the presence of *Nycteribia stylidiopsis* (Speiser, 1908) on *Miniopterus* sp. from the Comoros, and of *Penicillidia leptothrinax* (Speiser, 1908) from Madagascar. The latter were carrying Enterobacteriales and *Bartonella* and *Wolbachia* bacteria (Szentiványi *et al.*, 2019a: Suppl.). Enterobacteriales were also found in *Penicillidia* cf. *fulvida* (Szentiványi *et al.*, 2019a: Suppl.).

Verrett *et al.* (2022: 6) collected *Penicillidia fulvida* (Bigot, 1885) from bats they assigned to *Miniopterus* clades 1, 2, 3, 4, 7, 8 and/or 10.

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Miniopterus* sp.: *Nycteribia schmidlii scotti* Falcoz, 1923, *Penicillidia (Penicillidia) fulvida* (Bigot, 1885) and *Phthiridium tectum* (Theodor, 1957). *N. s. scotti* has also been reported from *Miniopterus* clade 1/4/5/7 and *Miniopterus inflatus/africanus*, whereas i P. f. fulvida had been reported from *Miniopterus* clade 1/4/7.

SIPHONAPTERA
Ischnopsyllidae
Members of the genus *Rhinolophopsylla* Oudemans, 1909 are known to be parasites of *Miniopterus* and *Rhinolophus* (Haeselbarth *et al.*, 1966: 191).

VIRUSES:
Adenoviridae
These viruses were found by Waruhiu *et al.* (2017) in bats from Kenay.

Coronaviridae
18 out of 300 Kenyan *Miniopterus* bats tested by Tao *et al.* (2017: Suppl.) was positive for CoV (6 %).

Flaviviridae
Raulino *et al.* (2022: 256) found antibodies against Zika virus.

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that 13 out of 77 examined Kenyan *Miniopterus* sp. specimens tested positive for *Paramyxovirus* sequences. This was also the case for two out of 41 specimens from the DRC.

Retroviridae
Farkašová *et al.* (2017: 3145) described an endogenous Deltaretrovirus, which only occurs in this family of bats and not in the closely related Vespertilionidae and Cistugonidae. This suggests that the endogenization occurred between 20 and 45 million years ago.

Rhabdoviridae
Lyssavirus - Rabies related viruses
West Caucasian Bat virus (WCBV)
Kuzmin *et al.* (2008b) detected WCBV in four of five localities sampled in Kenya with a seroprevalence of 17-26%.

Ikoma lyssavirus (IKOV)
Horton *et al.* (2014: Table S1) tested 229 Kenyan *Miniopterus* sp. specimens but failed to find neutralising antibodies.

Duvenhage lyssavirus (DUVV)
Banyard A. C. and Fooks A. R. (2017: 18) reported this virus from *Miniopterus* sp. specimens from South Africa and Kenya.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Angola, Cameroon, Comoros, Congo (Democratic Republic of the), Ethiopia, Gabon, Kenya, Madagascar, Malawi, Mozambique, Namibia, South Africa, South Sudan, Tanzania, Tunisia, Uganda, Zambia, Zimbabwe.

Miniopterus 'incertae-sedis'

2014. *Miniopterus sp. P3:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.
2014. *Miniopterus sp. P4:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.
2014. *Miniopterus sp. P5:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.
2014. *Miniopterus sp. P6:* Christides, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.
2014. *Miniopterus sp. P7:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.
2014. *Miniopterus X3:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014. - Comments: Christidis *et al.* (2014: 4) found this haplotype - represented by a single specimen - forming a sub-clade with *Miniopterus sororculus* and *M. mahafaliensis*.
2019. *Miniopterus manavi 2:* Demos, Webala, Lutz, Kerbis Peterhans, Goodman, Cortés-Delgado, Bartonjo and Patterson, Zool. Scr., 49 (1): 5. Publication date: 22 October 2019.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus aelleni Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi and Appleton, 2009

*2009. *Miniopterus aelleni* Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi and Appleton, Zool. Scr., 38 (4): 339, 353, figs 3d, 3e, 4, 7 - 10. Publication date: 22 June 2009. Type locality: Madagascar: Antsiranana province: Ankarana special reserve, Canyon d'Antsiroandoa Centre,: 6.2 km NW Mahamasina [12 55.1 S 49 07.6 E, 120 m]. Holotype: FMNH 173067: ad ♂, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG 12809. See Goodman and Cardiff (2004: 230). Paratype: FMNH 173069: ad ♀, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG. See Goodman and Cardiff (2004: 230). Paratype: FMNH 173070: ad ♀, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG. See Goodman and Cardiff (2004: 230). Paratype: FMNH 173072: ad ♂, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG. See Goodman and Cardiff (2004: 230). Paratype: FMNH 173075: ad ♂, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG. See Goodman and Cardiff (2004: 230). Paratype: FMNH 173076: ad ♂, skull and alcoholic. Collected by: H. Vola Razakarivony and Scott G. Cardiff; collection date: 8 April 2002; original number: SMG. See Goodman and Cardiff (2004: 230). - Etymology: The name *aelleni* is a patronym for Villy Aellen (1926 - 2000) who was a mammalogist at the Muséum d'histoire naturelle de Genève from 1954 to his retirement in 1989, where he also served as curator, assistant director, and director (Mahnert, 2000; Goodman *et al.*, 2009a: 353). (Current Combination).

2014. *Miniopterus aelleni A:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.

2022. *Miniopterus aellini:* Kettenburg, Kistler, Ranaivoson, Ahyong, Andrianiaina, Andry, DeRisi, Gentles, Raharinosy, Randriambolamanantsoa, Ravelomanantsoa, Tato, Dussart, Heraud and Brook, Front. Public Health, 10 (786060): 10. Publication date: 11 February 2022. (Lapsus).

Taxonomy:

See Goodman *et al.* (2009a).

Schoeman *et al.* (2014: 19) refer to Christidis *et al.* (2014) indicating that - from a phylogenetic species perspective - there is evidence that two sister species are present, which are tentatively named: *M. aelleni* A and *M. aelleni* B.

Common Names:

Czech: létavec Aellenův. English: Aellen's Long-fingered Bat, Aellen's Bent-winged Bat. French: Minioptère d'Aellen. German: Aellens Langflügelfledermaus.

Etymology of common name:

In honour of Villy Aellen (1926 - 2000), who was a mammalogist at the Muséum d'histoire naturelle de Genève from 1954 to his retirement in 1989, where he also served as curator, assistant director, and director. He devoted much of his professional interests to the study of bats, particularly those of Africa (see Goodman *et al.*, 2009a: 353).

Conservation status:

Global Justification

This species occurs at several sites in the western half of Madagascar (Goodman and Ramasindrazana, 2013); it is also known from a few specimens obtained on Anjouan Island in the Comoros Archipelago (Goodman *et al.*, 2010c). It is apparently not forest-dependant and may not be subjected to any important habitat degradation or other human pressures (Goodman *et al.*, 2010c).

Assessment History

Global

2016: LC ver. 3.1 (2001) (Goodman, 2017g).

Regional

None known.

Conservation actions:

Goodman (2017g) report that on Madagascar, this species is known from several protected areas, which include Ankarana, Namoroka and Bemaraha. While to their knowledge the sites this species occurs on Anjouan Island are not under any special protection.

General distribution:

Lowland portions of northern and western Madagascar up to 1,350 m (Goodman *et al.*, 2009a; Schoeman *et al.*, 2014: 28). Schoeman *et al.* (2014: 31) assigned *M. aelleni* A to the western or dry deciduous region bioclimatic zone, whereas *M. aelleni* B was classified to the humid forest region.

Goodman *et al.* (2010c: 131), O'Brien (2011: 289) and Garbutt (2022: 105) reported it also from the Comoros (Anjouan), where it occurs in more humid forests between 220 and 690 m..

General description of external morphology:

See Goodman *et al.* (2009a).

Dental Formula:

The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^2/_3$, $M^3/_3$ = 36.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2009a).

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls as *M. manavi sen lat.*, these calls were broadband FM/QCF sweeps produced at low duty cycle with most energy at about 58.1 kHz in the fundamental, with pulses having a short duration of about 4 ms.

Ramasindrazana *et al.* (2011: 294) recorded 19 calls from 7 *Miniopterus aelleni* specimens, and found the following echolocation call values: Frequency of maximum energy: 51.9 ± 1.57 (49.5 - 54.8) kHz, Maximum frequency: 99.8 ± 8.48 (75.0 - 119.0) kHz, Minimum frequency: 48.0 ± 1.43 (46.0 - 50.0) kHz, Call duration: 4.1 ± 0.65 (3.0 - 5.0) ms, Inter pulse interval: 87.3 ± 16.75 (61.0 - 118.5) ms.

MOLECULAR BIOLOGY:
Genetics
See Goodman *et al.* (2009a).

HABITAT:
Dammhahn and Goodman (2013: 108) mention the lower portion of forest structure and partially open areas as the foraging habitat for this species.

Also see Goodman *et al.*, 2009a).

ROOST:
This species seems to prefer roosting in caves (Garbutt, 2022: 105); see also Goodman *et al.* (2009a).

POPULATION:
Structure and Density
See Goodman *et al.*, 2009a). While Goodman (2017g) report that it is not known.

Trend
2016: (Goodman, 2017g).

REPRODUCTION AND ONTOGENY:
Somewhere between 17 November and 8 December, three bats reported by Goodman *et al.* (2025: 215) were one male with enlarged testes, another one with slightly enlarged testes and a non-reproductive female.

PARASITES:
Tortosa *et al.* (2013: 4) report the presence of the Nycteribiid bat fly *Nycteribia stylidiopsis* Speiser, 1908. Wilkinson *et al.* (2016) and Urushadze *et al.* (2017: 9) report *Penicillidia leptothrinax* Speiser, 1908, which in turn carried *Bartonella* bacteria and the blood parasite *Polychromophilus melanipherus* (Szentiványi *et al.*, 2019a: Suppl.). Ramasindrazana *et al.* (2017: Suppl.) report both flies.

Ramasindrazana *et al.* (2016: 6) reported the presence of *Litosoma* Clade 3 (Nematoda: Onchocercidae) on this bat species. They also mention *Litosoma goodmani* Martin, Bain, Jouvenet, Raharimanga, Robert & Rousset, 2006 from a *M. aelleni* specimen, that was previously identified as "*M. manavi*".

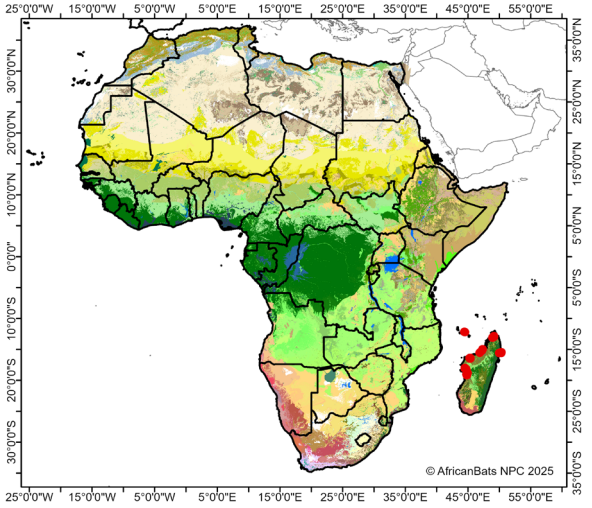

Figure 223. Distribution of *Miniopterus aelleni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros, Madagascar.

Miniopterus africanus Sanborn, 1936

*1936. *Miniopterus africanus* Sanborn, Field Mus. Nat. Hist., Zool. Ser., (362) 20 (14): 111. Publication date: 15 August 1936. Type locality: Ethiopia: Shoa province: Mulo, Sanford's Ranch [ca. 09 00 N 39 00 E, 8000 ft]. [Goto Description]. Holotype: FMNH 28769: ad ♀, skin and skull. Collected by: Alfred Marshall Bailey; collection date: 25 October 1926; original number: 73. (Current Combination).

? *Miniopterus inflatus africanus:* (Name Combination).

TAXONOMY:
Included in *inflatus* by Koopman (1993a: 230), but considered a valid species by Peterson *et al.* (1995: 120), Lavrenchenko *et al.* (2004b: 144), Simmons (2005).

COMMON NAMES:
Chinese: 非洲长翼蝠. Czech: létavec východoafrický. English: African Long-fingered Bat. French: Minioptère d'Afrique orientale. German: Afrikanische Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Assessed as Data Deficient (DD ver 3.1 (2001)) as there are no data regarding its distribution, population, habitat, threats, or conservation measures following its recognition as a valid species by Juste [B.] *et al.* (2007). Additional clarification of this species complex is required to complete an assessment (Waldien and Webala, 2020).

Assessment History
Global
2019: DD ver 3.1 (2001) (Waldien and Webala, 2020). 2004: LC ver 3.1 (2001) (IUCN, 2004; Schlitter, 2004h).

MAJOR THREATS:
Waldien and Webala (2020) state that given the uncertainties surrounding the species, there is little data regarding the threats to the species. As it inhabits moist montane rainforest deforestation (logging and conversion to agricultural lands) are likely threats.

CONSERVATION ACTIONS:
Waldien and Webala (2020) suggest that given the uncertainties surrounding the species, there are few insights into current and needed conservation actions for the species. Protection of moist montane rainforest is a logical first step. Research is needed on the species taxonomy, population, distribution, and ecology.

GENERAL DISTRIBUTION:
Native: Botswana; Eritrea; Ethiopia; Kenya; Namibia; Tanzania.

MOLECULAR BIOLOGY:
Karyotype
Tolera *et al.* (2021: 127) reported *2n* = 46 and FN = 54 for an Ethiopian male. The chromosomes included two large, two medium and one small pair of metacentrics and 17 pairs of acrocentrics. The X chromosome is probably a small metacentric and the Y chromosome a small dot-like acrocentric.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 87 minutes, and the digestibility rate about 78.7 %.

POPULATION:
Structure and Density
Population size and trends are unknown (Waldien and Webala, 2020).

Trend
2019: Unknown (Waldien and Webala, 2020).
2004: Not assessed.

PARASITES:
Lutz *et al.* (2016: 9) examined 20 *M. africanus* specimens from East Africa and found four of them infected with the haemosporidan parasite *Polychromophilus melanipherus* Dionisi, 1899.

Polychromophilus sp. Parasites were also found in 11 of the 22 Kenyan bats examined by Lutz *et al.* (2021: Suppl.)

Uchikawa (1985a: 19) reported that the type specimen of *Miniopterus africanus* harboured the "atypical" form of *Calcarmyobia congoensis* Uchikawa, 1982 (Acari: Myobiidae). This species is also a host of *Calcarmyobia kenyaensis* Uchikawa, 1982 in Kenya (see Uchikawa (1985a: 22) as *M. inflatus africanus*). Possibly some other records mentioned by Uchikawa (1985a: 22) as collected from *M. inflatus* from Cameroon, Liberia, and The Democratic Republic of Congo should be included here.

Uchikawa (1985c: 110) also reported on the presence of the mite *Pteracarus miniopteri* Uchikawa, 1978 on some specimens from Kenya, that were identified as *M. inflatus africanus*.

Tortosa *et al.* (2013: 5) and Ramasindrazana *et al.* (2017: Suppl.) mention this species as host for the Nycteribiid bat flies *Nycteribia schmidlii* Schiner, 1853 and *Pencillidia fulvida* Bigot, 1885.

DIPTERA
Nycteribiidae
Lutz *et al.* (2021: Suppl.) found Kenyan *M. africanus* bats to be hosts for *Eucampsipoda africana* Theodor, 1955, *Nycteribia schmidlii* Schiner, 1853 and *Penicillidia fulvida* (Bigot, 1885). Dick *et al.* (2023) reported these flies as *Nycteribia schmidlii scotti* Falcoz, 1923 and *Penicillidia (Penicillidia) fulvida* (Bigot, 1885).

Streblidae
Raymondia intermedia Jobling, 1936 (Shapiro *et al.*, 2016: 255). *Raymondia seminuda* Jobling, 1954 (Shapiro *et al.*, 2016: 255).

VIRUSES:
In their study of bats from three Kenyan caves, Kamau *et al.* (2022:) found astrovirues,

herpesviruses and retroviruses, as well as one occurrence of Bole tick virus 4.

Coronaviridae - Coronaviruses
SARS-CoV
Tong *et al.* (2009) tested 1 bat collected in Kenya during 2006 positive for the presence of coronavirus RNA in a fecal sample. One Kenyan bat tested by Tao *et al.* (2017: Suppl.) was negative for CoV.

Polyomaviridae
Polyomavirus
Of the nine specimens tested from the Chyulu National Park (Kenya), one tested positive (Conrardy *et al.*, 2014: 259).

Rhabdoviridae
Rhabdovirus
One of the nine specimens tested from the Chyulu National Park (Kenya) tested positive (Conrardy *et al.*, 2014: 259).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Eritrea, Ethiopia, Kenya, Somalia.

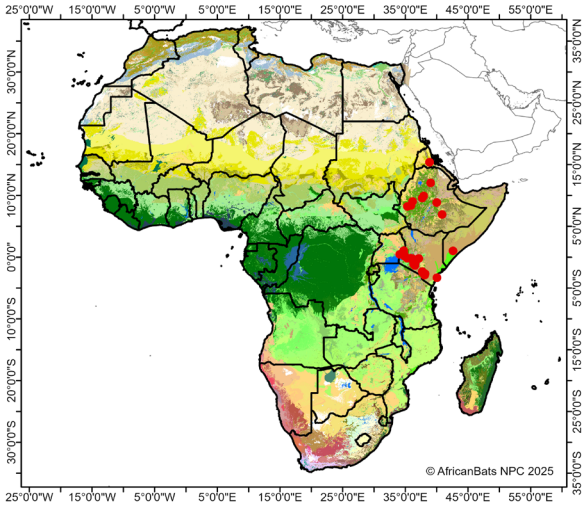

Figure 224. Distribution of *Miniopterus africanus*.

Miniopterus ambohitrensis Goodman, Ramasindrazana, Naughton and Appleton, 2015

2014. *Miniopterus aelleni B:* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: 1. Publication date: 18 March 2014.

*2015. *Miniopterus ambohitrensis* Goodman, Ramasindrazana, Naughton and Appleton, Zootaxa, 3936 (4): 538, 543, figs 2 - 5. Publication date: 23 March 2015. Type locality: Madagascar: Province d'Antsiranana: Parc National de la Montagne d'Ambre: Joffreville (Ambohitra), 5.5 km SW: Station Forestière des Roussettes [12 31 37.3 S 49 10 19.1 E, 1000 m]. Holotype: FMNH 202450: ad ♂, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 9 May 2009; original number: SMG 16169. Paratype: FMNH 202452: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 9 May 2008; original number: SMG-16171. See Demos *et al.* (2023: 4, fig. 1). - Etymology: The name *ambohitrensis* is derived from the geographical name of the type locality, which in Malagasy is Ambohitra and in French is Montagne d'Ambre. The nearby village of Joffreville is also referred to as Ambohitra. In the Malagasy language, the root word of Ambohitra is *vohitra* meaning mountain or highlands, giving an ecological context to the specific epithet of this bat, which occurs at higher elevations.

COMMON NAMES:
English: Montagne d'Ambre Long-fingered Bat, Ambohitra long-fingered bat, Malagasy Northern Long-fingered Bat, Montagne D'Ambre Bent-winged Bat. French: Minioptère de Montagne d'Ambre. German: Ambre-Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
This species is known from several sites in the northern portion of Madagascar (Goodman *et al.*, 2015b), most of which are montane and apparently not subjected to any important habitat degradation or other human pressures. It is notably common at several of these sites (Goodman, 2017h).

Assessment History
Global
LC 3.1 (2001) (Goodman, 2017h).

Regional
Endemic to Madagascar, therefore Global assessment should be consulted.

CONSERVATION ACTIONS:
Goodman (2017h) reports that this species is known from several protected areas, which include Marojejy, Montagne d'Ambre, Ambohitantely, and Bemanevika.

GENERAL DISTRIBUTION:
Only known from four localities, three in far north (including Mt D'Ambre and Marojejy National Parks) and one in Central Highlands (Ambohitantely) of Madagascar. These are in the wetter montane forest areas at altitudes between 810 and 1,570 m (Garbutt, 2022: 107).

Native: Madagascar.

HABITAT:
Chakravarty *et al.* (2024: 7) considers this species to be a "highland dwelling species".

ROOST:
This species roosts in caves and rock crevices (Garbutt, 2022:107).

DIET:
Fecal pellets of two individuals revealed Coleoptera (45.7 %), Hymenoptera (24.8 %), and Lepidoptera (24.4 %). (see Goodman *et al.*, 2023b: 241).

POPULATION:
Structure and Density
Not known (Goodman, 2017h).

Trends
2016: Unknown (Goodman, 2017h).

PARASITES:
Wilkinson *et al.* (2016) report the presence of *Penicillidia leptothrinax* on "*Miniopterus* cf. *ambohitrensis*", which was carrying Enterobacteriales bacteria (Szentiványi *et al.*, 2019a: Suppl.).

Referring to Rasoanoro *et al.* (2021), Minozzo *et al.* (2021: 8) report the presence of the haemosporidian *Polychromophilus* in *M. ambohitrensis*. Bajić *et al.* (2023: Suppl.) identified this parasite as *Polychromophilus melanipherus* (Dionisi, 1899).

VIRUSES:
Paramyxoviridae
Mélade *et al.* (2016b: 4) found one out of 19 *M.* cf. *ambohitrensis* specimens they tested to be infected with paramyxoviruses.

Rhabdoviridae
Four out of 15 *M.* cf. *ambohitrensis* specimens tested by Mélade *et al.* (2016a: 6) showed a reaction against *Duvenhage Lyssavirus*.

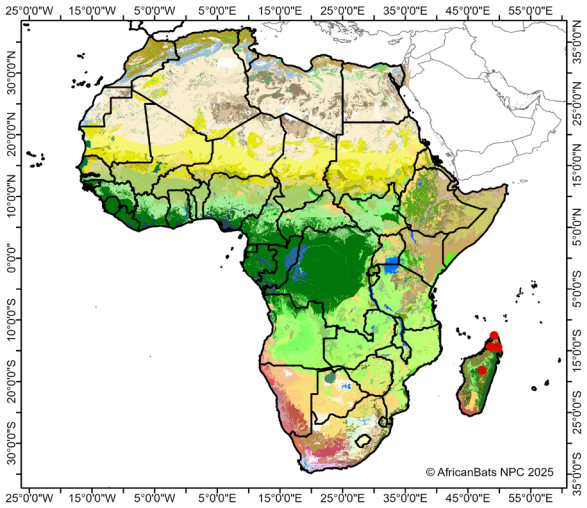

Figure 225. Distribution of *Miniopterus ambohitrensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus arenarius Heller, 1912

*1912. *Miniopterus natalensis arenarius* Heller, Smiths. Misc. Coll., 60 (12): 2. Publication date: 4 November 1912. Type locality: Kenya: Central province: Nanyuki district: Northern Guaso Nyiro: Nyuki (=Nanyuki) river [00 01 N 37 04 E]. [Goto Description]. Holotype: USNM 181811: ad ♀. Collected by: Edmund Heller; collection date: 4 October 1911; original number: 4413. - Comments: Coordinates mentioned as 00 21 N 36 55 E by Thorn *et al.* (2009: 49).
2010. *Miniopterus arenarius:* Benda, Vespertilio, 13-14: 307. (Name Combination).
? *Miniopterus cf. arenarius VG-2013*
? *Miniopterus schreibersi arenarius:* (Name Combination).

TAXONOMY:
Formerly included in either *Miniopterus schreibersii* or *Miniopterus natalensis*, but based on genetic and biometrical data considered a valid species by Farkašová *et al.* (2017: Suppl.), Kruskop *et al.* (2014: 102), Kassahun *et al.* (2015: 168), Farkašová *et al.* (2017: Suppl.), Wilson and Mittermeier (2019: 704) and Monadjem *et al.* (2020e: 242, 255), although the exact assignment still needs to be confirmed by material from the type locality.

Benda *et al.* (2025: 108) assigned their Kenyan material tentatively to Miniopterus aff. arenarius, indicating that this is a parataxon which contains several taxonomically undefined genetic lineages, at least two of which occur in Kenya (and one of them being *M. mossambicus*)..

COMMON NAMES:
Czech: létavec pískový. English: Sandy long-fingered bat, Aequatorial Broad Winged Bat.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
This species occurs in northeastern Africa, from the boundary between Tanzania and Kenya, through Uganda, South Sudan and Ethiopia to the Arabian Peninsula, where it has been reported from Saudi Arabia and Yemen (Harrison and Bates, 1991 [as *M. schreibersii*], Benda *et al.*, 2011b: 45 [as *M. natalensis*]).

HABITAT:
Primarily occurring in *Acacia - Commiphora* bushlands and thickets Ibáñez and Juste (2019: 704).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 42 *M. natalensis* specimens from East Africa and found 20 of them infected with *Polychromophilus melanipherus* Dionisi, 1899.

PROTOZOA
Kassahun *et al.* (2015: 168) examined two *M. arenarius* specimens from Masha (Ethiopia), and found one of them to be infected by *Leishmania* parasites (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 4).

ARACHNIDA
Myobiidae
Uchikawa (1985a: 15) corrected the type host for *Calcarmyobia rhinolophi* from *Rhinolophus lobatus* to *Miniopterus natalensis arenarius*. Uchikawa (1985a: 22) mentioned *Calcarmyobia kenyaensis* Uchikawa, 1982 on "*Miniopterus schreibersi*" from Belgian Congo and on "*Miniopterus schreibersi arenarius*" (and *M. natalensis arenarius*) from Kenya. Uchikawa (1985c: 110) furthermore reported on the presence of *Pteracarus miniopteri* Uchikawa, 1978 on bats Kenya, Uganda (as either *M. natalensis arenarius* or *M. schreibersi arenarius*).

Spinturnicidae
Orlova *et al.* (2024: 152) reported a first host-parasite association for *Miniopterus* cf. *arenarius* and *Spinturnix faini* Benoit, 1959. They also reported (p. 153) a first host-parasite association between *Miniopterus arenarius* and *Spinturnix semilunaris* de Meillon and Lavoipierre, 1944.

SIPHONAPTERA
Ischnopsyllidae
Oxyparius isomalus (Waterston, 1915) from the foothills of Mt. Elgon, Kenya (Haeselbarth *et al.*, 1966: 188). *Rhinolophopsylla ectopa* (Jordan, 1937) found in a cave in the foothills of Mt. Elgon, Kenya (Haeselbarth *et al.*, 1966: 191). The hosts for these fleas might be *M. arenarius*.

DIPTERA)
Streblidae
Lutz *et al.* (2021: found one Ugandan "*Miniopterus natalensis*" to be parasitized by an *Ascodipteron* sp., another by *Penicillidia fulvida*, and 18 by *Nycteribia schmidlii* Schiner, 1853. Given the country of origin, the bats should probably be assigned to *M. arenarius*.

Nycteribiidae
Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Miniopterus arenarius*: *Nycteribia latitergum* Theodor, 1957 and *Phthiridium tectum* (Theodor, 1957).

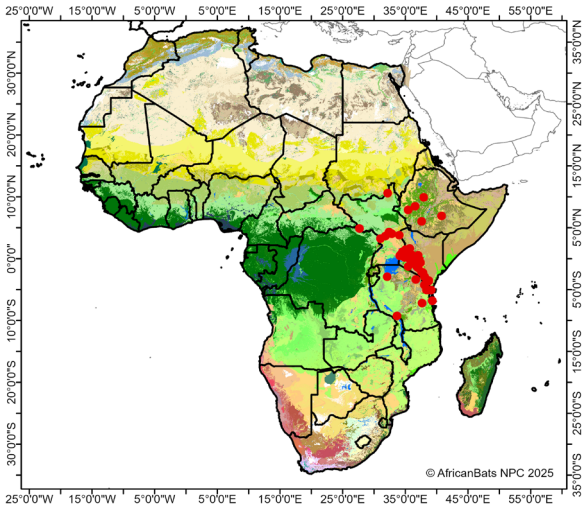

Figure 226. Distribution of *Miniopterus arenarius*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Kenya, South Sudan, Sudan, Tanzania, Uganda.

Miniopterus brachytragos Goodman, Maminirina, Bradman, Christidis and Appleton, 2009

*2009. *Miniopterus brachytragos* Goodman, Maminirina, Bradman, Christidis and Appleton, Am. Mus. Novit., 3669: 1, 9, figs 3, 4A–C, 5. Publication date: 30 November 2009. Type locality: Madagascar: Province de Mahajanga: Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National]: Forêt d'Ambovonomby: 26 km NW Andranomavo [16 28.2 S 45 20.9 E, 200 m]. Holotype: FMNH 175840: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 9 October 2002; original number: SMG 13040. Paratype: FMNH 172685:; collection date: 5 November 2001. Collected in Antsiranana Province, Forêt de Binara, near Analamazava River, 7.5 km SW Daraina (village), 13°15.3'S, 49°37.0'E, 325 - 600 m. Paratype: FMNH 172686:; collection date: 5 November 2001. Collected in Antsiranana Province, Forêt de Binara, near Analamazava River, 7.5 km SW Daraina (village), 13°15.3'S, 49°37.0'E, 325 - 600 m. Paratype: FMNH 172867:; collection date: 2 December 2001. Collected at the Parc National de Bemaraha, south bank Manambolo River, near Tombeau Vazimba, 3.5 km E Bekopaka, 19°08.4'S, 44°49.7'E, 100 m,. Paratype: FMNH 175846:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175847:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175850:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175851:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175852:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175856:; collection date: 9 - 10 October 2002. Same locality as holotype. Paratype: FMNH 175864:; collection date: 11 October 2002. Collected just outside limit of Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], along Ampandra River, 22 km NW Andranomavo, 16°26.4429'S, 45°24.723'E, 120 m. Paratype: FMNH 175865:; collection date: 11 October 2002. Collected just outside limit of Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], along Ampandra River, 22 km NW Andranomavo, 16°26.4429'S, 45°24.723'E, 120 m. Paratype: FMNH 175867:; collection date: 11 October 2002. Collected just outside limit of Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], along Ampandra River, 22 km NW Andranomavo, 16°26.4429'S, 45°24.723'E, 120 m. Paratype: FMNH 175869:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175870:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175871:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175872:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175873:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175874:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175875:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175877:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175879:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175880:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175881:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175882:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175883:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175884:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 175885:; collection date: 14 - 15 October 2002. Collected at the Réserve Naturelle Intégrale de Namoroka [status subsequently changed to Parc National], near source of Mandevy River, 32 km NW Andranomavo, 16°22.8'S, 45°20.7'E, 100 m. Paratype: FMNH 188651:; collection date: 14 February 2006. Collected in Antsiranana Province, Nosy Komba, 0.9 km SW Ampangorinana, on trail to Station Forestière d'Antanampoera, 13°26.835'S, 48°20.466'E, 100 m. Paratype: FMNH 202523:; collection date: 26 November 2007. Collected in Toamasina Province, Masoala Peninsula, 1.8 km S Ambanizana (village), 15°38.291'S, 49°57.944'E, 5 m. - Etymology: From the Greek *brachys* ("short") and *tragos*, meaning "goat," a word ultimately borrowed into New Latin to mean "tragus," and has been chosen as this taxon is easily distinguished from its congeners by its diminutive tragus (see Goodman *et al.*, 2009c: 17).. (Current Combination).

COMMON NAMES:
English: Broad-tragused Long-fingered Bat, Short-tragus Long-fingered Bat. Frnech: Minioptère à tragus court. German: Namoroka-Langflügelfledermaus

CONSERVATION STATUS:
Global Justification
This species is known from seven sites in the northern and western portions of Madagascar (Goodman and Ramasindrazana, 2013; Goodman *unpublished data* in Goodman (2017i)), many of which are within existing protected areas. This species is apparently not forest-dependant and by extrapolation not subjected to any important habitat degradation or other human pressures.

Assessment History
Global
2016: LC ver. 3.1 (2001) (Goodman, 2017i).

Regional
Endemic to Madagascar, therefore Regional assessment is the same as Global.

MAJOR THREATS:
Not known (Goodman, 2017i).

Trend:- Unknown (Goodman, 2017i).

CONSERVATION ACTIONS:
Goodman (2017i) report that this species is known from several protected areas: Bemaraha, Loky-Manambato, Masoala and Namoroka.

GENERAL DISTRIBUTION:
Occur on Madagascar, from the Masoala Peninsula in the northeast, the Daraina region in the central northeast, and in the karstic zones of the Namoroka and Bemaraha massifs, as well as on the island of Nosy Komba (Goodman *et al.*, 2009c: 11).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the northwestern part of the island (western or dry deciduous region). It occurs at altitudes between sea level and 600 m in dry forest and humid forest locations, but also in adjacent disturbed and anthropogenic areas (Garbutt, 2022: 106).

ECHOLOCATION:
Ramasindrazana *et al.* (2011: 294) recorded 30 calls from 8 *Miniopterus brachytragos* specimens, and found the following echolocation call values: Frequency of maximum energy: 59.0 ± 1.06 (57.3 - 61.7) kHz, Maximum frequency: 105.8 ± 11.20 (85.0 - 128.0) kHz, Minimum frequency: 55.7 ± 0.84 (54.0 - 57.0) kHz, Call duration: 3.4 ± 0.49 (2.6 - 4.3) ms, Inter pulse interval: 84.6 ± 18.99 (56.1 - 122.5) ms.

ROOST:
M. brachytragos roosts in caves near native forests (Garbutt, 2022: 106).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
Rasoanoro *et al.* (2019: 67) refer to Raharimanga *et al.* (2003), who reported *Trypanosoma* sp. from "*Miniopterus manavi*", but one of these bats belonged to the current species.

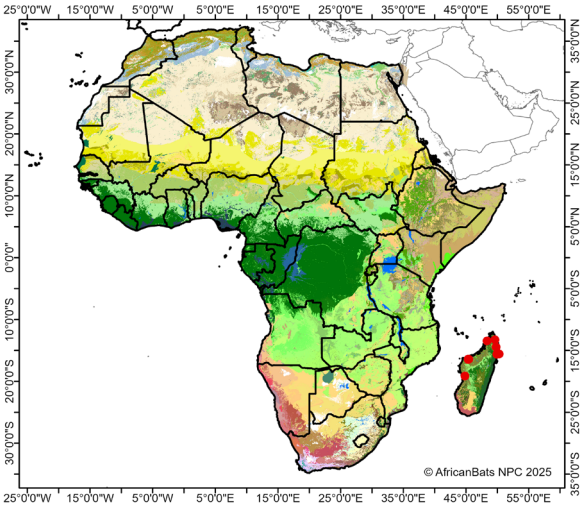

Figure 227. Distribution of *Miniopterus brachytragos*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus cf. fraterculus Tanshi, Chigozie Obitte, Monadjem and Kingston, 2022

2022. *Miniopterus cf. fraterculus* Tanshi, Chigozie Obitte, Monadjem and Kingston, Acta Chiropt., 23 (2): 318 (for 2021). Publication date: 14 February 2022.

TAXONOMY:
Tanshi *et al.* (2022a: 318) considered Nigerian specimens from the ROM that were identified as *Miniopterus fraterculus* actually to represent a separate species (*Miniopterus* cf. *fraterculus*), which is not likely to be related to *M. fraterculus*.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

PARASITES:
Ceballos-Pérez *et al.* (2024: 3) [referring to Lutz *et al.* (2016)] mention the presence of *Polychromophilus melanipherus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Nigeria.

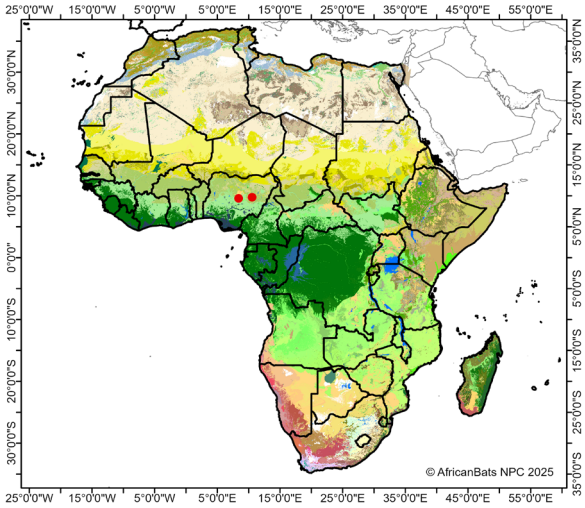

Figure 228. Distribution of *Miniopterus* cf. *fraterculus*.

Miniopterus cf. inflatus Monadjem, Shapiro, Richards, Karabulut, Crawley, Broman Nielsen, Hansen, Bohmann and Mourier, 2020

2020. *Miniopterus cf. inflatus* Monadjem, Shapiro, Richards, Karabulut, Crawley, Broman Nielsen, Hansen, Bohmann and Mourier, Acta Chiropt., 21 (2): 239.

TAXONOMY:
Monadjem *et al.* (2020e: 252) found that *M. inflatus* s.s. from the lower Guinea region isn't closely related fo *M.* cf. *inflatus* from eastern and southern Africa, which might indicate that these two forms represent different species, but further investigation remains necessary (see also Monadjem *et al.*, 2020b: 12).

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Monadjem *et al.* (2020e: 246) indicate that *M.* cf. *inflatus* from eastern and southern Africa has a light pelage

ECHOLOCATION:
For two caves in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data for *Miniopterus* cf. *inflatus*: Boundou cave: 1 M: F_{pmax}: 55.5 kHz, F_{pmean}: 54.2 kHz, F_{ppeak}: 51.2 kHz, F_{max}: 105.3 kHz, F_{flat}: 98.8 kHz, F_{knee}: 104 kHz, F_{min}: 44 kHz, F_{mean}: 69.2 kHz, Duration: 2.2 ms; 7 FF: F_{pmin}: 39.6 ± 3.3 kHz, F_{pmax}: 69.6 ± 11.1 kHz, F_{pmean}: 54.6 ± 6.2 kHz, F_{ppeak}: 47.6 ± 2.7 kHz, F_{max}: 82 ± 17.8 kHz, F_{flat}: 53.5 ± 16.6 kHz, F_{knee}: 56.2 ± 16.2 kHz, F_{min}: 44.6 ± 2.9 kHz, F_{mean}: 58.7 ± 9 kHz, Duration: 4.1 ± 0.2 ms. Mont Belo cave: 24 MM: F_{pmin}: 37.3 ± 8.6 kHz, F_{pmax}: 62.5 ± 9.9 kHz, F_{pmean}: 52.5 ± 7.7 kHz, F_{ppeak}: 48.1 ± 7.5 kHz, F_{max}: 77.1 ± 14.5 kHz, F_{flat}: 47.3 ± 8.4 kHz, F_{knee}: 51 ± 8.2 kHz, F_{min}: 44.9 ± 5.2 kHz, F_{mean}: 55.4 ± 7.6 kHz, Duration: 2.8 ± 0.5 ms.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

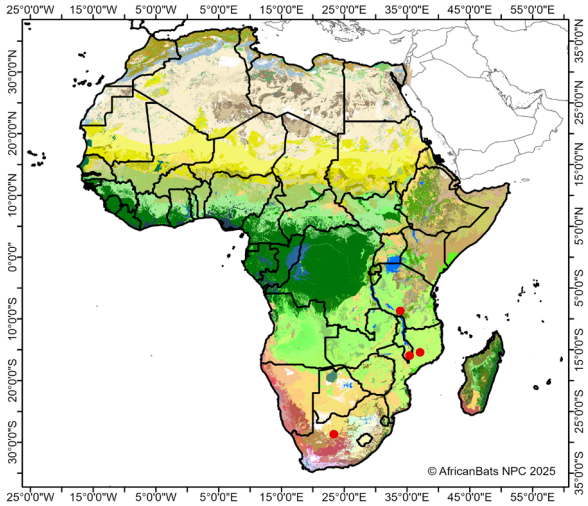

Figure 229. Distribution of *Miniopterus* cf. *inflatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Malawi, Mozambique, South Africa, Tanzania.

Miniopterus egeri Goodman, Ramasindrazana, Maminirina, Schoeman and Appleton, 2011

*2011. *Miniopterus egeri* Goodman, Ramasindrazana, Maminirina, Schoeman and Appleton, Zootaxa, 2880: 1, 9, figs 3, 4, 5A, 6, 7. Publication date: 17 May 2011. Type locality: Madagascar: Toamasina Province: Sahafina forest: Brickaville, 9.5 km W [18 48 37 S 48 58 48 E, 50 m]. Holotype: FMNH 209160: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman and Beza Ramasindrazana; collection date: 5 December 2009; original number: SMG 16602. - Etymology: In honour of Dr. Judith Eger, Senior Curator, Department of Mammalogy, Royal Ontario Museum, Toronto, for her contribution to taxonomic studies of Old World bats, including Madagascar (see Goodman *et al.*, 2011: 13). (Current Combination).

? *Miniopterus sp. BRA-2011*

COMMON NAMES:
English: Eger's long-fingered bat, Eger's Bent-winged Bat. French: Minioptère d'Eger. German: Eger-Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
This newly described species is known from numerous sites in the eastern portions of Madagascar (Goodman and Ramasindrazana, 2013), several of which are within existing protected areas. This species is apparently not forest-dependent and by extrapolation not subjected to any important habitat degradation or other human pressures (Goodman, 2017j).

Assessment History
Global
2016: LC ver 3.1 (2001) (Goodman, 2017j).

Regional
Endemic to Madagascar, therefore, see global assessment.

CONSERVATION ACTIONS:
Goodman (2017j) report that this species is known from several protected areas, which include Masoala, Sahafina, and Andohahela.

GENERAL DISTRIBUTION:
Based on current knowledge it is known from scattered sites occurring across two-thirds of Madagascar's lowland area from near sea level to 550 m (Goodman *et al.*, 2011: 15).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the eastern coastal part of the island (eastern humid forest or lowland forest region - humid).

Native: Madagascar (Goodman *et al.*, 2011: 15).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 63) could not find a baculum in the one specimen they examined.

ECHOLOCATION:
Low-duty cycle, frequency modulated/quasi constant (FM/QCF) echolocation call, with a peak frequency of 54.7 kHz (53.2 - 56.3 kHz) and a duration of 2.9 ms (2.5 - 3.4 ms) (Goodman *et al.*, 2011: 8).

Ramasindrazana *et al.* (2011: 294) recorded 16 calls from 2 *Miniopterus egeri* specimens, and found the following echolocation call values: Frequency of maximum energy: 54.7 ± 1.02 (53.2

- 56.3) kHz, Maximum frequency: 113.8 ± 3.62 (107.0 - 123.0) kHz, Minimum frequency: 49.0 ± 0.52 (48.0 - 50.0) kHz, Call duration: 2.9 ± 0.26 (2.5 - 3.4) ms, Inter pulse interval: 62.6 ± 12.57 (43.2 - 81.1) ms.

HABITAT:
Often associated with disturbed forests with mixed native and introduced trees or at the ecotone between degraded anthropogenic habitats and native forest (Goodman *et al.*, 2011: 15).

ROOST:
A day roost site of this species was found in a natural rock shelter in the Poste Forestier de Farankaraina surrounded by slightly disturbed natural lowland humid forest (Goodman *et al.*, 2011: 15).

DIET:
Rasoanoro *et al.* (2015: 63, 64) found that the diet of *M. egeri* mainly consisted of Coleoptera (51.5 vol %), Hymentoptera (28 %), Lepidoptera (10.8 %), and Isoptera (9.7 %).

POPULATION:
Structure and Density
Further information is needed (Goodman *et al.*, 2011: 15). Not known (Goodman, 2017j).

Trend
2016: Unknown (Goodman, 2017j).

In the short term this species does not appear to face a risk of dramatic population decline (Goodman *et al.*, 2011: 15).

PARASITES:
HAEMOSPORIDA
Referring to Rasoanoro *et al.* (2021), Minozzo *et al.* (2021: 8) report the presence of *Polychromophilus* in *M. egeri*.

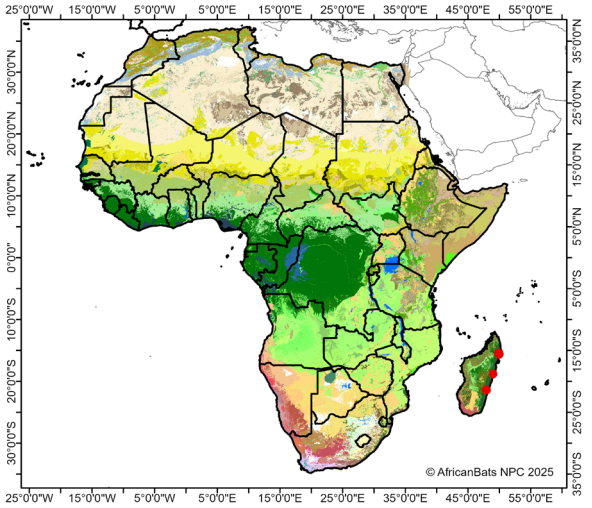

Figure 230. Distribution of *Miniopterus egeri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus fraterculus Thomas and Schwann, 1906

*1906. *Miniopterus fraterculus* Thomas and Schwann, Proc. zool. Soc. Lond., 1906, I: 162. Publication date: 7 June 1906. Type locality: South Africa: Southern Cape Province: Knysna [33 53 S 22 59 E]. [Goto Description]. Holotype: NHMUK 1905.5.7.18: ad ♂, skin and skull. Collected by: Captain Claude Henry Baxter Grant; collection date: 3 October 1905; original number: 1073. See Thomas and Schwann (1906a: 162). - Comments: Coordinates mentioned as 35 56 S 23 06 E by Thorn *et al.* (2009: 49). - Etymology: From the Latin meaning "little brother" (see Goodman *et al.*, 2007b: 1222). (Current Combination).

1917. *Miniopterus breyeri vicinior* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 450. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 49019: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 16 December 1911; original number: 1770. See Allen (1917: 450). - Comments: Considered a subspecies of *fraterculus* by Thorn *et al.* (2009: 49).

1978. *M[iniopterus] fraterreulus:* Herzit-Straschil and Robinson, Koedoe, 21: 104. (Lapsus).

? *Miniopterus fraterculus fraterculus:* (Name Combination).

TAXONOMY:
Meester *et al.* (1986) state that Harrison and Clancey (1952) and Harrison (1953) have demonstrated that Ellerman *et al.* (1953) are mistaken in regarding *fraterculus* as a synonym of *M. schreibersii natalensis*. Koopman (1966) regards *fraterculus* instead as a subspecies of the extralimital (to southern Africa) *M. minor* Peters, 1867, but Hayman and Hill (1971) disagree. Corbet and Hill (1980) retain *fraterculus* as species, as do Swanepoel *et al.* (1980) and Koopman (1982).

Specimens from Madagascar assigned to *M. fraterculus* by Peterson *et al.* (1995) and Simmons (2005: 519) are now considered to be a distinct species: *Miniopterus sororculus* (Goodman *et al.*, 2007b).

COMMON NAMES:
Afrikaans: Klein grotvlermuis. Chinese: 小长翼蝠. Czech: létavec jihoafrický. English: Lesser Long-fingered Bat, Black Clinging Bat, Lesser bent-winged bat. French: Minioptère d'Afrique

australe, Petit minioptère. German: Kleine Langflügelfledermaus. Portuguese: Morcego pequeno de dedos compridos. SiSwati: Lilulwane.

CONSERVATION STATUS:
Global Justification
Known from a number of discrete ranges. This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread distribution on the African mainland and its ability to live in a wide variety of habitat types (Schlitter *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bs). On Madagascar, it is quite rare and further surveys are required.

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bs). 2008: LC ver 3.1 (2001) (Schlitter *et al.*, 2008; IUCN, 2009). 2004: LC ver 3.1 (2001) (Schlitter, 2004g; IUCN, 2004). 1996: EN (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (MacEwan *et al.*, 2016c). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).
Eswatini: 2003: NT B2ab(iv); D2 ver 3.1 (2001) (Monadjem *et al.*, 2003).

MAJOR THREATS:
There are no major threats to this species on the African mainland (Schlitter *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bs).

CONSERVATION ACTIONS:
Schlitter *et al.* (2008) [in IUCN (2009)] and Monadjem *et al.* (2017bs) report that this species is presumably present in a number of protected areas. In Tanzania it is present in the Manga Forest Reserve of Tanzania (Doggart *et al.*, 1999b). Further studies are needed to better define the range of this species.

GENERAL DISTRIBUTION:
Traditionally, *Miniopterus fraterculus* was considered to be present in Central Africa, East Africa and southern Africa, where it was known from a number of discrete ranges, the largest of which stretched along south-eastern Africa, from Malawi, Mozambique and Zimbabwe, down to South Africa (where it extended along the south coast and its distribution was mostly affected by the annual temperature range (Babiker Salata, 2012: 50)). It was also known from eastern Democratic Republic of Congo near the borders with Uganda and Rwanda (although this population needed to be confirmed as *Miniopterus fraterculus*), and recorded from localities in Tanzania, Zambia, and Kenya. A small recorded range in Kenya near the border with Tanzania probably does not represent *Miniopterus fraterculus*.

Taylor *et al.* (2018b: 62) mention *Miniopterus* cf. *fraterculus* from Angola, however based on acoustic evidence only. Beja *et al.* (2019: 388) believe the Angolan records to be misidentifications.

ROM has 28 specimens from two localities in Cameroon, which need verification as they are well outside the presently known distribution of the species. This is also the case for the specimens from DRC, Kenya and Nigeria.

Specimens from Madagascar assigned to *M. fraterculus* (Peterson *et al.* (1995; Russ *et al.*, 2001; Simmons, 2005: 519) are now considered to be a distinct species: *Miniopterus sororculus* (Goodman *et al.*, 2007b).

However, recent changed in the taxonomy of the genus *Miniopterus* have led to the recognition of several new species, which reduced the distribution of *M. inflatus* to the southern and eastern parts of the Republic of South Africa, Swaziland and possibly extreme southern Mozambique (Ibáñez and Juste, 2019: 706, Monadjem *et al.*, 2020e: 239).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 297,363 km^2. In the RSA, its distribution is most affected by the annual temperature range (Babiker Salata, 2012: 50).

Native: Eswatini (Monadjem *et al.*, 2010d: 539, Monadjem *et al.*, 2021: 5); Mozambique (Monadjem *et al.*, 2010d: 539; Monadjem *et al.*, 2010c: 385 as *M.* cf. *fraterculus*); South Africa (Monadjem *et al.*, 2010d: 539).

DENTAL FORMULA:
van der Merwe (1985b: 251) examined 44 skulls and found 95 % of them vestigial teeth between the upper canine and the first premolar. In 44 % of the skulls, the teeth were present on both sides.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 6.4 Pa, aspect ratio 6.3 for a wingspan of 29 cm and a wing area of 137 cm^2 and a body mass of 9 g.

ECHOLOCATION:
Schoeman and Waddington (2011: 291) mention a F_{peak}: 62.1 ± 1.7 kHz and a duration: 3.7 ± 0.6 ms for specimens from Durban, South Africa.

The 135 calls analysed by Eisenring *et al.* (2016: SI 2) from bats in the Aberdares Range in Kenya had the following values: F_{peak}: 56.2 ± 1.4 (53.3 - 60.0) kHz, F_{max}: 87.1 ± 15.9 (63.8 - 127.6) kHz, F_{min}: 52.2 ± 1.6 (47.4 - 56.2) kHz, duration: 34.9 ± 15.9 (11.5 - 80.1) ms, interpulse interval: 0.8 ± 0.6 (0.3 - 4.8) ms.

For calls from specimens from Swaziland, Monadjem *et al.* (2017c: 179) recorded: F_{min}: 58.5 ± 0.50 (58.1 - 58.8) kHz, F_{knee}: 63.6 ± 1.27 (62.7 - 64.4) kHz, F_c: 59.2 ± 0.40 (58.9 - 59.5) kHz and duration: 2.9 ± 0.32 (2.7 - 3.1) ms.

Weier *et al.* (2020: Suppl.) reported on 27 "*M.* cf. *fraterculus* calls from the Okavango River Basin with the following characteristics: F_{max}: 70.82 ± 8.03 kHz, F_{min}: 55.21 ± 14.04 kHz, F_{knee}: 62.13 ± 1.59 kHz, F_{char}: 59.99 ± 1.53 kHz, slope: 36.47 ± 32.94 OPS, duration: 3.88 ± 1.45 ms.

5 calls recorded at the Venatia mine (Limpopo province, RSA) by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 3.14 ± 0.73 ms, F_{min}: 61.22 ± 2.88 kHz, F_{max}: 70.57 ± 3.36 kHz, F_{knee}: 65.56 ± 1.07 kHz and F_{char}: 63.43 ± 1.90.

950 calls of 52 bats from southern KwaZulu-Natal and Eastern Cape reported by Moir (2020: 29) and Moir *et al.* (2021a: 371) had the following parameters: F_{max}: 83.21 ± 8.26 (68.35 - 101.11) kHz, F_{min}: 58.59 ± 1.65 (53.43 - 61.19) kHz, F_{char}: 58.59 ± 1.65 (56.43 - 61.19) [identical to F_{min}?], F_{knee}: 59.35 ± 1.43 (57.80 - 61.46) kHz, and duration: 2.07 ± 0.51 (1.33 - 3.78) ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 62.30 ± 1.90 kHz.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003).

Karyotype
Rautenbach *et al.* (1993) described the karyotype as having a diploid number $2n$ = 46, aFN = 50, BA = 6, X = SM, Y = A.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 75 minutes, and the digestibility rate about 80.3 %.

POPULATION:
Structure and Density
It is common and widespread (Schlitter *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017bs).

Trend
2016: Unknown (Monadjem *et al.*, 2017bs).
2008: Unknown (Schlitter *et al.*, 2008; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Delayed implantation (lasting two-and-a-half months), insemination, ovulation and fertilization occur in the autumn. Embryogenesis proceeds to the blastocyst stage and development is then retarded until arousal in spring, when the blastocyst implants and embryogenisis resumes. The active foetal growth period takes about four months (Bernard, 1980a: 55; Bernard, 1980c).

Bernard (1980b: 111) found that the ovarian and uterine function is asymmetrical as ovulations occurred primarily in the left ovary (94 %), whereas all implantations occurred in the right uterine horn.

PARASITES:
HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 6 *M.* cf. *fraterculus* specimens from East Africa and found two of them infected with the haemosporidan parasite *Polychromophilus melanipherus* Dionisi, 1899.

ACARI
Myobiidae
Uchikawa (1985a: 16) reported mites belonging to *Calcarmyobia rhinolophia* (Radford, 1940) on bats identified as *M. fuscus fraterculus* from Natal, South Africa.

Trombiculidae
Leptotrombidium lawrencei Vercammen-Grandjean and Langston, 1976 (see Stekolnikov, 2018a: 143; Zajkowska *et al.*, 2018: 112).

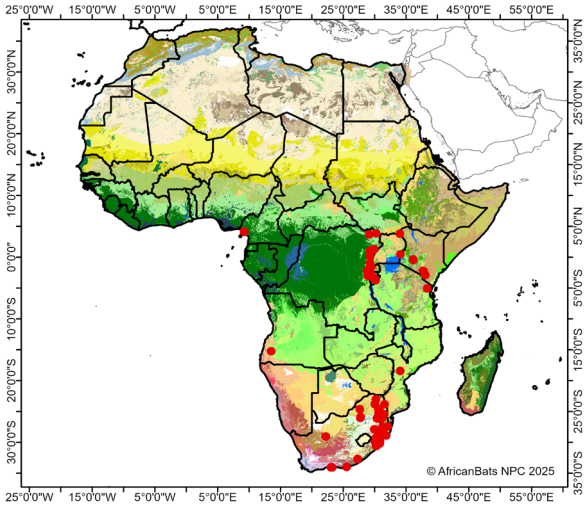

Figure 231. Distribution of *Miniopterus fraterculus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Cameroon, Congo (Democratic Republic of the), Eswatini, Kenya, Madagascar, Mozambique, Rwanda, South Africa, Tanzania, Uganda.

Miniopterus gleni Peterson, Eger and Mitchell, 1995

*1995. *Miniopterus gleni* Peterson, Eger and Mitchell, Faune de Madagascar, Chiroptères, 84: 128, figs 60, 61. Type locality: Madagascar: 20 km S Tuléar: Sarodrano and Saint-Augustin, in a marine cave [23 33 S 43 45 E]. [Goto Description]. Holotype: ROM 42567: ad ♂, skin and skull. Collection date: 9 May 1967. (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: létavec Glenův. English: Glen's Long-fingered Bat, Glen's Bent-winged Bat. French: Minioptère malgache, Minioptère de Glen. German: Glens Langflügelfledermaus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Muldoon *et al.* (2009: 1114) report on subfossil remains from the Ankilitelo fauna (late Holocene, appr. 500 years ago).

Gunnell *et al.* (2014: 3) refer to Goodman and Junker (2013) who also report fossils from the Andrahomana cave.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread distribution in Madagascar. It may be locally threatened in parts of its range by hunting and roost disturbance, but is not thought to be declining fast enough to place it in a higher category of threat (Andriafidison *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017ce).

Assessment History
Global
2016: LC ver 3.1 (Monadjem *et al.*, 2017ce). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008e; IUCN, 2009). 2000: LR/nt (IUCN, 2000). 1994: LR/nt ver 2.3 (1994) (Groombridge, 1994).

Regional
None known.

MAJOR THREATS:
It is threatened by roost site disturbance. This species is locally hunted in the south-west and north-west of Antananarivo (Goodman, 2006; Goodman *et al.*, 2008d) and as a relatively large species may be subject to similar exploitation elsewhere. There is no evidence that hunting presents a major threat. It is unclear if this species is forest dependent (Andriafidison *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017ce).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008e) [in IUCN (2009)] and Monadjem *et al.* (2017ce) report that this species is known to exist in a number of protected areas in the north-east (Eger and Mitchell, 2003) and many along the west coast (Goodman *et al.*, 2005a).

GENERAL DISTRIBUTION:
Miniopterus gleni is endemic to the island of Madagascar where it appears to be widely distributed (Eger and Mitchell, 2003; Goodman *et al.*, 2005a). The areas from where it has yet to be recorded may reflect low sampling effort rather than a genuine absence. North of Onilahy river (incl. Ile Sainte-Marie; Rakotonandrasana and Goodman, 2007: 6).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the coastal areas of northeast, north, west, and the south of the island (western or dry deciduous region).

Native: Madagascar (Eger and Mitchell, 2003; Goodman *et al.*, 2005a; Rakotonandrasana and Goodman, 2007: 6)

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
This is the largest *Miniopterus* species occurring on Madagascar (Garbutt, 2022: 106).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 63) could not find a baculum in the three males they examined.

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls of eight individuals, which were characterized by broadband FM/QCF pulses produced at low duty cycle with a frequency of maximum energy at about 44.8 kHz, while the fundamental was always the most intense call and pulses are short duration.

Ramasindrazana *et al.* (2011: 294) recorded 16 calls from 6 *Miniopterus gleni* specimens, and found the following echolocation call values: Frequency of maximum energy: 42.3 ± 1.29 (40.1 - 44.6) kHz, Maximum frequency: 82.6 ± 8.22 (70.0 - 93.2) kHz, Minimum frequency: 37.4 ± 0.94 (36.0 - 38.9) kHz, Call duration: 3.7 ± 0.49 (3.0 - 4.4) ms, Inter pulse interval: 88.9 ± 17.75 (66.7 - 124.1) ms.

HABITAT:
Dammhahn and Goodman (2013: 108) mention the lower portion of forest structure and partially open areas as the foraging habitat for this species. Garbutt (2022: 106) mentions this species occurs in all forest types and anthropogenic areas up to 1,250 m. Falimiarintsoa (2022: 28) found this species in a vanilla plantation.

ROOST:
On Madagascar, Wilkinson *et al.* (2012: 160) reported the typical roosting site to be caves, where the colony size is usually 2 to 8 bats, but in Ankarana 90 bats were found in a colony (Garbutt, 2022: 106).

DIET:
The fecal pellets of one individual from Sarahandrano contained primarily Diptera and much less Coleoptera (see Falimiarintsoa, 2022).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 84 minutes, and the digestibility rate about 79.1 %.

POPULATION:
Structure and Density
There was a maximum of 90 individuals recorded at a roost in Ankarana (S. G. Cardiff *pers. comm.*), but otherwise this species always appears to roost in rather small colonies (Robinson *et al.*, 2006). Its relative abundance, as determined by mist netting, varies from rare (Kofoky *et al.*, 2007) to locally common (Robinson *et al.*, 2006).

Trend
2016: Unknown (Monadjem *et al.*, 2017ce).
2008: Unknown (Andriafidison *et al.*, 2008e; IUCN, 2009).

PARASITES:
Lagadec *et al.* (2012: 1696) and Dietrich *et al.* (2014: Suppl.) report the presence of spirochaetes bacteria of the genus *Leptospira*, and which were identified as *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

Ramasindrazana *et al.* (2016: 2) indicate that *Litomosa goodmani* Martin, Bain, Jouvenet, Raharimanga, Robert & Rousset, 2006 (Onchocercidae, Nematoda) was described from a *M. gleni* from northern Madagascar. They also recovered *Litomosa* Clade 1 from this bat species.

Perkins and Schaer (2016: Suppl.) report the presence of the haemosporidan *Polychromophilus* sp. Ramasindrazana *et al.* (2018: Suppl.) identified this parasite as *Polychromophilus melanipherus* Dionisi, 1899 (see also Bajić *et al.*, 2023: Suppl.).

Tortosa *et al.* (2013: 4) and Ramasindrazana *et al.* (2017: Suppl.) reported the following Nycteribiid bat flies: *Nycteribia stylidiopsis*, *Penicillidia leptothrinax*, and *Penicillidia* sp. The first one was also mentioned by Wilkinson *et al.* (2016) and Urushadze *et al.* (2017: 9), who reported that these flies carried Enterobacteriales and *Bartonella* bacteria, as well as the blood parasite *Polychromophilus melanipherus* (Szentiványi *et al.*, 2019a: Suppl.).
Rasoanoro *et al.* (2021: 8) mentions one *Nycteribia stylidiopsis* Speiser, 1908 specimen on a *Miniopterus gleni*.

VIRUSES:

Astroviridae

One of two *M. gleni* specimens tested by Lebarbenchon *et al.* (2017: Suppl.) was positive for Astroviridae.

Paramyxoviridae

Wilkinson *et al.* (2012: 160) tested 7 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

Hoarau *et al.* (2021: Suppl.) reported two specimens from Madagascar carrying viruses of this family.

Mélade *et al.* (2016b: 4) found four out of 22 *M. gleni* specimens they tested to be infected with paramyxoviruses.

UTILISATION:

Goodman (2006) describes the hunting method used by local inhabitants. See also Goodman *et al.* (2008d) and Jenkins and Racey (2008).

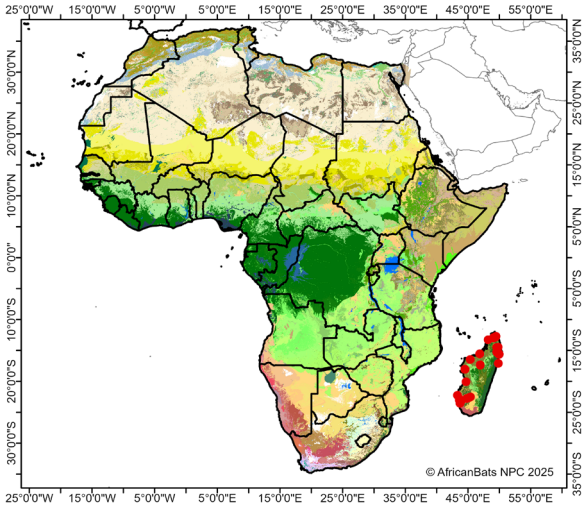

Figure 232. Distribution of *Miniopterus gleni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Madagascar.

Miniopterus griffithsi Goodman, Maminirina, Bradman, Christidis and Appleton, 2009

*2009. *Miniopterus griffithsi* Goodman, Maminirina, Bradman, Christidis and Appleton, J. Syst. Evol. Res., 38: 75, 81, figs 4, 6. Publication date: prior to 25 October 2009. Type locality: Madagascar: Province de Toliara: Grotte d'Androimpano: 4.2 km NE Itampolo (village), on old road to Ejeda [24 39.012 S 43 57.797 E, 110m]. Holotype: FMNH 184214: ad ♂, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 23 February 2005; original number: SMG 14593. Paratype: FMNH 184153: ad ♂. Grotte de Vitane (Vitany), 4.1 km SE Itampolo, 244208.5S 435749.4E, 25m. Paratype: FMNH 184154: ad ♂. Grotte de Vitane (Vitany), 4.1 km SE Itampolo, 244208.5S 435749.4E, 25m. Paratype: FMNH 184167: ad ♂. Grotte de Vitane (Vitany), 4.1 km SE Itampolo, 244208.5S 435749.4E, 25m. Paratype: FMNH 184215: ad ♂. same locatlity as the holotype. Paratype: FMNH 184216: ad ♂. Same locatlity as the holotype. Paratype: FMNH 184236: ad ♀. Same locatlity as the holotype. Paratype: USNM 577076. Fivondronana de Tolagnaro, 20 km WNW Ranopiso, 12 km ENE Amboasary, near Itaranta River, 2501S 4630E, 40m. Paratype: USNM 577077. Fivondronana de Tolagnaro, 20 km WNW Ranopiso, 12 km ENE Amboasary, near Itaranta River, 2501S 4630E, 40m. (Current Combination).

2021. *M[iniopterus] grifthsi:* Minozzo, da Silva Mathias, Riediger, de Oliveira Guimarães, dos Anjos, Monteiro, dos Santos, Biondo and Kirchgatter, Microorganisms, 9 (6): 7. Publication date: 7 June 2021. (Lapsus).

2022. *Miniopterus griffiths:* Esteves, Gaeta, Batista, Dias and Heinemann, Transb. Emerg. Dis., xxx (x): 9. Publication date: 9 May 2022. (Lapsus).

TAXONOMY:

Goodman *et al.* (2009b) examining the phylogeography of the *M. gleni* complex, found that the Onilahy River is a major barrier to gene flow. Subsequently, morphological characters (tragus shape, pelage coloration and skull proportions) were identified, that supported the separation of the populations found on either side of the Onilahy River (Goodman *et al.*, 2009b).

COMMON NAMES:

English: Griffiths' Long-fingered Bat, Griffiths's Bent-winged Bat. French: Minioptère de Griffiths. German: Griffiths Langflügelfledermaus.

ETYMOLOGY OF COMMON NAME:

In honour of Owen Griffiths, founder of Biodiversity Conservation Madagascar, who is a specialist on the terrestrial mollusc fauna of the western Indian Ocean and has been instrumental in preserving key important areas of habitat on Mauritius and Madagascar. He has generously supported many initiatives for documenting the rich Malagasy fauna (including genetic studies on *Miniopterus*) (see Goodman *et al.*, 2009a: 346).

CONSERVATION STATUS:

Global Justification

This species is known from few localities in the southern portion of Madagascar (Goodman and Ramasindrazana, 2013). Research is needed to

better define the geographical distribution of *Miniopterus griffithsi* and new field data are necessary to assess properly this taxon (Goodman, 2017k).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2016: DD ver 3.1 (2001) (Goodman, 2017k).
2009: EN (Goodman *et al.*, 2009b).

Regional
Endemic to Madagascar therefore global assessment should be used.

MAJOR THREATS:
Threats to this species are not known (Goodman, 2017k).

CONSERVATION ACTIONS:
Goodman (2017k) report that this species is not currently known from any protected area. Two of the three sites it has been documented are in degraded forested ecosystems (Goodman *et al.*, 2009b). If indeed it is not forest dependent, these human pressures may not directly impact this species.

GENERAL DISTRIBUTION:
Miniopterus griffithsii is endemic to Madagascar, where it seems to be restricted to the region between the southern banks of the Onilahy River and the Mandrare River (Itampolo east to near Ranopiso). It is actually known from three localities between 15 and 100 m of altitude (Garbutt, 2022: 109).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the south/southwestern coastal part of the island (south-west sub-arid or spiny bush).

Native: Madagascar.

ECHOLOCATION:
Ramasindrazana *et al.* (2011: 294) recorded 8 calls from 2 *Miniopterus griffithsi* specimens, and found the following echolocation call values: Frequency of maximum energy: 44.1 ± 0.67 (43.5 - 45.3) kHz, Maximum frequency: 80.4 ± 15.66 (61.0 - 99.0) kHz, Minimum frequency: 40.0 ± 0.0 (40.0 - 40.0) kHz, Call duration: 3.2 ± 0.29 (2.9 - 3.6) ms, Inter pulse interval: 89.2 ± 27.42 (56.4 - 128.5) ms.

ROOST:
Wilkinson *et al.* (2012: 160) indicate that caves are the typical roosting sites for these bats on Madagascar.

MIGRATION:
Reher *et al.* (2019: 121) found that *M. griffithsi* was only present in the Vintany Cave (southwestern Madagascar) during the wet season, whereas other species such as *Triaenops menamena* and *Miniopterus mahafaliensis* were present in both the dry and wet season.

POPULATION:
Structure and Density
Population size and trends are not known for this species (Goodman, 2017k).

Trends
2016: Unknown (Goodman *et al.*, 2009b).

PARASITES:
Lagadec *et al.* (2012: 1696), Dietrich *et al.* (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of spirochaetes bacteria of the genus *Leptospira*, and which were further identified as *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

The haemosporidian *Polychromophilus melanipherus* Dionisi, 1899 was reported from this species by Ramasindrazana *et al.* (2018: Suppl.) (see also Bajić *et al.*, 2023: Suppl.).

Ramasindrazana *et al.* (2016: 6) recovered *Litomosa* Clade 2 (Nematoda: Onchocercidae) from this bat species.

VIRUSES:
Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 2 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

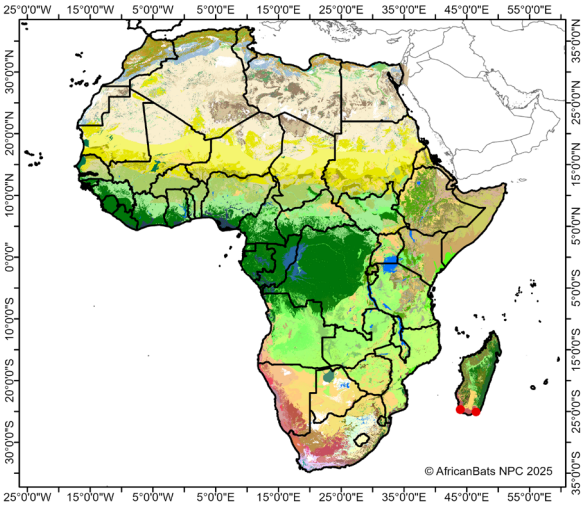

Figure 233. Distribution of *Miniopterus griffithsi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus griveaudi Harrison, 1959

*1959. *Miniopterus minor griveaudi* Harrison, Durban Mus. Novit., 5 (15): 192. Publication date: 30 April 1959. Type locality: Comoros: Grand Comoro [11 35 S 43 20 E]. [Goto Description]. Holotype: NHMUK 1967.1231: ad ♀, alcoholic (skull not removed). Collected by: Paul Griveaud; collection date: 10 August 1958. Formerly HZM 3.2803, see Harrison (1959a: 192). - Comments: The museum labels of the two other specimens, on which Harrison (1959a) based his description (HZM 4.2804 and 5.2805), have the following note by P. Griveaud: "couloir souterrain et grotte sous coulée de lave Niombadjée". Niombadjée is a toponym for Niombadjou (also spelled as Niumbadju), located on the western lower flank of Mt. Karthala at 11° 47′ 57" S, 43° 17′ 50" E (approximately 600 m) and where members of the expedition were based from 8 August 1958 to 23 August 1958: see Goodman *et al.* (2009a: 342). - Etymology: In honour of Mr. Paul Griveaud, the collector of the type specimen.

2022. *Miniopterus griveaud:* Esteves, Gaeta, Batista, Dias and Heinemann, Transb. Emerg. Dis., xxx (x): 8. Publication date: 9 May 2022. (Lapsus).

? *Miniopterus griveaudi (Clade 3):* Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi and Appleton, Zool. Scr., 38: 351 - 353, 362 - 363.

? *Miniopterus griveaudi:* (Current Combination).

TAXONOMY:
Originally synonymised with *Miniopterus minor*. Then moved as a synonym of *Miniopterus manavi* (Peterson *et al.*, 1995: 135; Simmons, 2005: 520). Peterson *et al.* (1995: 119) suggest that it may be a valid species, which Simmons (2005: 520) recognises as a valid subspecies. Juste [B.] *et al.* (2007: 32) consider *griveaudi* a valid species based on mtDNA data, a view supported by Weyeneth *et al.* (2008).

COMMON NAMES:
Czech: létavec komorský. English: Griveaud`s Long-fingered bat, Griveaud's Bent-winged Bat. French: Minioptère des Comores. French: Minioptère de Griveaud. German: Komoren-Langflügelfledermaus.

ETYMOLOGY OF COMMON NAME:
In honour of Mr. Paul Griveaud, the collector of the type specimen.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Juste, 2008a; IUCN, 2009; Juste, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) (Juste, 2019a). 2008: DD ver 3.1 (2001) (Juste, 2008a; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Juste, 2008a; IUCN, 2009; Juste, 2019a).

CONSERVATION ACTIONS:
Juste (2008a) [in IUCN (2009)] and Juste (2019a) reports that it is not known if the species is present in any protected areas. Further studies

are needed into the distribution, abundance, natural history, and threats to this species.

GENERAL DISTRIBUTION:
Miniopterus griveaudi is endemic to Grand Comore Island and Anjouan in the Comoros.

O'Brien (2011: 289) also reports it from Madagascar. Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the northwestern part of the island (western or dry deciduous region) up to 400 m.

Native: Comoros (Koopman, 1993a: 231 [as *minor*], Simmons, 2005: 521 [as *minor*], Juste [B.] *et al.*, 2007: 32), Madagascar.

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls as *M. manavi s.l.*, these calls were broadband FM/QCF sweeps produced at low duty cycle with most energy at about 58.1 kHz in the fundamental, with pulses having a short duration of about 4 ms.
Ramasindrazana *et al.* (2011: 294) recorded 49 calls from 17 *Miniopterus griveaudi* specimens from Madagascar, and found the following echolocation call values: Frequency of maximum energy: 59.9 ± 1.73 (56.4 - 62.4) kHz, Maximum frequency: 105.6 ± 12.05 (82.0 - 130.0) kHz, Minimum frequency: 55.9 ± 1.36 (53.0 - 58.0) kHz, Call duration: 3.5 ± 0.54 (2.7 - 4.4) ms, Inter pulse interval: 85.7 ± 19.80 (40.0 - 123.6) ms.
For 27 calls of 8 specimens from the same species from Anjoun, Ramasindrazana *et al.* (2011: 294) reported the following echolocation call values: Frequency of maximum energy: 59.2 ± 0.73 (58.2 - 60.8) kHz, Maximum frequency: 104.3 ± 8.86 (86.0 - 123.0) kHz, Minimum frequency: 54.5 ± 1.22 (53.0 - 57.0) kHz, Call duration: 3.2 ± 0.53 (2.7 - 4.6) ms, Inter pulse interval: 83.8 ± 15.60 (57.6 - 128.1) ms.
And 22 calls of 6 specimens from Grande Comore gave the following echolocation call values: Frequency of maximum energy: 59.4 ± 0.78 (58.2 - 60.9) kHz, Maximum frequency: 110.0 ± 11.10 (74.0 - 124.0) kHz, Minimum frequency: 55.0 ± 0.76 (53.0 - 56.0) kHz, Call duration: 3.1 ± 0.34 (2.6 - 3.6) ms, Inter pulse interval: 83.5 ± 13.18 (66.1 - 123.9) ms.

MOLECULAR BIOLOGY:
Karyotype
Richards *et al.* (2010) reported one female with a 2*n*=46 and a FNa=50. The karyotype consists of two large metacentric, one medium metacentric and 19 acrocentric chromosomal pairs. As FISH with the complete set of *Myotis* probes was applied, the X chromosome could be identified as a submetacentric element. Volleth and Eick (2012: 167) also mention a segment number of 23.

HABITAT:
Dammhahn and Goodman (2013: 108) mention the lower portion of forest structure and partially open areas as the foraging habitat for this species.

ROOST:
Wilkinson *et al.* (2012: 160) indicated that caves are the typical roosting site for this species on the Comoros.

DIET:
Goodman *et al.* (2023b: 241) [referring to Falimiarintsoa (2022), Rafanomezanjanahary (2021), Manana (2022)] mentioned fecal pellets of four bats from Sarahandrano containing Coleoptera (54.0 %), Diptera (35.0 %), and Lepidoptera (9.5 %); pellets of 10 individuals from Antsahabe contained Coleoptera (50 %), Lepidoptera (33 %), and Diptera (11 %), and pellets of five bats from the eastern slopes of the Marojejy National Park contained Coleoptera (42.4 %), Lepidoptera (37.2 %), and Hymenoptera (25.4 %).

PREDATORS:
Razakaratrimo *et al.* (2019: 112) mention *Macheiramphus alcinus anderssoni* (Gurney, 1866) as predator of *M.* cf. *griveaudi*, which makes 4.6 % of its prey in the Mandrozo Protected Area.

POPULATION:
Structure and Density
The abundance and population size of this species are not known (Juste, 2008a; IUCN, 2009; Juste, 2019a).

Trend
2018: Unknown (Juste, 2019a). 2008: Unknown (Juste, 2008a; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Goodman *et al.* (2023b: 242) mentioned that eight females captured at Antsahabe between 29 September and 19 November 2019 of which three had small mammae and four carried embryos (crown-rump 4 to 18 mm). Of the 12 males, seven had abdominal testes and non-convoluted epididymes and five had abdominal testes and partially convoluted epididymes. Three bats collected at Andratsakala between 6 March and 25 April 2022 included two subadult females and one male with convoluted epididymes. This would indicate that the gestation period is at the end of the year when

the rainy season starts and the insects are available at their highest densities.

Goodman *et al.* (2025: 215) reported on three non-reproductive males and 31 (out of 39) pregnant females collected between mid November and early December. Two of the latter had single embryos with crown-rump lengths of 18 and 19 mm.

PARASITES:
Lagadec *et al.* (2012: 1696), Lei and Olival (2014: Suppl.) and Gomard *et al.* (2016: 5) found this species to be infected by *Leptospira* bacteria on the Comoro Islands. These were further identified as *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

The haemosporidian *Polychromophilus melanipherus* Dionisi, 1899 was reported from this species by Ramasindrazana *et al.* (2018: Suppl.), as wel as an unidentified *Haemosporida* sp.

Tortosa *et al.* (2013: 4) reported these bats to be parasitized by *Nycteribia stylidiopsis* on both the Comoro Islands and on Madagascar. On the latter island, two additional Nycteribiid bat flies were found: *Penicillidia leptothrinax* and *Penicillidia* sp. *N. stylidiopsis* and *P. leptothrinax* were also reported by Wilkinson *et al.* (2016) and Ramasindrazana *et al.* (2017: Suppl.). Wilkinson *et al.* (2016) furthermore reported the presence of "*Penicillidia* sp. (cf. *fulvida*)" (see also Attaullah *et al.*, 2023: 4). The *N. stylidiopsis* flies were found to carry Enterobacteriales, and the *P.* cf. *fulvida* was host for the blood parasite *Polychromophilus murinus* as well as Enterobacteriales and *Bartonella* bacteria, whereas *P. leptothrinax* was carrying Enterobacteriales and *Bartonella* and *Wolbachia* bacteria (Szentiványi *et al.*, 2019a: Suppl.).

Ramasindrazana *et al.* (2016: 6) recovered *Litomosa* Clades 1, 2 and 3 (Nematoda: Onchocercidae) from this bat species, as well as an unnamed filariod.

VIRUSES:
Astroviridae
26 bats were tested by Lebarbenchon *et al.* (2017: Suppl.) of which 15 were positive for Astroviridae.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 20 individuals from the Comoros using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 3 positive results for viral nucleic acids. Wilkinson *et al.* (2014) tested 17 individuals from Amabhibe in Madagascar with an RT-PCR specific for the *Respiro-*, *Morbilli-* and *Henipavirus* genera, four of the 17 individuals tested positive for paramyxovirus RNA.

18 out of 116 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

Rhabdoviridae
Mélade *et al.* (2016a: 6) tested 33 specimens for *Lagos bat lyssavirus* and two of them showed seroreactivity. This was also the case for 10 out of 29 specimens they tested for *Duvenhage lyssavirus*.

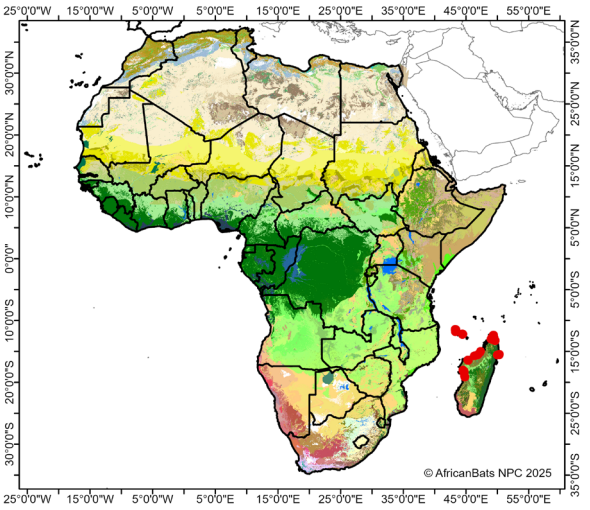

Figure 234. Distribution of *Miniopterus griveaudi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros, Madagascar.

†*Miniopterus horaceki* Gunnell, Eiting and Geraads, 2011

*2011. *Miniopterus horaceki* Gunnell, Eiting and Geraads, N. Jb. Geol. Paläont. Abh., 260 (1): 63, figs 3B, 7C, 8D-F. Publication date: January 2011. Type locality: Morocco: Ahl al Oughlam [ca. 33 35 N 07 30 W]. Holotype: INSAP AaO 4605. Right dentary with p2-p4, m1 trigonid. - Etymology: In honour of Ivan Horáček, in recognition of his many contributions to the understanding of the evolutionary history of bats, and especially of vespertilionids (see Gunnell *et al.*, 2011: 63). (Current Combination).

TAXONOMY:
Gunnell *et al.* (2011: 63) describe it as larger than nearly all extant African and European *Miniopterus* species (including *M. gleni, M. inflatus, M. newtoni, M. fraterculus, M. natalensis, M. manavi, M. noreenae, M. minor, M. williamsi*, and *M. schreibersi*). Generally similar in size to *M. africanus* but differs in having PM_{3-4} relatively broader and more exodaenodont, PM_3 larger than PM_2, and in having relatively taller lower premolars. Larger than *M. schreibersi* with PM_2 smaller compared to PM_3, but *M. schreibersi* does possess relatively broad premolars similar to the Moroccan species.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene (Brown *et al.*, 2019: Suppl.).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Libya.

Miniopterus inflatus Thomas, 1903

*1903. *Miniopterus inflatus* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (72): 634. Publication date: 1 December 1903. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1903.2.4.8: ad ♂, skin only. Collected by: George Latimer Bates Esq. Collection date: 24 July 1901. - Etymology: From the masculine Latin adjective *inflatus*, meaning "inflated, swollen", referring to its inflated skull (see Lanza *et al.*, 2015: 329). (Current Combination).
? *Miniopterus infatus:* (Lapsus).

TAXONOMY:
Koopman (1975: 230) included *africanus*, but see Peterson *et al.* (1995: 120), Simmons (2005: 520) and Juste [B.] *et al.* (2007: 28).

Simmons (2005: 520) recognises *rufus* Sanborn, 1936 as a valid subspecies.

Based on cytochrome *b* and morphometric analyses, Monadjem *et al.* (2020b: 12; 2020e: 237) found that *M. inflatus* is paraphyletic with the populations from the central African rainforest (Cameroon, Gabon and possibly Congo, DRC and CAR) not being closely related to the savanna forms from eastern and southern Africa.

Until a more profound analysis is performed, Benda *et al.* (2025: 105-106) assigned their Kenyan specimens tentatively to *Miniopterus* aff. *Inflatus* as this is a parataxon, which covers multiple genetic lineages.

COMMON NAMES:
Afrikaans: Groot grotvlermuis. Castilian (Spain): Murciélago de Ala Larga. Chinese: 大长翼蝠. Czech: létavec větší. English: Greater Long-fingered Bat, High-crowned bat. French: Grand minioptère africain, Grand minioptère, Minioptère à couronne. German: Aufgeblasene Langflügelfledermaus. Italian: Miniòttero maggióre di Thòmas, Miniòptero maggióre di Thòmas. Portuguese: Morcego grande de dedos compridos.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Schlitter, 2008h; IUCN, 2009; Monadjem and Schlitter, 2017d).

Assessment History
Global
2016: LC ver 3.1 (2001) [includes *africanus* Sanborn, 1936] (Monadjem *et al.*, 2017cm). 2008: LC ver 3.1 (2001) [includes *africanus* Sanborn, 1936] (Schlitter, 2008h; IUCN, 2009). 2004: LC ver 3.1 (2001) (Schlitter, 2004j; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: NT D1 ver 3.1 (2001) (Richards *et al.*, 2016c).

MAJOR THREATS:
There do not appear to be any major threats to this species. Some roosting caves are disturbed by tourism activities (Schlitter, 2008h; IUCN, 2009; Monadjem and Schlitter, 2017d).

CONSERVATION ACTIONS:
Schlitter (2008h) [in IUCN (2009)] and Monadjem and Schlitter (2017d) report that this species has been recorded from a number of protected areas. There is a need to limit disturbance of important roosting caves. Further studies are needed into the distribution of this species in West Africa.

GENERAL DISTRIBUTION:
Patchily recorded over much of sub-Saharan Africa. It has been reported from Liberia and Guinea in West Africa; from Cameroon, Equatorial Guinea, Gabon, Central African Republic and the Democratic Republic of the Congo in Central Africa; from Ethiopia, Uganda, Kenya and Tanzania in East Africa; and from Namibia, Zimbabwe and Mozambique in southern Africa.

The distribution of this species is somewhat unclear in West Africa due to confusion with records of "*Miniopterus schreibersii*" (Hutterer *et al.*, 1992: 397: Simmons, 2005:520) and *M. villiersi* (Tanshi *et al.*, 2022a: 314). Additionally, Monadjem et al. () only recognize two species in West Africa: a larger *Miniopterus nimbae* and a smaller sized *M. villiersi*. The animals from Guinea and Liberia previously assigned to *M. inflatus* therefore rather represent *M. nimbae*.

Native: Burundi (Simmons, 2005: 520); Cameroon (Simmons, 2005: 520); Central African Republic; Congo (Bates *et al.*, 2013: 329 - 1st authenticated records); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Simmons, 2005: 520; Monadjem *et al.*, 2010d: 539); Equatorial Guinea; Gabon (Simmons, 2005: 520); Kenya (Simmons, 2005: 520); Malawi (Monadjem *et al.*, 2010d: 539); Mozambique (Smithers and Lobão Tello, 1976; Simmons, 2005: 520; Monadjem *et al.*, 2010d: 539; Monadjem *et al.*, 2010c: 385); Namibia (Monadjem *et al.*, 2010d: 539); Nigeria (Tanshi *et al.*, 2022a: 317); South Africa (Monadjem *et al.*, 2010d: 539); Tanzania; Uganda (Kityo and Kerbis, 1996: 62; Simmons, 2005: 520); Zambia (Ansell, 1974; Monadjem *et al.*, 2010d: 539); Zimbabwe (Monadjem *et al.*, 2010d: 539).

Dental Formula:

van der Merwe (1985b: 251) examined three skulls and found vestigial teeth between the upper canine and the first premolar in all of them.

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.6 Pa, aspect ratio 8.7 and tip shape index of 2.15 for a wingspan of 29 cm and a wing area of 97 cm^2 and a body mass of 13 g.

Molecular Biology:

Genetics

See Hoofer and Van Den Bussche (2003).

Karyotype

Ruedas *et al.* (1990) described the karyotype as having a diploid number of 2*n* = 46, aFN = 50, BA = 6, X = M, Y = A.

Habitat:

In the Mount Nimba area, Monadjem *et al.* (2016y: 371) recorded this species from a variety of forested and disturbed habitats between 500 and 1,000 m.

Roost:

Monadjem *et al.* (2016y: 371) found a roost of this species in an old mine adit.

Happold and Happold (2023: 178) indicate that these bats generally roost singly and sometimes in small groups, but also that - in Gabon - females congregated in a maternity cave, which housed about 40,000 bats.

Diet:

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 106 minutes, and the digestibility rate about 76.6 %.

Population:

Structure and Density

This is generally considered to be a locally rare species, although it can be common in some areas (Schlitter, 2008h; IUCN, 2009; Monadjem and Schlitter, 2017d).

Trend

2016: Unknown (Monadjem and Schlitter, 2017d).
2008: Unknown (Schlitter, 2008h; IUCN, 2009).

Reproduction and ontogeny:

Brosset and Saint Girons (1980: 227) indicate that in Gabon all females were pregnant between August and September, and births were taking place in October. Between January and July, none of the females were either having any foetuses or young or were lactating. The males were non-reproductive between 9 October and 10 February.

Parasites:

Fain (1959b: 342) described *Nycteridocoptes miniopteri* (Acari: Sarcoptidae) from a *M. inflatus* specimen collected in Mulungu, Kivu, DRC.

Uchikawa (1985a: 22) reported *Calcarmyobia kenyaensis* Uchikawa, 1982 (Acari: Myobiidae) from *Miniopterus inflatus* specimens from Cameroon, Liberia, The Democratic Republic of Congo, Uganda and Kenya. Some Kenyan bats were identified as belonging to *Miniopterus inflatus africanus*, which might indicate that the host should actually be *M. africanus*.

Uchikawa (1985b: 52) further collected two paratypes of *Calcarmyobia producta* from a *M. inflatus* specimen from N Chyulu Hills, Kenya.

Uchikawa (1985c: 110) furthermore reported on several specimens from Kenya and The Democratic Republic of Congo, infected with four female *Pteracarus miniopteri* Uchikawa mites.

Justine (1989b: 555) described a new stomach parasite: *Capillaria magnova* from a *M. inflatus* from Belinga (Gabon).

Duval *et al.* (2012: 1559) indicate that the haemosporidan *Polychromophilus (Polychromophilus) corradetti* Landau et al., 1980 was described from *M. inflatus* specimens from Gabon (see Landau *et al.*, 1980b: 22). They also report (p. 1561) on five haplotypes belonging to the *Polychromophilus melanipherus* group and isolated during their study in Gabon (see also Bajić *et al.*, 2023: Suppl.).

Arnuphapprasert *et al.* (2020: Suppl.) refer to GenBank data for *Polychromophilus* sp. (haplotypes 3, 4, and 5) from Gabonese *M. inflatus*.

ARACHNIDA
Laelapidae
Neospinolaelaps Illiniopteri Zumpt and Patterson, 1952 was reported by Taufflieb (1962: 112).

Sarcoptidae
Fain (1959e: 157) described *Notoedres (Metanotoedres) miniopteri* from *M. inflatus* from Thysville (= Mbanza-Ngungu), DRC.

Spinturnicidae
Taufflieb (1962: 112) reported *Spinturnix semilunaris* de Meillon and Lavolplerre, 1944.

DIPTERA
Streblidae
Brachytarsina allaudi (Falcoz, 1923) in Gabon (Obame-Nkoghe *et al.*, 2016: 5). *Raymondia huberi* Frauenfeld 1856 in Guinea-Bissau (Haeselbarth *et al.*, 1966: 102). *Raymondia seminuda* Jobling, 1954 (Shapiro *et al.*, 2016: 255). *Raymondia tauffliebi* Theodor, 1968 in Congo (Shapiro *et al.*, 2016: 256).

Nycteribiidae
Nycteribia exacuta Theodor, 1957 from Dalaba, Guinea (Haeselbarth *et al.*, 1966: 108). *Nycteribia schmidlii* Schiner, 1853 (Haeselbarth *et al.*, 1966: 108; Tortosa *et al.*, 2013: 5; Duron *et al.*, 2014: 2108; Obame-Nkoghe *et al.*, 2016: 5; Ramasindrazana *et al.*, 2017: Suppl.), which was in Gabon carrying the blood parasite *Polychromophilus melanipherus* (Szentiványi *et al.*, 2019a: Suppl.). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114; Duron *et al.*, 2014: 2109; Obame-Nkoghe *et al.*, 2016: 5), which in Gabon was also carrying the same blood parasite as above (Szentiványi *et al.*, 2019a: Suppl.). *Eucampsipoda africana* Theodor, 1955 (Obame-Nkoghe *et al.*, 2016: 5; Júnior *et al.*, 2020: Suppl.).

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibody to SARS-CoV in sera in 34 individuals from Oriental Province, DRC, one tested positive (1/34, 2.9 %). Tong *et al.* (2009) tested 7/12 bats collected in Kenya during 2006 positive for the presence of coronavirus RNA in a fecal sample.

Anthony *et al.* (2017b: Suppl.) mention the alpha-coronaviruses: Kenya_Cov_KY33 and Predict_CoV_28. One out of two Kenyan specimens tested by Tao *et al.* (2017: Suppl.) was positive for CoV. One out of 249 Gabonese bats (0.4 %) tested by Maganga *et al.* (2020: 2) was found to be positive for an infection by *Alphacoronavirus*.

Filoviridae - Filoviruses
Marburgvirus
This virus is reported by Becquart *et al.* (2010: 1), Kuzmin *et al.* (2010b: 353), Luis *et al.* (2013: Suppl), Changula *et al.* (2014: 486), Simons *et al.* (2014: 2090), and Willoughby *et al.* (2017: Suppl.). Markotter *et al.* (2020: 6) mention the bat species as "*Miniopterus* cf. *inflatus*" (see also below).

Ebolavirus
On 24 January 2019, a series of newspaper articles was published, where several scientists from EcoHealth Alliance were quoted (Simon J. Anthony, Jonathan Epstein) stating that in a mouth swab one Liberian *Miniopterus inflatus* (out of 150 tested) RNA material of the Zaire Ebolavirus was found. Epstein, however, pointed out that if the bat was a natural host for the virus, it would have been found in more than one bat. He also pointed out that the bat could have become infected by another bat species living in the same habitat. Fabian Leendertz (veterinary epidemiologist at the Robert Koch Institute - not involved in the study) indicated that the virus itself wasn't isolated but only about one-fifth of its genome (Grady, 2019; Kupferschmidt, 2019; Su, 2019; Brainard, 2019).

Demos *et al.* (2019c: "11") pointed out that *M. inflatus* - as currently understood - has a very wide distribution, ad might be paraphyletic, indicating that further research is needed to confirm the true identity of the bat involved. Markotter *et al.* (2020: 6) therefore listed the bat as "*Miniopterus* cf. *inflatus*".

Nairoviridae
Orthonairovirus
9 out of 51 *M. inflatus* specimens from Gabon tested by Müller *et al.* (2016: 3) were positive for Crimean Congo haemorrhagic fever virus (CCHFV).

Paramyxoviridae
Orthorubulavirus
Drexler *et al.* (2012a: Suppl. Table S1) indicated that two of the 125 specimens they examined from Gabon tested positive for *Rubulavirus* (Human orthorubulavirus-related viruses according to Markotter *et al.*, 2020: 6).

Polyomaviridae
Nieto-Rabiela *et al.* (2019: Suppl.) mentioned the presence of Bat Polyomavirus.

In their overview table, Maganga *et al.* (2014a: 8) reported the following viruses were already found on *M. inflatus*: Marburg virus (MBGV), Coronavirus, Rubulavirus.

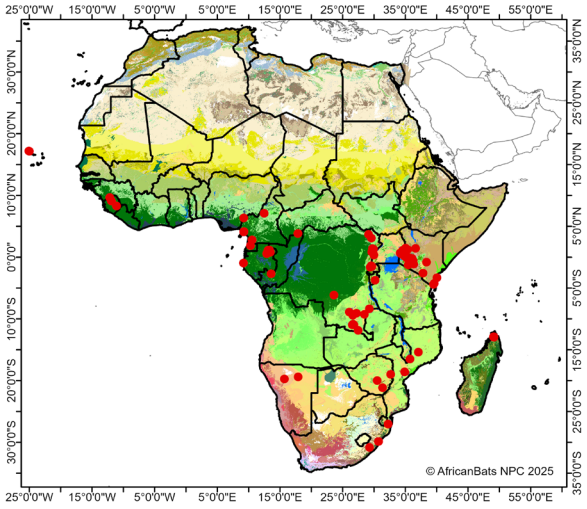

Figure 235. Distribution of *Miniopterus inflatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Cape Verde, Central African Republic, Congo (Democratic Republic of the), Gabon, Kenya, Madagascar, Mozambique, Namibia, Nigeria, Rwanda, Sierra Leone, South Africa, Uganda, Zambia, Zimbabwe.

Miniopterus inflatus inflatus Thomas, 1903

*1903. *Miniopterus inflatus* Thomas, Ann. Mag. nat. Hist., ser 7, 12 (72): 634. Publication date: 1 December 1903. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. - Etymology: From the masculine Latin adjective *inflatus*, meaning "inflated, swollen", referring to its inflated skull (see Lanza *et al.*, 2015: 329). (Current Combination).
? *Miniopterus inflatus inflatus:* (Name Combination).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burundi, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Kenya, Madagascar, Uganda.

Miniopterus inflatus rufus Sanborn, 1936

*1936. *Miniopterus rufus* Sanborn, Field Mus. Nat. Hist., Zool. Ser., (362) 20 (14): 112. Publication date: 15 August 1936. Type locality: Congo (Democratic Republic of the): Tanganyika-Moero: Lualaba River, 40 mi (64 km) below Bukama: Katobwe [08 51 S 26 05 E]. [Goto Description]. Holotype: FMNH 29416: ad ♂, skin and skull. Collected by: John Todd Zimmer; collection date: 28 November 1926; original number: 566.
? *Miniopterus inflatus rufus:* (Name Combination, Current Combination).

PARASITES:
Lutz *et al.* (2016: 9) examined 31 "*M. rufus*" specimens from East Africa and found 22 of them infected with the haemosporidan parasite *Polychromophilus melanipherus* Dionisi, 1899.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Kenya, Uganda.

Miniopterus maghrebensis Puechmaille, Allegrini, Benda, Bilgin, Ibañez and Juste, 2014

*2014. *Miniopterus maghrebensis* Puechmaille, Allegrini, Benda, Bilgin, Ibañez and Juste, in: Puechmaille, Allegrini, Benda, Gürün, Šrámek, Ibáñez, Juste and Bilgin, Zootaxa, 3794 (1): 108, 112, figs 2, 3a-b, 4a-b, 5a-b. Publication date: 5 May 2014. Type locality: Morocco: Er Rachidiyah Province: 5.7 km S of Ksar Tazougart, 19 km W-NW of Boudenib: Kef Azigza Cave (or Tazzouguert Cave) [32 01 46.6 N 03 47 16.7 W, 1060 m]. Holotype: NMP 94426: ad ♂, skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 28 April 2008; original number: pb3907. Paratype: EBD 25780M: ad ♂, alcoholic (skull not removed). Collected by: Carlos J. Ibáñez Uargui, Javier Juste, J.A. Garrido and Juan

Quetglas; collection date: 30 April 2000. Kef Azigza Cave. Paratype: NMP 90047: ♂, alcoholic (skull not removed). Collected by: Petr Benda; collection date: 30 August 2003. Talknout, Oued Tessaoud. Paratype: NMP 90051: ♂, skull and alcoholic. Collected by: Petr Benda; collection date: 30 August 2003. Talknout, Oued Tessaoud. Paratype: NMP 90103: ♀, skull and alcoholic. Collected by: Petr Benda; collection date: 9 September 2003. Sebt-es-Âït-Serhrouchèn, Oued El Ammar. Paratype: NMP 94505: alcoholic (skull not removed). Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94506: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94507: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94508: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94509: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94510: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94511: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94512: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94513: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94514: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. Paratype: NMP 94515: skull and alcoholic. Collected by: Petr Benda, Jaroslav Červený, Adam Konečný and Peter Vallo; collection date: 26 April 2008. Kef Azigza Cave. - Etymology: The name maghrebensis refers to the region (the Maghreb; the region of northern Africa located between the Atlantic Ocean, the Mediterranean Sea, and the Sahara) where the new species was discovered (see Puechmaille *et al.*, 2014a: 118). (Current Combination).

Taxonomy:

Bilgin *et al.* (2016: 330) calculated that the split between *M. maghrebensis* and *M. schreibersii* took place some 72,041 years ago (95 % HDP Interval = 5,637 - 139,570 years).

Common Names:

Castilian (Spain): Murrcielago de cueva magrebí. Czech: létavec maghrebský. Dutch: Maghrebijns langvleugelvleermuis. English: Maghrebian bent-wing bat. French: Minioptere du Maghreb. German: Maghreb-Langflügelfledermaus.

Conservation status:

Global Justification

This species is known from very few sites only, all representing underground spaces threatened by human activities. Listed as Near Threatened (NT ver 3.1 (2001)) because actual levels of disturbance are likely to lead the habitat of this species to decline of at least 30% in the next 15 years (Benda and Piraccini, 2017).

Assessment History

Global

2016: NT ver 3.1 (2001) (Benda and Piraccini, 2017).

Regional

None known.

Major threats:

Threats to the species are mainly human disturbance of roost sites, and perhaps the use of pesticides against insects (Benda and Piraccini, 2017).

Conservation actions:

Benda and Piraccini (2017) report that no specific measures are known to be in place for this species, but it occurs in protected areas across its range.

General distribution:

Northern Morocco to south of the High Atlas Mountains and northern Tunisia.

Gili *et al.* (2025: 533) report the first European record for this species from the Island of Lampedusa.

Based on cyt *b* sequences from GenBank, Derouiche *et al.* (2024: 34) conclude that this species hasn't been found in Algeria yet, but given its distribution in the surrounding countries, it probably is present in that country.

Native: Lampedusa (Gili *et al.*, 2025: 533); Morocco (Dbiba *et al.*, 2025: 7); Tunisia.

Sexual dimorphism:

Šrámek and Benda (2014: 222) found that most of the cranio-dental measurements in males were larger than in females, except for the dimensions associated with skull and rostral width. In dental characters, on the other hand, females were larger in 38 of 57 variables and the sexes highly diverged ($P < 0.001$) in the length of the lower canine; slightly diverged in widths of the second lower incisor, second upper molar (in central part) and third lower molar.

Echolocation:

Puechmaille *et al.* (2014a: 113) provide the following data [(avg ± sd (min - max)]: Peak

frequency: 52.89 ± 0.74 (51.00 - 54.78) kHz; Start frequency: 74.69 ± 7.66 (63.57 - 101.07) kHz; End frequency: 50.36 ± 0.81 (48.92 - 51.85) kHz; Duration: 4.48 ± 0.67 (3.20 - 5.60) ms; Interval between pulses: 107.14 ± 27.35 (67.20 - 239.20) ms.

MOLECULAR BIOLOGY:
Genetics
The GenBank sequence (partial Cytochrome *b*, tRNA-Threonine, tRNA-Proline, HV1) of the holotype corresponds to the accession numbers KJ535784 & KJ535824 (see Puechmaille *et al.*, 2014a: 117).

POPULATION:
This species has been found in the Mediterranean and steppe habitats of the Maghreb (Benda and Piraccini, 2017).

Trend:- 2016: Unknown (Benda and Piraccini, 2017).

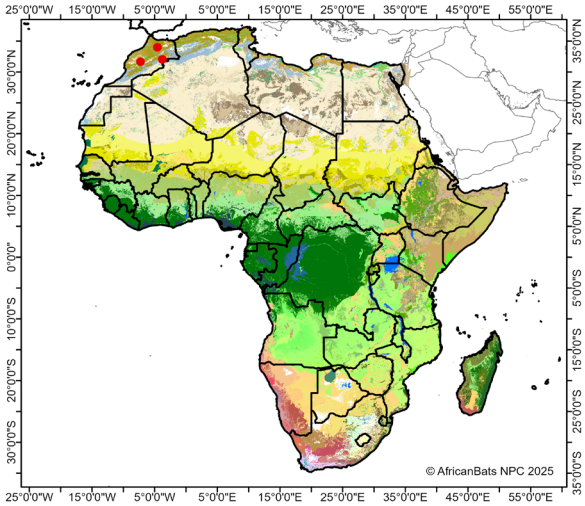

Figure 236. Distribution of *Miniopterus maghrebensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Morocco.

Miniopterus mahafaliensis Goodman, Bradman, Christides and Appleton, 2009

*2009. *Miniopterus mahafaliensis* Goodman, Bradman, Christides and Appleton, Am. Mus. Novit., 3669: 1, 17, figs 4D-E, 6, 7. Publication date: 30 November 2009. Type locality: Madagascar: Province de Toliara: Parc National de Tsimanampetsotsa: 6.5 km NE Efoetse: near Mitoho Cave [24 03.0 S 43 45.0 E, 50 m]. Holotype: FMNH 173197: ad ♂. Collected by: Steven M. Goodman; collection date: 2 March 2002; original number: SMG 12649. Paratype: FMNH 172918:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172919:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172920:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172921:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172922:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172923:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172924:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172925:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172926:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172927:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172928:; collection date: 7 May 2002. Grotte d'Ambanilia, 3.7 km SSE Sarodrano, 23°32.397' S, 43°44.763' E, sea level. Paratype: FMNH 172929:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 172930:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 172931:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 172932:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 172933:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 173154. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173189. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173190. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173191. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173192. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173193. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173194. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173195. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173196. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173198. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173199. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173200. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173201. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173202. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH 173203. Parc National de Tsimanampetsotsa, 6.5 km NE Efoetse, near Mitoho Cave, 24°03.0' S, 43°45.0' E, 50 m. Paratype: FMNH

173204:; collection date: 4 March 2002. Parc National de Tsimanampetsotsa, Malaza Manga Aven, 24°1.827' S, 43°45.283' E, 80 m. Paratype: FMNH 173252:; collection date: 24 July 2001. Antafiky, 23°29'16.0" S, 44°04'39.1" E, 50 m. Paratype: FMNH 173253:; collection date: 4 February 2002. Antafiky, 23°29'16.0" S, 44°04'39.1" E, 50 m. Paratype: FMNH 175991:; collection date: 9 December 2002. Province de Fianarantsoa, Parc National de l'Isalo, along Sahanafa River, at foot of Bevato, 28 km SE Berenty-Betsileo, 22°19.0' S, 45°17.6' E, 550 m. Paratype: FMNH 176096:; collection date: 11 November 2002. Province de Toliara, Parc National de Kirindy-Mite, 13 km W Marofihitsa, 20°47.4' S, 44°08.8' E, 30 m. Paratype: FMNH 176097:; collection date: 11 November 2002. Province de Toliara, Parc National de Kirindy-Mite, 13 km W Marofihitsa, 20°47.4' S, 44°08.8' E, 30 m. Paratype: FMNH 176098:; collection date: 11 November 2002. Province de Toliara, Parc National de Kirindy-Mite, 13 km W Marofihitsa, 20°47.4' S, 44°08.8' E, 30 m. Paratype: FMNH 176099:; collection date: 11 November 2002. Province de Toliara, Parc National de Kirindy-Mite, 13 km W Marofihitsa, 20°47.4' S, 44°08.8' E, 30 m. Paratype: FMNH 176100:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176101:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176102:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176103:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176104:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176105:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176106:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176107:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176108:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176109:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176110:; collection date: 16-17 November 2002. Parc National de Kirindy-Mite, near village of Betakilotra, 11 km SE Marofihitsa, 20°53.2' S, 44°04.8' E, 35 m. Paratype: FMNH 176167:; collection date: 14, 15, and 18 February 2003. Forêt des Mikea, 9.5 km W Ankililoaka, 22°46.7' S, 43°31.4' E, 80 m. Paratype: FMNH 176168:; collection date: 14, 15, and 18 February 2003. Forêt des Mikea, 9.5 km W Ankililoaka, 22°46.7' S, 43°31.4' E, 80 m. Paratype: FMNH 176169:; collection date: 14, 15, and 18 February 2003. Forêt des Mikea, 9.5 km W Ankililoaka, 22°46.7' S, 43°31.4' E, 80 m. Paratype: FMNH 176170:; collection date: 14, 15, and 18 February 2003. Forêt des Mikea, 9.5 km W Ankililoaka, 22°46.7' S, 43°31.4' E, 80 m. Paratype: FMNH 176508:; collection date: 4 June 2002. Mahaleotse, 23°31'38.8" S, 44°05'16.1" E, 70 m. Paratype: FMNH 176509:; collection date: 27 November 2002. Fiherenana, 23°14'17" S, 43°52'23" E. Paratype: FMNH 176510:; collection date: 27 November 2002. Fiherenana, 23°14'17" S, 43°52'23" E. Paratype: FMNH 177376:; collection date: 16 August 2003. Ranobe, 23°14.033' S, 43°52.493' E, approximately 50 m. Paratype: FMNH 184155. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184156. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184157. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184158. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184159. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184160:; collection date: 29 May 2005. Grotte d'Amborombe, 4.0 km Itampolo, 24°37'42.7" S, 43°58'56.9" E, 70 m. Paratype: FMNH 184168. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184217:; collection date: 18 February 2005. 10.5 km SE Itampolo (village), 24°44.2' S, 44°1.79' E, 120 m. Paratype: FMNH 184218:; collection date: 18 February 2005. 10.5 km SE Itampolo (village), 24°44.2' S, 44°1.79' E, 120 m. Paratype: FMNH 184219:; collection date: 18 February 2005. 10.5 km SE Itampolo (village), 24°44.2' S, 44°1.79' E, 120 m. Paratype: FMNH 184220:; collection date: 18 February 2005. 10.5 km SE Itampolo (village), 24°44.2' S, 44°1.79' E, 120 m. Paratype: FMNH 184221:; collection date: 18 February 2005. 10.5 km SE Itampolo (village), 24°44.2' S, 44°1.79' E, 120 m. Paratype: FMNH 184222. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184223. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184224. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184225. Grotte d'Andraimpano, 4.2 km NE Itampolo, 24°39.012' S, 43°57.797' E.m,. Paratype: FMNH 184226:; collection date: 26 February 2005. Grotte d'Antagneotsy, 5.0 km NE Vohombe, 24°23.001' S, 43°50.742' E, 100 m. Paratype: FMNH 184470:; collection date: 1 November 2004. Ihosy, commune rurale d'Akily, Grotte d'Andranomilitry, 22°23.111' S, 46° 03.355' E, 950 m. Paratype: FMNH 184471:; collection date: 1 November 2004. Ihosy, commune rurale d'Akily, Grotte d'Andranomilitry, 22°23.111' S, 46° 03.355' E, 950 m. Paratype: FMNH 184472:; collection date: 1 November 2004. Ihosy, commune rurale d'Akily, Grotte d'Andranomilitry, 22°23.111' S, 46° 03.355' E, 950 m. Paratype: FMNH 184473:; collection date: 1 November 2004. Ihosy, commune rurale d'Akily, Grotte d'Andranomilitry, 22°23.111' S, 46° 03.355' E, 950 m. Paratype: FMNH 202484:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 202485:; collection date: 8 May 2002. Grotte de Bisihiko, 0.75 km E St. Augustin, 23°32.933' S, 43°46.044' E, 10 m. Paratype: FMNH 75774:; collection date: 18 June 1953. Betroka, 23°15'50" S, 46°05'30" E, 800 m. - Etymology: The name *mahafaliensis* is derived from the Malagasy word mahafaly, meaning ''to make taboos,'' but here specifically referring to one of the local cultural groups in southwestern Madagascar, the Mahafaly, and the Mahafaly Plateau, a limestone karst area, from whence many of the specimens of this taxon were collected. In the region of the Forêt des Mikea (see Goodman *et al.*, 2009c: 28). (Current Combination).

COMMON NAMES:
English: Mahafaly Long-fingered Bat, Mahafaly Bent-winged Bat. French: Minioptère Mahafaly. German: Mahafaly-Langflügelfledermaus. Malagasy: kitrotroke.

CONSERVATION STATUS:
Global Justification
This species is known from numerous sites in the dry southern portion of Madagascar (Goodman and Ramasindrazana, 2013); a few of these localities are within existing protected areas. This species is apparently not forest-dependant and may not be very sensitive to any important habitat degradation or other human pressures (Goodman, 2017l).

Assessment History
Global
2016: LC ver. 3.1 (2001) (Goodman, 2017l).

Regional
Endemic to Madagascar therefore global assessment should be used.

CONSERVATION ACTIONS:
Goodman (2017l) this species is known from several protected areas, which include: Isalo, Kirindy Mité, Mikea, and Tsimanampetsotsa.

GENERAL DISTRIBUTION:
Madagascar (known from numerous sites on or in close proximity to the limestone Mahafaly Plateau in the southwestern portion of the island, including the zone from Itampolo north across the Onilahy River to Sarodrano spanning the elevational range from sea level to 120 m. Its distribution then continues further north to the Forêt des Mikea (70 - 80 m) and based on current data ends in the Kirindy-Mite region (30 - 35 m). Further, it is known from the more inland and upland sites of Ihosy and near Betroka from 800 - 950 m and within the Isalo formation at 550 m.).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the southwestern quarter of the island (south-west sub-arid or spiny bush).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 63) could not find a baculum in the one specimen they examined.

ECHOLOCATION:
Ramasindrazana *et al.* (2011: 294) recorded 24 calls from 9 *Miniopterus mahafaliensis* specimens, and found the following echolocation call values: Frequency of maximum energy: 59.6 ± 1.46 (57.3 - 62.2) kHz, Maximum frequency: 113.7 ± 8.08 (95.0 - 123.0) kHz, Minimum frequency: 55.1 ± 1.47 (53.0 - 57.0) kHz, Call duration: 3.3 ± 0.25 (2.9 - 3.8) ms, Inter pulse interval: 68.7 ± 14.04 (43.5 - 95.3) ms.

HABITAT:
M. mahafaliensis is found in dry deciduous forests, spiny forests and open anthropogenic areas from sea level to 950 m (Garbutt, 2022: 108).

ROOST:
Wilkinson *et al.* (2012: 160) reported caves to be the typical roosting site for these bats on Madagascar, but it might possibly also use hollow trees.

DIET:
Ramasindrazana *et al.* (2012: 120-121) examined faecal pellets from bats in the Tsimanampetsotsa NP, and found them to contain 47.5 ± 5.5 volume percent Lepidoptera, 39.9 ± 5.5 Coleoptera, 6.9 ± 2.9 Hymenoptera, 3.4 ± 0.6 Psocoptera, 1.1 ± 0.4 Diptera, 1.0 ± 0.2 Aranea, and 0.1 ± 0.0 Homoptera/Hemiptera. During the dry season, 52.9 ± 6.1 volume percent Coleoptera were found and 35.2 ± 5.7 Lepidoptera. The latter order was represented by 82.3 ± 7.7 percent in the wet season, whereas the Coleoptera dropped to 3.2 ± 0.8 percent.

POPULATION:
Structure and Density
Not known (Goodman, 2017l).

Trends
Unknown (Goodman, 2017l).

PARASITES:
Lagadec *et al.* (2012: 4696), Dietrich *et al.* (2014: Suppl.), Lei and Olival (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of spirochaetes bacteria of the genus *Leptospira*, which were identified as *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

The haemosporidian *Polychromophilus melanipherus* Dionisi, 1899 was reported from this species by Ramasindrazana *et al.* (2018: Suppl.), as wel as an unidentified *Haemosporida* sp. Rasoanoro *et al.* (2019: 67) refer to Raharimanga *et al.* (2003) who reported *Trypanomsoma* sp. from a "*Miniopterus manavi*".

Ramasindrazana *et al.* (2016: 6) recovered *Litomosa* Clade 2 (Nematoda: Onchocercidae) from *M. mahafaliensis*.

On Madagascar, Tortosa *et al.* (2013: 4) found Nycteribiid bat flies belonging to *Penicillidia leptothrinax*.

VIRUSES:
Astroviridae
Hoarau *et al.* (2021: Suppl.) reported the presence of these viruses in bats from Madagascar.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 11 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids.

In their extensive study, Mélade *et al.* (2016b: 3) found that *M. mahafaliensis* was the least infected species of Madagascan bat, with only 4 out of 89 specimens (4.5 %) infected.

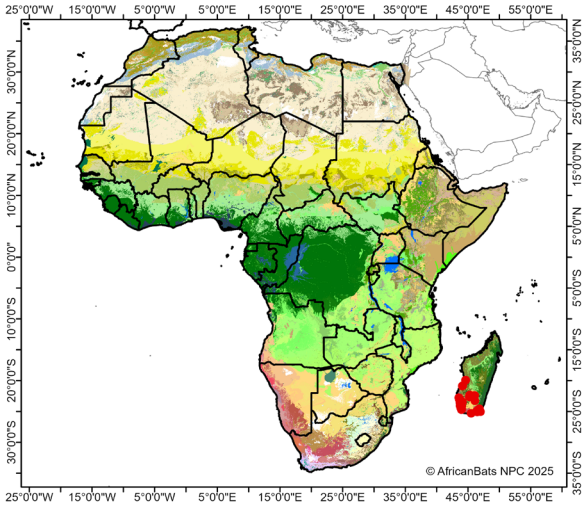

Figure 237. Distribution of *Miniopterus mahafaliensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus majori Thomas, 1906

*1906. *Miniopterus Majori* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (98): 175. Publication date: 1 February 1906. Type locality: Madagascar: SE Betsileo: Imasindrary [=Sahamananina] [20 17 S 47 31 E, 1 600 m]. [Goto Description]. Holotype: NHMUK 1897.9.1.38: ad ♀, skin and skull. Collected by: Dr. Charles Immanuel Forsyth-Major; collection date: 3 July 1895; original number: 457. - Etymology: In honour of Dr. C.I. Forsyth Major, collector of the type specimen (see Thomas, 1906a: 176). (Current Combination).
? *Miniopterus majori majori:* (Name Combination).
? *Miniopterus majori:* (Current Spelling).

TAXONOMY:
Included in *schreibersi* by Koopman (1993a: 231), but considered a valid species by Peterson *et al.* (1995: 131), Hutson *et al.* (2001: 32), Russ *et al.* (2001), Simmons (2005: 520).

COMMON NAMES:
Czech: létavec východomadagaskarský. English: Major Long-fingered Bat, Major's Long-fingered Bat, Major's Bent-winged Bat. French: Grand minioptère malgache, Minioptère de Major. German: Majors Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its relatively wide range, ability to live in a wide variety of habitats from intact forests to heavily degraded areas, and because there is no evidence of a decline that would warrant listing in a higher category of threat (Jenkins and Rakotoarivelo, 2008a; IUCN, 2009; Monadjem *et al.*, 2017br).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017br). 2008: LC ver 3.1 (2001) (Jenkins and Rakotoarivelo, 2008a; IUCN, 2009). 2003: DD (IUCN, 2003). 2001: DD (IUCN/SSC Action Plan, 2001).

Regional
None known.

MAJOR THREATS:
The major threats to this species are not known. It could be susceptible to cave disturbance in some sites and it could perhaps be hunted in some areas (Jenkins and Rakotoarivelo, 2008a; IUCN, 2009; Monadjem *et al.*, 2017br).

CONSERVATION ACTIONS:
Jenkins and Rakotoarivelo (2008a) [in IUCN (2009)] and Monadjem *et al.* (2017br) report that this species is reported from a few protected areas, such as Parc National de Masoala and Parc National de Mantadia (Russ and Bennet, 1999; Randrianandrianana *et al.*, 2006). Some of these records may need to be reassessed in view of the ongoing taxonomy of this genus in Madagascar (Goodman and Maminirina, 2007).

GENERAL DISTRIBUTION:
Miniopterus majori is endemic to Madagascar and has a sympatric distribution with *Miniopterus*

sororculus in the highlands of Madagascar (Goodman *et al.*, 2007b) and is widely, but patchily, distributed across the island (Peterson *et al.*, 1995; Eger and Mitchell, 2003).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the eastern part of the island (higher elevations (< 1,200 m) of the Central Highlands - sub-humid region).

Goodman and Maminirina (2007) suggest that the only specimens known form the Comoro Islands were collected by M. Humbolt and may have been incorrectly provenanced. Until new material is available from the island to confirm that *M. majori* exists, it is removed from the known distribution of the species and is restricted at this time to Madagascar.

Native: Madagascar (Peterson *et al.*, 1995; Eger and Mitchell, 2003; Simmons, 2005: 520; Goodman and Maminirina, 2007).

Presence incorrectly assigned: Comoro Islands (Simmons, 2005: 520).

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls as *Miniopterus majori/sororculus*, which produced broadband FM/QCF echolocation calls at low duty cycle, but with a lower maximum energy, at about 48.5 kHz. The fundamental being most intense with short duration pulses of about 4.5 ms.

Ramasindrazana *et al.* (2011: 294) recorded 39 calls from 12 *Miniopterus majori* specimens, and found the following echolocation call values: F_{peak}: 48.5 ± 1.15 (46.1 - 52.0) kHz, F_{max}: 82.5 ± 11.78 (64.0 - 102.0) kHz, F_{min}: 44.4 ± 0.97 (43.0 - 46.0) kHz, duration: 3.6 ± 0.42 (2.8 - 4.5) ms, Inter pulse interval: 85.0 ± 16.34 (59.5 - 134.8) ms.

HABITAT:
M. majori is found in humid forest and spiny forest areas (Garbutt, 2022: 107).

ROOST:
This bat roosts in caves, often together with *M. gleni, M. manavi* and/or *M. sororculus*. Occasionally, it is also found in tree holes (Garbutt, 2022:107).

DIET:
Kemp *et al.* (2018: Suppl.) used DNA metabarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Lepidoptera (*Ericeia inangulata* (Guenée, 1852), *Pandemis* sp., *Celsumaria elongata* Brown, 2017, *Meyrickiella homosema* (Meyrick, 1887), *Emmalocera* sp., *Palpita* sp., *Pandemis retroflua* Diakonoff, 1960, *Achaea euryplaga* (Hampson, 1913), *Eublemma viettei* (Berio, 1954), *Herpetogramma licarsisalis* (Walker, 1859), *Chloroclystis androgyna* Herbulot, 1957, *Idiodes oberthuri* Dognin 1911, *Scopula* AH01Md, *Ectropis* AH27Md), Hemiptera, Blattodea, Trombidiformes, Diptera (*Simulium lineatum* (Meigen, 1804)), Coleoptera, Hymenoptera, Ephemeroptera, Trichoptera, Sarcoptiformes, Astigmata.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 84 minutes, and the digestibility rate about 79.1 %.

POPULATION:
Structure and Density
There is no information on its population status (Jenkins and Rakotoarivelo, 2008a; IUCN, 2009; Monadjem *et al.*, 2017br).

Trend
2016: Unknown (Monadjem *et al.*, 2017br). 2008: Unknown (Jenkins and Rakotoarivelo, 2008a; IUCN, 2009).

PARASITES:
Dietrich *et al.* (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of spirochaetes of the genus *Leptospira* in bats from Fianarantsoa, Madagascar. These were identified as *L. borgpetersenii* by Dietrich *et al.* (2018a: 3).

Uchikawa (1985b: 45) reports *Calcarmyobia comoresensis* mites of bat specimens from Vobima and Bersroha, Madagascar. Uchikawa (1985c: 111) mentions the presence of *Pteracarus miniopteri* Uchikawa, 1978 mites on *M. schreibersi majori* specimens from Madagascar. Tortosa *et al.* (2013: 4), furthermore, reported the presence of Nycteribiid bat flies: *Nycteribia stylidiopsis* and *Penicillidia leptothrinax*. The *Nycteribia* is also reported by Ramasindrazana *et al.* (2017: Suppl.).

Ramasindrazana *et al.* (2016: 6) recovered *Litomosa* Clade 1 (Nematoda: Onchocercidae) from this bat species.

Ramasindrazana *et al.* (2018: 7) refer to Ramasindrazana *et al.* (2018) to report the presence of the Haemosporidian *Polychromophilus* in this bat species.

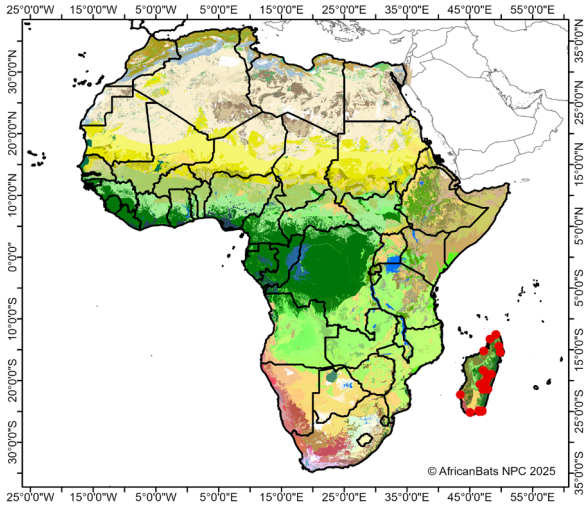

Figure 238. Distribution of *Miniopterus majori*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Miniopterus manavi Thomas, 1906

*1906. *Miniopterus manavi* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (98): 176. Publication date: 1 February 1906. Type locality: Madagascar: Eastern/Northeastern Betsileo: Fandriana region [20 17 S 47 31 E]. [Goto Description]. Holotype: NHMUK 1897.9.1.37: ad ♂, skin and skull. Collected by: Dr. Charles Immanuel Forsyth-Major; collection date: 3 July 1895; original number: 453. See Peterson *et al.* (1995: 135). Topotype: MCZ 45101: ♀, complete skeleton. Collected by: The Grandidier Collection; collection date: 3 July 1895. - Comments: [Imansindrary = ? Masindrary, 15 km ESE Fandriana, see Jenkins and Carleton, 2005 (in Goodman *et al.*, 2009a: 340)]. (Current Combination).
1993. *Miniopterus minor grivaudi:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 231. (Lapsus).
2001. *Miniopterus menavi:* Hutson, Mickleburgh and Racey, Microchiropteran bats, 89. (Lapsus).
2007. *Miniopterus (griveaudi) manavi:* Goodman and Maminirina, Mammalia, 71 (4): 151. (Name Combination).
2009. *Miniopterus manavi (Clade 1):* Goodman, Maminirina, Weyeneth, Bradman, Christidis, Ruedi and Appleton, Zool. Scr., 38: 346-351, 362.
? *Miniopterus manavi manavi:* (Name Combination).

TAXONOMY:
Included in *minor* by Koopman (1993a: 231), but considered a valid species by Peterson *et al.* (1995: 135), Hutson *et al.* (2001: 32), Russ *et al.* (2001), and Simmons (2005: 520).

Simmons (2005: 520) recognised *griveaudi* Harrison, 1959 as a valid subspecies of *M. manavi*, Juste [B.] *et al.* (2007: 33) elevated *griveaudi* as a separate species, which is followed in this account.

Weyeneth *et al.* (2008) used mitochondrial DNA markers to demonstrate that the specimens from the Comoro islands are not closely related to *M. minor* from the African mainland, and that these islands were probably populated as a result of two or three invasions originating from Madagascar.

COMMON NAMES:
Czech: létavec manavijský. English: Manavi Long-fingered Bat, Manavil Bent-winged Bat. French: Petit minioptère malgache. French: Minioptère manavi. German: Manavi-Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread distribution (near suitable caves) across Madagascar. While it is locally threatened by hunting, this is not thought to be a major threat of this species across its range (Andriafidison *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017cf).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cf). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008f; IUCN, 2009). 2003: DD [as *M. menavi*] (IUCN, 2003). 2001: DD [as *M. menavi*] (IUCN/SSC Action Plan, 2001). 2000: DD.

Regional
None known.

MAJOR THREATS:
There are no major threats to the species. In Makira, this species is eaten by people (Golden, 2005), but it is not known if this species is hunted

in other parts of its range. It is probably not forest dependent, but is rarely netted in areas without vegetation stands (Andriafidison *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017cf).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008f) [in IUCN (2009)] and Monadjem *et al.* (2017cf) report that this species occurs in many of the forest protected areas in western and eastern Madagascar and as such does not require specific conservation measures. Additional information on its ecology would be helpful to better understand how it responds to deforestation and roost disturbance. There is some uncertainty about the taxonomy of *M. manavi* and that this taxon is actually a complex of new species (F. Ratromomanarivo *pers. comm.*). Further studies on morphology, acoustics and genetics are therefore needed.

GENERAL DISTRIBUTION:
Miniopterus manavi was originally reported from a wide area on Madagascar including the islands of Nosy Be and Nosy Komba (Rakotonandrasana and Goodman, 2007: 6), where it appeared to be widely distributed (Eger and Mitchell, 2003; Goodman *et al.*, 2005a) and occurreing over a wide elevational range, from 20 to 1,500 m above sea-level.

However, Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the eastern part of the island, but not along the coast (higher elevations of the Central Highlands - sub-humid region).

Due to the split off of several recently recognized species,.the above range has been restricted to the southern part of the Central Highlands, which also restricted the altitudinal range to between 900 and 1,500 m (Garbutt, 2022: 108).

Grand Comoro (Peterson *et al.*, 1995; Simmons, 2005: 520). Removed by Juste [B.] *et al.* (2007: 33), due to the removal of *griveaudi* as a separate species.

Native: Madagascar (Peterson *et al.*, 1995; Eger and Mitchell, 2003; Goodman *et al.*, 2005a; Simmons, 2005: 520; Rakotonandrasana and Goodman, 2007: 6).

ECHOLOCATION:
Russ *et al.* (2003) describe the echolocation as a frequency-modulated sweep that terminates in a constant-frequency portion with maximum energy around 57 kHz. Kofoky *et al.* (2009: 382) reported the calls as *M. manavi s.l.*, these calls were broadband FM/QCF sweeps produced at low duty cycle with most energy at about 58.1 kHz in the fundamental, with pulses having a short duration of about 4 ms. Low-duty cycle, frequency modulated/quasi constant (FM/QCF) echolocation call, with a peak frequency of 57.2 kHz (55.5 - 58.2 kHz) and a duration of 2.5 ms (2.1 - 3.0 ms) (Goodman *et al.*, 2011: 9).

Ramasindrazana *et al.* (2011: 294) recorded 9 calls from 2 specimens tentatively assigned to *Miniopterus 'manavi'*, and found the following echolocation call values: Frequency of maximum energy: 57.2 ± 0.77 (55.5 - 58.2) kHz, Maximum frequency: 98.4 ± 7.60 (89.0 - 110.0) kHz, Minimum frequency: 53.0 ± 0.0 (53.0 - 53.0) kHz, Call duration: 2.5 ± 0.32 (2.1 - 3.0) ms, Inter pulse interval: 66.0 ± 8.70 (54.1 - 84.7) ms.

HABITAT:
M. manavi is found In native forests, degraded forests and cultivated areas (rice paddies) (Garbutt, 2022: 108).

ROOST:
These bats roost in caves and large hollow trees (Garbutt, 2022: 108).

DIET:
Razakarivony *et al.* (2005) found Araneae in 2 % of stomachs examined. Rakotoarivelo *et al.* (2007), in Madagascar, found *M. manavi* to mainly consume Hemiptera.

Kemp *et al.* (2018: Suppl.) used DNA metacarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Lepidoptera (*Pandemis retroflua* Diakonoff, 1960), Hymenoptera, Coleoptera, Hemiptera, Blattodea, Diptera (*Simulium lineatum* (Meigen, 1804), *Anopheles squamosus* Theobald, 1901, *Coquillettidia* sp.), Ephemeroptera, Mesostigmata, Sarcoptiformes, Trombidiformes, Astigmata, Neuroptera.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 73 minutes, and the digestibility rate about 80.5 %.

POPULATION:
Structure and Density
It is locally abundant in cavities or rocky overhangs that provide suitable roosting features.

Bayliss and Hayes (1999) reported on a colony of approximately 4,000 found in Makira, but this locality is outside the currently accepted distribution area for this species.

Trend
2016: Unknown (Monadjem *et al.*, 2017cf). 2008: Unknown (Andriafidison *et al.*, 2008f; IUCN, 2009).

PARASITES:
Gomard *et al.* (2016: 5) reported the presence of *Leptospira* bacteria in 5 out of 7 tested bats (73.7 %).

Megali *et al.* (2010: 1042), Duval *et al.* (2012: 1563), and Arnuphapprasert *et al.* (2020: Suppl.) reported Genbank data for *Polychromophilus* sp. (*Haemosporida*) from *M. manavi*. Ramasindrazana *et al.* (2018: Suppl.) identified the parasite as *Polychromophilus melanipherus* Dionisi, 1899, and the bat as "*M. manavi* s.l." (see also Bajić *et al.*, 2023: Suppl.).

Raharimanga *et al.* (2003: 72) reported *Trypanosoma* sp. from *M. manavi*, but these bats were later re-identified as *M. mahafaliensis* and *M. brachytragos* (see Rasoanoro *et al.*, 2019: 67).

Uchikawa (1985b: 45) reported a mite belonging to *Calcarmyobia comoresensis* from the type specimen of *M. manavi*. From the same specimen, Uchikawa (1985c: 110) also reported mites belonging to *Pteracarus miniopteri* Uchikawa, 1978. Furtermore, he also described two mite subspecies: *Calcarmyobia steatosetae steatosetae* and *Calcarmyobia steatosetae rectipenis* from several other bat specimens.

The presence of the Nycteribiid bat fly *Penicillidia leptothrinax* was reported by Tortosa *et al.* (2013: 4), Ramasindrazana *et al.* (2017: Suppl.) and Urushadze *et al.* (2017: 10). Additionally, Ramasindrazana *et al.* (2017: Suppl.) reported both "*Penicillidia* sp. and *P. leptothrinax* from one and the same bat identified as "*Miniopterus* cf. *manavi*".

Ramasindrazana *et al.* (2016: 6) reported the presence of *Litosoma* Clade 1 (Nematoda: Onchocercidae) on this bat species.

VIRUSES:
Astroviridae
Hoarau *et al.* (2021: Suppl.) reported viruses of this family in organs of bats from Madagascar.

Picornaviridae
Zeghbib *et al.* (2019: Suppl.) refer to the presence of a Hepatovirus.

UTILISATION:
In Makira, this species is eaten by people (Golden, 2005), also see Goodman *et al.* (2008d).

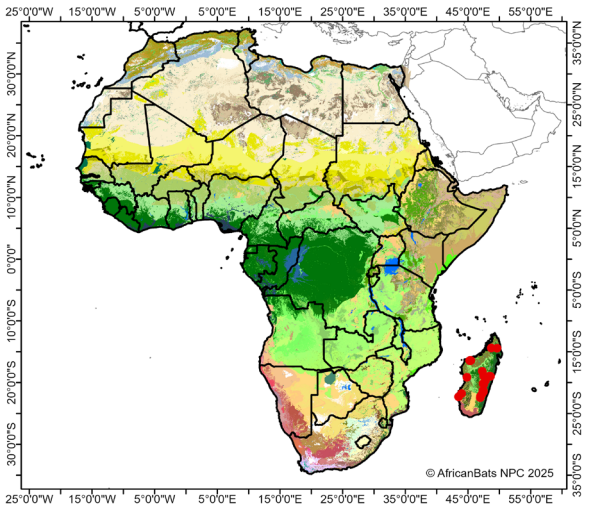

Figure 239. Distribution of *Miniopterus manavi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus minor Peters, 1867

*1867. *Miniopterus minor* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 870 (for 1866). Publication date: 1867. Type locality: Tanzania: Zanzibar Island. [Goto Description]. Holotype: ZMB 3268: ♂, skin and skull. Collected by: Baron Karl Klaus von der Decken. See Turni and Kock (2008: 52). - Comments: Peters (1867a: 885) mentions "Ein einziges ausgewachsenes Männchen von der Küste von Zanzibar". However, Benda *et al.* (2025: 32, 111-112 Footnote) suggest that the type locality is actually (the coast part of) Zanzibar Island itself. - Etymology: From the masculine Latin adjective *minor*, meaning "smaller", used as comparative of *parvus*, meaning "small", referring to the relatively small size of the species (see Lanza *et al.*, 2015: 334). (Current Combination).

1992. *Miniopterus minor occidentalis* Juste and Ibáñez, Bonn. zool. Beitr., 43 (3): 358, 362. Publication date: 21 October 1992. Type locality: Congo: Koilou, Meya-Nzouari Cave [03 53 S 14 31 E]. Holotype: MHNG 1074.013: ad ♀, skull and alcoholic. Collected by: M. Taufflieb; collection date: 1 July 1961. - Comments: (see Simmons, 2005). - Etymology: From the Latin for western. (Name Combination).

? *Miniopterus minor minor:* (Name Combination).

TAXONOMY:



Figure 240. *Miniopterus minor*, Zanzibar Island.

Koopman (1993a: 231) included *griveaudi* Harrison, 1959 and *manavi* Thomas, 1906, but Peterson *et al.* (1995: 119, 135) and Simmons (2005: 520) recognised *manavi* as a distinct species, with *griveaudi* as a subspecies. Juste [B.] *et al.* (2007: 33) elevated *griveaudi* as a separate species.

Simmons (2005: 521) recognised *newtoni* Bocage, 1889 and *occidentalis* Juste and Ibáñez, 1992 as vaild subspecies of *M. minor*. Juste [B.] *et al.* (2007: 33) elevated *newtoni* as a separate species.

Reviewed by Juste and Ibáñez (1992).

Morphometric analyses by Monadjem *et al.* (2020b: 12, 14) indicate that the specimens from Tanzania (*M. m. minor*) are clearly different from those from the Central African Republic and the Democratic Republic of the Congo (*M. m. occidentalis*) and possibly may represent different species. Although they do mention "*Miniopterus occidentalis*" throughout the text and in the appendix, they conclude that further investigation is needed to confirm its species status.

COMMON NAMES:

Chinese: 侏长翼蝠. Czech: létavec nejmenší. English: Least Long-fingered Bat. French: Petit minioptère africain, Minioptère minuscule. German: Zwerg-Langflügelfledermaus. Italian: Miniòttero minóre, Miniòptere minóre.

CONSERVATION STATUS:

Global Justification

Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, ecological requirements and threats (Jacobs *et al.*, 2008n; IUCN, 2009; Jacobs *et al.*, 2019j).

Assessment History

Global

2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019j). 2008: DD ver 3.1 (2001) [includes *occidentalis* Juste and Ibáñez, 1992] (Jacobs *et al.*, 2008n; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004o; IUCN, 2004). 2003: LR/nt (IUCN, 2003). 2001: LR/nt (IUCN/SSC Action Plan, 2001). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

This species is presumably threatened in parts of its range by habitat loss resulting from logging operations and the conversion of land to agricultural use (Jacobs *et al.*, 2008n; IUCN, 2009; Jacobs *et al.*, 2019j).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008n) [in IUCN (2009)] and Jacobs *et al.* (2019j) report that there appear to be no direct conservation measures in place. It has been recorded from the Kambai Forest Reserve in Tanzania by Cunneyworth (1996b). Further studies are needed into the taxonomy, distribution, natural history and threats to this poorly known species.

GENERAL DISTRIBUTION:

Miniopterus minor recorded from very few locations over a wide area. It has been reported from a small area on the border between Congo and the Democratic Republic of the Congo, a single locality in southwestern Democratic Republic of the Congo, and from a small area of coastal Kenya and Tanzania (including the island of Unguja [see O'Brien, 2011: 289]).

São Tomé (Koopman, 1993a: 231; Simmons, 2005: 521) removed by Juste [B.] *et al.* (2007: 33) due to the removal of *newtoni* as a separate species.

Native: Angola; Congo (Juste and Ibáñez, 1992: 363; Simmons, 2005: 521; Bates *et al.*, 2013: 337); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Juste and Ibáñez, 1992: 363; Van Cakenberghe *et al.*, 1999; Simmons, 2005: 521; Monadjem *et al.*, 2010d: 539); Kenya (Simmons, 2005: 521); Tanzania (Simmons, 2005: 521).

ECHOLOCATION:

For two caves in the Republic of Congo, Labadie *et al.* (2025b: 11) provided the following data for *Miniopterus* cf. *minor*: Boundou cave: 5 FF: F_{pmin}: 53.2 ± 1 kHz, F_{pmax}: 76.2 ± 6.7 kHz, F_{pmean}: 67.9 ±

5.8 kHz, F_{ppeak}: 64.8 ± 6 kHz, F_{max}: 107 ± 12.9 kHz, F_{flat}: 60 ± 3.2 kHz, F_{knee}: 64.4 ± 5.7 kHz, F_{min}: 58 ± 3.1 kHz, F_{mean}: 75 ± 6 kHz, Duration: 2.4 ± 0.4 ms; 10 MM: F_{pmin}: 52.5 ± 2.1 kHz, F_{pmax}: 78.1 ± 5 kHz, F_{pmean}: 68.9 ± 4.9 kHz, F_{ppeak}: 68.7 ± 13.1 kHz, F_{max}: 97.9 ± 21.9 kHz, F_{flat}: 60.3 ± 6.9 kHz, F_{knee}: 58.5 ± 21.5 kHz, F_{min}: 57.2 ± 2.7 kHz, F_{mean}: 73 ± 7.3 kHz, Duration: 2.9 ± 0.8 ms. Mont Belo cave: 10 FF: F_{pmin}: 46 ± 3.8 kHz, F_{pmax}: 71.1 ± 11.9 kHz, F_{pmean}: 62.7 ± 8.8 kHz, F_{ppeak}: 56.7 ± 5 kHz, F_{max}: 93 ± 15.1 kHz, F_{flat}: 55 ± 6.5 kHz, F_{knee}: 61.3 ± 8 kHz, F_{min}: 51.7 ± 4.6 kHz, F_{mean}: 66 ± 9 kHz, Duration: 2.8 ± 0.8 ms; 8 MM: F_{pmin}: 47.3 ± 3.2 kHz, F_{pmax}: 72.9 ± 7.6 kHz, F_{pmean}: 66.8 ± 7.3 kHz, F_{ppeak}: 61.1 ± 4 kHz, F_{max}: 96.4 ± 20.3 kHz, F_{flat}: 59 ± 6.6 kHz, F_{knee}: 68.6 ± 19.3 kHz, F_{min}: 55.3 ± 3.9 kHz, F_{mean}: 69.7 ± 8.7 kHz, Duration: 2.6 ± 0.5 ms.

ROOST:
McWilliam (1982: 176) found this bat to be roosting in caves.

MIGRATION:
In Kenya, McWilliam (1982: 175) found that most long-distance movements were made by females, whereas males showed a larger site specificity.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 73 minutes, and the digestibility rate about 80.5 %.

POPULATION:
Structure and Density
There are very few records of this species (Jacobs *et al.*, 2008n; IUCN, 2009; Jacobs *et al.*, 2019j).

Trend
2018: Unknown (Jacobs *et al.*, 2019j). 2008: Unknown (Jacobs *et al.*, 2008n; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
In Kenya, *M. minor* exhibits seasonal torpor between April and September, when the temperatures are lower (McWilliam, 1982: 184).

MATING:
McWilliam (1982: 176, 177) described a small "mating dome" within the Homa Lime cave in Kenya, which was almost exclusively occupied by mature males, which returned the following years. Immature males were excluded from the dome. During the mating period (May to July), the males produced a pungent odour (resembling rotting cocoa) in their urine (McWilliam, 1982: 181).

PARASITES:
Uchikawa (1985b: 50) described the mite *Calcarmyobia minoris* from *Miniopterus minor minor* from Similani Cave, 16 km S. of Mombasa, Coast Province, Kenya. Uchikawa (1985c: 110) also reported three female mites belonging to *Pteracarus miniopteri* Uchikawa, 1978 from bats from Kenya.

Adam and Landau (1973a: 5) and Landau and Adam (1973: 6) report on the presence of a protozoan parasite of the genus *Polychromophilus* (Haemoproteidae) in *M. minor minor* from the Republic of Congo. About 50 % of the specimens they examined, were found to be infected. Gametocytes were found year-round. The bats were also infested by the nycteribiids *Penicillidia fulvida* Bigot, 1885 and *Nycteribia schmidlii scotti* Falcoz, 1923, of which the prior was a major carrier of *Polychromophilus* sporozoites. Garnham (1973: 237) reports the parasite as *Polychromophilus melanipherus* Dinoisi, 1899 (see also Bajić *et al.*, 2023: Suppl.).

Polychromophilus sp. was also reported by Rosskopf *et al.* (2018: 31) from Gabonese *M. minor occidentalis*, where both examined specimens were infected.

Landau and Adam (1973: 6) also report on another protozoan parasite: *Hepatocystis*, of which schizonts were found in the liver and lungs.

Duval *et al.* (2012: 1559) and Landau *et al.* (2012: 142) indicate that the haemosporidan *Polychromophilus (Polychromophilus) adami* Landau *et al.*, 1980 was described from *M. minor minor* specimens in the Republic of Congo (see Landau *et al.*, 1980b: 27). Landau *et al.* (2012: 142) also mention this bat as the type host for *Bioccala murinus* (Dionisi, 1899).

Lutz *et al.* (2016: 9) examined 13 *M. minor* specimens from East Africa and found five of them infected with *Polychromophilus melanipherus* Dionisi, 1899.

11 out of 17 Kenyan bats examined by Lutz *et al.* (2021: Suppl.) were infected by *Polychromophilus* Haemosporidia.

BACTERIA
Bartonellae
McKee *et al.* (2021: Suppl.) reported *Bartonella* sp. from Kenyan bats.

ARACHNIDA
Spinturnicidae
Orlova *et al.* (2024: 153) mention this species as host for *Spinturnix semilunaris* de Meillon & Lavoipierre, 1944.

DIPTERA
Nycteribiidae
Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108; Lutz *et al.*, 2021: Suppl.).

Lutz *et al.* (2021: Suppl.) also found *Penicillidia fulvida* (Bigot, 1885).

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Miniopterus minor*: *Eucampsipoda africana* Theodor, 1955, *Nycteribia schmidlii scotti* Falcoz, 1923 and *Penicillidia (Penicillidia) fulvida* (Bigot, 1885), but they also mention that *E. africana* might be an erroneous record.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Miniopterus minor*: Astroviruses, Coronaviruses, Paramyxoviruses and Polyomaviruses.

Coronaviridae - Coronaviruses
SARS-CoV
Tong *et al.* (2009) tested 1 bat collected in Kenya during 2006 positive for the presence of coronavirus RNA in a faecal sample. 22.6 % (66 out of 292) of the Kenyan bats tested by Tao *et al.* (2017: 3) were positive for CoV.

Paramyxoviridae
Paramyxovirus
Conrardy *et al.* (2014: 259) tested 16 bats from the Three Caves (Kenya) and found one of them to be positive. Mortlock *et al.* (2015: 1841) tested 151 Kenyan bats and found 14 to be positive.

Nieto-Rabiela *et al.* (2019: Suppl.) mention Bat paramyxovirus and Miniopterus paramyxovirus to be present.

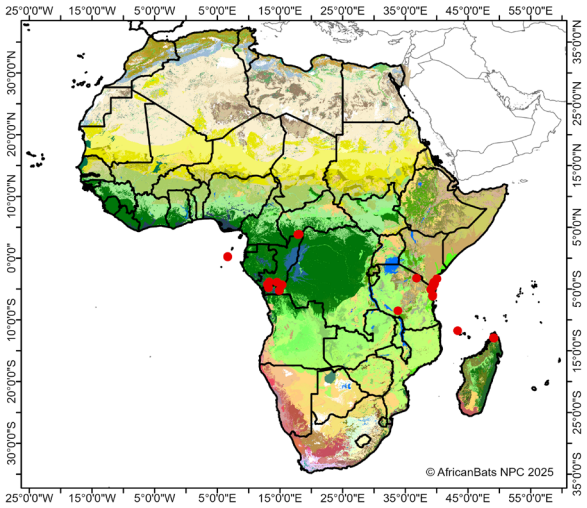

Figure 241. Distribution of *Miniopterus minor*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Central African Republic, Comoros, Congo, Congo (Democratic Republic of the), Kenya, Madagascar, São Tomé and Príncipe, Tanzania.

Miniopterus mossambicus Monadjem, Goodman, Stanley and Appleton, 2013

*2013. *Miniopterus mossambicus* Monadjem, Goodman, Stanley and Appleton, Zootaxa, 3746 (1): 123, 129, figs 3, 6, 7. Publication date: 10 December 2013. Type locality: Mozambique: Nampula province: outskirts of Nampula town: Bamboo Inn [15.10306 S 39.21748 E, 420 m]. Holotype: FMNH 213651: ad ♂, skull and alcoholic. Collected by: Steven M. Goodman and Ara Monadjem; collection date: 9 October 2010; original number: SMG-16875. Paratype: FMNH 213652: ad ♂, alcoholic (skull not removed). Collected by: Steven M. Goodman and Ara Monadjem; collection date: 9 October 2010; original number: SMG-16876. - Etymology: Refers to the country from which the species was collected (see Monadjem *et al.*, 2013a: 129). (Current Combination).

COMMON NAMES:
Chinese: 莫桑比克长翼蝠. English: Mozambique long-fingered bat. German: Mossambique-Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Kenya (López-Baucells *et al.*, 2017: 20); Malawi; Mozambique; Zambia; Zimbabwe.

ECHOLOCATION:
Monadjem *et al.* (2013a: 139) mention a knee frequency of 55 kHz.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

REPRODUCTION AND ONTOGENY:
In a colony of about 2,000 bats at Bwarenunka Cave near Chisakila (Zambia), Benda *et al.* (2022: 322) found that all examined females were lactating on 1 December.

PARASITES:
BACTERIA
Dietrich *et al.* (2018a: 4) report the presence of *Leptospira borgpetersenii*.

DIPTERA
Streblidae
Raymondia aspera Maa, 1968 from Mozambique (Shapiro *et al.*, 2016: 254).

VIRUSES:
Astroviridae
Two out of 21 bats tested positive in the study by Hoarau *et al.* (2018: 2).

Coronaviridae
Hoarau *et al.* (2021: Suppl.) reported such viruses to be present in these bats.

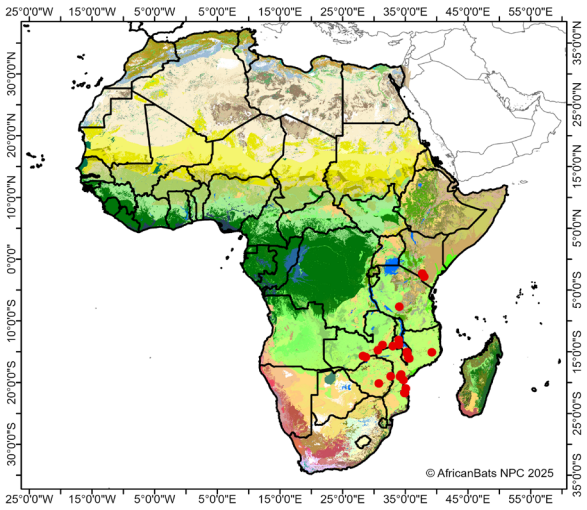

Figure 242. Distribution of *Miniopterus mossambicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Malawi, Mozambique, Tanzania, Zambia, Zimbabwe.

Miniopterus natalensis (A. Smith, 1833)

*1833. *Vespertilio Natalensis* A. Smith, S. Afr. Quart. J., ser 2, 1 (2): 59. Publication date: November 1833. Type locality: South Africa: KwaZulu-Natal: Durban [29 52 S 31 00 E]. [Goto Description]. Syntype: NHMUK 1846.6.2.19. Shared cotype for *Vespertilio natalensis* and *Vespertilio scotinus* - this needs further investigation as it is unlikely that Sundeval examined material described by Andrew Smith. It is possible that this co-type should only be assigned to one of these species. Cotype: NHMUK 1848.6.12.19. - Comments: Concerning the type locality, Meester *et al.* (1986: 46) remark: "Durban nominated by Roberts (1951: 73)").

1840. *Vespertilio d'asythrix* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome Seconde, 2 (13): 268. Publication date: 1840. Type locality: South Africa: "Interior of Caffraria". [Goto Description]. Holotype: RMNH MAM.25093: ad, skin and skull. Collected by: Jean Baptiste Edouard Verreaux. The RMNH catalog mentions two numbers: 25093.a (skull + loose bones) and 25093.b (skin). - Comments: .

*1846. *Vesperugo scotinus* Sundevall, Öfvers. kongl. Sv. Vet.-Akad. Förhandl., 3 (4): 119. Publication date: 1846. Type locality: South Africa: KwaZulu-Natal: Durban [29 52 S 31 00 E]. [Goto Description]. Syntype: NHMUK 1846.6.2.19. Shared cotype for *Vespertilio natalensis* and *Vespertilio scotinus* - this needs further investigation as it is unlikely that Sundeval examined material described by Andrew Smith. It is possible that this co-type should only be assigned to one of these species. Syntype: NRM 631071:; collection date: 28 November 1843. Syntype: NRM 641070:; collection date: 28 June 1840. - Comments: Type locality originally mentioned as "variis Caffrariæ locis allata"; Meester *et al.* (1986: 46) state: "Durban nominated by Roberts (1951: 74)". .

1909. *Miniopterus breyeri* Jameson, Ann. Mag. nat. Hist., ser 8, 4 (23): 471. Publication date: 1 November 1909. Type locality: South Africa: N Transvaal province: Waterberg district: Gat(s)koppies. [Goto Description]. Holotype: NHMUK 1909.7.2.6: imm ♀. Collected by: Henry Paul William Lyster Jameson; original number: 398.

1927. *Miniopterus smitianus* Thomas, Proc. zool. Soc. Lond., 373. Publication date: 12 July 1927. Type locality: Namibia: E Damaraland, 40 mi (64 km) W of Gobabis: Witvlei. Holotype: NHMUK 1926.12.7.15.

2014. *Miniopterus 'natalensis':* Christidis, Goodman, Naughton and Appleton, PLoS ONE, 9 (3) e92440: Suppl. Publication date: 18 March 2014.

2018. *Miniopteris schriebersii:* Adams and Kwiecinski, Diversity, 10 (3) 103: 7. Publication date: 18 September 2018. (Lapsus).

2020. *Miniopterus cf. natalensis:* Monadjem, Guyton, Naskrecki, Richards, Kropff and Dalton, Acta Chiropt., 22 (1): 3. Publication date: 3 September 2020. (Name Combination).

2021. *Miniopterus nataliensis:* Hayward and Tachedjian, mBio, 12 (5) e0194-21: 3. Publication date: 7 September 2021. (Lapsus).

? *Miniopterus africanus natalensis:* (Name Combination).

? *Miniopterus breyeri breyeri:*

? *Miniopterus natalensis dasythrix:* (Name Combination).
? *Miniopterus natalensis natalensis:* (Name Combination).
? *Miniopterus natalensis smitianus:* (Name Combination).
? *Miniopterus natalensis:* (Name Combination, Current Combination).
? *Miniopterus schreibersi dasythrix:*
? *Miniopterus schreibersi natalensis:* (Name Combination).
? *Miniopterus schreibersi:*
? *Miniopterus schreibersii natalensis A:*
? *Miniopterus schreibersii natalensis B:*
? *Miniopterus schreibersii natalensis:* (Name Combination).
? *Miniopterus schreibersii:*
? *Vespertilio scotinus:*

TAXONOMY:



Figure 243. *Miniopterus natalensis*.

Considered a synonym of *schreibersi* by Koopman (1993a: 231). O'Shea and Vaughan (1980), Koopman (1994), Peterson *et al.* (1995) and Horáček *et al.* (2006: 105) suggested that *natalensis* may be distinct from *schreibersi*. Considered a valid species by Simmons (2005: 521).

Simmons (2005: 521) recognised *arenarius* Heller, 1912 as valid subspecies. However, see Kruskop *et al.* (2014: 102), Kassahun *et al.* (2015: 168), Farkašová *et al.* (2017: Suppl.), Wilson and Mittermeier (2019: 704) and Monadjem *et al.* (2020e: 242, 255), who consider this to be a valid species.

Based on mitochondrial data, Demos *et al.* (2019c: "9") indicate that *natalensis* is sister to all of the other African and Madagascan forms, although this was not confirmed by the nuclear data.

COMMON NAMES:

Chinese: 纳塔尔长翼蝠. Czech: létavec natalský. English: Natal Long-fingered Bat, Natal Clinging Bat. French: Minioptère du Natal. German: Natal-Langflügelfledermaus, Südafrikanischen Sackfledermaus, Kaffern-Sackfledermaus. SiSwati: Lilulwane.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

This species is present in the latter half of the upper Pleistocene sequence and in the late Holocene at Border Cave, and probably at Nkupe during the middle and late Holocene (Avery, 1991: 6). Further Holocene material is reported by Avery and Avery (2011: 20) from Blinkklipkop, Limerock, and Zoovoorbij (Northern Cape province, South Africa), who also reported Pleistocene remains from Wonderwerk.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008aj; IUCN, 2009; Monadjem *et al.*, 2017bg).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bg). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008aj; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004ai; IUCN, 2004).

Regional

South Africa: 2016: LC ver 3.1 (2001) (MacEwan *et al.*, 2016b). 2004: NT ver 3.1 (2001) [assessed as *M. schreibersii*] (Friedmann and Daly, 2004:263).

Eswatini:- 2003: NT B2ab(iv); D2 ver 3.1 (2001) [assessed as *M. schreibersii*] (Monadjem *et al.*, 2003: 184).

MAJOR THREATS:

In view of its wide range, there appear to be no major threats to this species. In parts of the species distribution it is locally threatened by habitat loss resulting from conversion of land to agricultural use, incidental poisoning with insecticides, and the disturbance of roosting and maternity caves by tourist activities (Jacobs *et al.*, 2008aj; IUCN, 2009; Monadjem *et al.*, 2017bg).

Aronson (2022: 225) found this species to be the third most impacted species, with 5 % of the carcasses found near South African wind energy facilities.

CONSERVATION ACTIONS:
Jacobs *et al.* (2008aj) [in IUCN (2009)] and Monadjem *et al.* (2017bg) report that there appear to be no conservation measures in place for this species. There is a need to identify and protect important roost sites (especially maternity caves). In view of the species wide range, it is presumably present in some protected areas. There is a need to better determine the range of this species when compared to that of *Miniopterus schreibersii*.

GENERAL DISTRIBUTION:
Miniopterus natalensis is a widely distributed species, recorded from southern and East Africa, with some records from Central Africa. It ranges south from Angola and southern Democratic Republic of the Congo, into Namibia, Botswana, South Africa, Lesotho, Mozambique, Malawi, Zimbabwe and Zambia. Because of frequent misidentification between this species and *Miniopterus schreibersii*, there is a need to carefully review the distribution of *Miniopterus natalensis*.

Records from the Arabian Peninsula, Ethiopia, South Sudan and Uganda are currently assigned to *Miniopterus arenarius* (see Monadjem *et al.*, 2020e: 239; Ibáñez and Juste, 2019: 704). We also tentatively include the records from Kenya and Tanzania to this species.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,227,870 km^2. In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 539; Taylor *et al.*, 2018b: 62); Botswana (Smithers, 1971; Monadjem *et al.*, 2010d: 539); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 539); Eswatini (Monadjem *et al.*, 2010d: 540, Monadjem *et al.*, 2021: 5); Kenya?; Lesotho (Lynch, 1994: 191 [as "*M. schreibersii*"]; Monadjem *et al.*, 2010d: 539); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 35; Monadjem *et al.*, 2010d: 539); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 539; Monadjem *et al.*, 2010c: 385); Namibia (Monadjem *et al.*, 2010d: 340); South Africa (Simmons, 2005: 521, Seamark and Kearney, 2007: 4; Monadjem *et al.*, 2010d: 540); Tanzania? (Stanley and Goodman, 2011: 47 as *M. schreibersii*); Zambia (Ansell, 1974; Ansell, 1978; Monadjem *et al.*, 2010d: 540); Zimbabwe (Monadjem *et al.*, 2010d: 540).

Presence uncertain: Uganda, Kenya, Tanzania.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Schoeman and Jacobs (2002: 157) reported the following wing parameters for one "*M. schreibersii*" specimen from the Algeria Forestry Station (RSA): Fa: 46.6 mm, Wing area: 137.7 cm^2, Wing span: 30.9 cm, Wing loading: 7.8 N/m^2, and aspect ratio: 6.9.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$ $C^1/_1$ $PM^2/_3$ $M^3/_3$ = 36 (van der Merwe, 1985a: 73).

van der Merwe (1985a: 73) also indicates that the deciduous tooth replacement starts in the lower jaw and is completed prior to that of the upper jaw. The replacement starts at an age of one and a half weeks. In general, the replacement sequence is: I_3, I_1, C_1, I_2, PM_4, PM_3, and all teeth are replaced at week 5. In the upper jaw, the replacement starts two and a half weeks (PM^4, PM^3, I^2, I^3, C^1) and is generally completed in week 6.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Camacho *et al.* (2019: "5") describe the facial profile of *M. natalensis* as convex ("airorhynchy"), with an extreme upward orientation in its snout.

FUNCTIONAL MORPHOLOGY:
Moussy *et al.* (2012: 189), referring to Miller-Butterworth *et al.* (2003), indicate that isolation of different populations in South Africa has led to local adaptation in *Miniopterus schreibersii natalensis*, which is strongly associated with four biomes and results in differences in wing morphology and migratory behaviour. The animals from the northeastern population have a higher wing aspect ratio, which forms an advantage for long-distance flight, allowing for migrations over longer distances.

Brown (1999: 170) found that "*M. schreibersii*" is able to thermoregulate in temperatures between 5 and 40°C.

Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 7.8 Pa, aspect ratio 6.4 for a wingspan of 31 cm and a wing area of 146 cm^2 and a body mass of 12 g.

ECHOLOCATION:
See Jacobs (1999) and Taylor (1999b).

Schoeman and Waddington (2011: 291) mention a F_{peak}: 51.1 ± 0.9 kHz and a duration: 6.8 ± 0.4 ms for specimens from Durban, South Africa.

For *Miniopterus natalensis* specimens from Swaziland and Namibia, Taylor *et al.* (2013b: 17) recorded the following parameters for 21 calls: F_{max}: 65.9 ± 5.76 (59.0 - 80.9) kHz, F_{min}: 53.7 ± 0.58 (52.5 - 54.9) kHz, F_{knee}: 56.5 ± 0.31 (55.7 - 57.0) kHz, F_{char}: 54.1 ± 0.78 (52.7 - 55.5) kHz, duration: 2.6 ± 0.48 (1.9 - 3.8) ms. Values for a further 11 specimens from Swaziland were reported by Monadjem *et al.* (2017c: 179): F_{min}: 53.2 ± 0.87 (51.3 - 54.8) kHz, F_{knee}: 57.0 ± 0.96 (55.5 - 58.5) kHz, F_c: 53.6 ± 0.83 (51.6, 55.0) kHz and duration: 2.8 ± 0.37(2.2 - 3.7) ms. They also indicated that the maximum detection distance for this species is 5 m.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 56 (56 - 57) kHz.

Schoeman and Jacobs (2002: 157) reported a F_{peak} of 53.6 kHz for one "*M. schreibersii*" from the Algeria Forestry Station (RSA). Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg area (RSA): F_{min}: 52 - 55 kHz, F_{char}: 45 - 62 kHz, F_{knee}: 56 - 57 kHz, slope: 235 - 622 OPS, duration: 2 - 4 ms.

In the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded 15 calls with F_{char}: 49.91 ± 0.95 kHz, F_{max}: 67.84 ± 4.75 kHz, F_{min}: 49.39 ± 0.88 kHz, F_{knee}: 53.61 ± 2.27 kHz, duration: 4.96 ± 1.31 ms and 7.30 ± 2.65 calls/sec.

Moir (2020: 29) a,d Moir *et al.* (2021a: 371) registered 373 calls of 20 bats from southern KwaZulu-Natal and Eastern Cape: F_{max}: 71.72 ± 5.90 (62.55 - 85.55) kHz, F_{min}: 48.28 ± 1.65 (45.99 - 53.83) kHz, F_{char}: 50.37 ± 2.14 (47.26 - 53.25) kHz, F_{knee}: 52.79 ± 2.71 (49.07 - 61.60) kHz, and duration: 2.19 ± 0.49 (1.46 - 3.48) ms.

Eisenring *et al.* (2016: SI 2) reported for 17 calls of bats from the Aberdares Range in Kenya the follow values: F_{peak}: 44.1 ± 3.5 (41.5 - 54.8) kHz, F_{max}: 66.6 ± 17.7 (51.3 - 104.4) kHz, F_{min}: 40.4 ± 1.5 (38.5 - 44.0) kHz, DT: 0.1 ± 0.0 (0.1 - 0.1), duration: 26.1 ± 17.5 (12.5 - 63.9) ms, interpulse interval: 1.0 ± 0.5 (0.5 - 2.5) ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 27.90 ± 2.50 kHz, F_{max}: 33.20 ± 8.00 kHz, F_{min}: 25.70 ± 2.20 kHz.

10 calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 58.77 ± 2.45 kHz, F_{min}: 55.48 ± 1.10 kHz, F_{knee}: 57.07 ± 1.50 kHz, F_{char}: 55.90 ± 1.29 kHz, slope: 13.28 ± 20.65 OPS, duration: 3.92 ± 1.48 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 8) reported the following characteristics for 96 calls of 11 bats: F_{max}: 61.46 ± 7.55 kHz, F_{min}: 52.27 ± 5.9 kHz, F_{knee}: 55.55 ± 0.81 kHz, F_{char}: 54.08 ± 0.98 kHz, slope: -508.55 ± 3897.77 OPS, duration: 4.08 ± 1.61 ms. Three calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Tabls S1) had a duration: 3.91 ± 0.66 ms, F_{min}: 48.76 ± 0.31 kHz, F_{max}: 65.05 ± 11.73 kHz, F: 50.90 ± 0.74 kHz and F_{char}: 48.95 ± 0.24 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 23 *Miniopterus natalensis* calls from the Kruger Park (RSA): F_{min}: 50.5 ± 2.6 (46.6 - 54.2) kHz, duration: 3.2 ± 0.7 (2.4 - 4.6) ms, F_{max}: 65.8 ± 8.3 (51.5 - 85.9) kHz, F_{knee}: 53.8 ± 3.6 (48.5 - 60.3) kHz, F_{char}: 51.9 ± 2.9 (47.8 - 57.0) kHz.

28 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 52 - 55 kHz, F_{max}: 59 - 80 kHz, F_{char}: 53 - 56 kHz, F_{knee}: 56 - 57 kHz and duration 2 - 4 ms.

For 16 calls from 2 *Miniopterus natalensis* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 53.57 ± 0.50 kHz, F_{knee}: 58.78 ± 2.05 kHz, F_{min}: 53.26 ± 0.81 kHz, F_{max}: 73.89 ± 11.90 kHz, Bandwidth: 20.63 ± 11.92 kHz, Duration: 2.41 ± 0.27 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 49.91 ± 0.95 kHz, F_{max}: 67.84 ± 4.75 kHz and F_{min}: 49.39 ± 0.88 kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 51.4 kHz and duration: 3.4 ms.

Molecular Biology:

Karyotype

M. schreibersii from Namibia and South Africa now assigned to *M. natalensis*, were karyotyped by Rautenbach *et al.* (1993) who described the karyotype as having a diploid number of 2*n* = 46, aFN = 50, BA = 6, X = SM, Y = A.

Genetics

Teeling *et al.* (2017: 32) mention the assembly size for *M. natalensis* to be 1.80 Gb.

Banerjee *et al.* (2017: 10) detected potential c-Rel binding sites in *M. natalensis*. This protein has a

potential role in the DNA repair pathway as a regulator of inflammatory gene expression.

Shao *et al.* (2023: 3) investigated the genome of *M. natalensis* and found the 15 most diverse microsatellite motifs in this species to be $(A)_n$, $(CT)_n$, $(AC)_n$, $(TA)_n$, $(G)_n$, $(TAT)_n$, $(TTTA)_n$, $(ATAG)_n$, $(CATT)_n$, $(CCTT)_n$, $(CAA)_n$, $(TGGA)_n$, $(AACAA)_n$, $(AAAC)_n$ and $(TTATT)_n$ comprising of 94.10 % of all microsatellites identified.

Wang *et al.* (2025b: 6) report that the total length of the genome is 1.9 Gb.

Isotope
Pretorius *et al.* (2022: 802) found that male *M. natalensis* had a broader isotopic niche (in both $\delta^{13}C$ and $\delta^{15}N$ ranges). This may indicated different migration strategies to that of females or feeding on prey from a broader geographic origin.

HABITAT:
Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *M. natalensis* activity was not significantly, nor positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *M. natalensis* preferred trees and orchards surrounding wetlands (Sirami *et al.*, 2013: 35).

Voigt *et al.* (2013: 751) investigated stable isotope ratios of carbon, nitrogen and hydrogen in the fur keratin of *M. natalensis* on the slopes of Mount Kilimanjaro and found that this species migrates seasonally between low and high elevations. They found that *M. natalensis* captured before and after the cold period at around 1,800 m above sea level originated from around 1,400 m a.s.l. or lower, which they suggest might be the result of a search for colder hibernacula at higher elevations.

HABITS:
van der Merwe (1973b: 380) indicates that in the Transvaal *M. natalensis* forms hibernating (winter) and maternity (summer) colonies, and he reports on maternity caves housing 50,000 to 100,000 animals. The bats usually form closely packed clusters, hanging from the roofs of caves, although some might be hanging against the walls. Hibernation started at the beginning of May and lasted until the end of July.

At De Hoop Nature Reserve (Western Cape Province, South Africa), Thomas and Jacobs (2013: 124) found that *M. natalensis* emerged significantly later during early summer than in late summer. Norton and van der Merwe (1978: 219) already found that juveniles returned later in the night than adults, probably because they needed more food as their fat reserves would be insufficient to get them over the winter.

At Madimatle cave (RSA), Pretorius *et al.* (2020b: 409) found that the magnitude of activity of *Miniopterus natalensis* is primarily affected by photoperiod rather than by climatic variables (including rainfall). Their activity increased as the night length decreased. Pretorius *et al.* (2020c: 755) found that the time of moonrise did not affect the activity of these bats. Moonlight did not affect the bat's activity during the maternity season, but bright moonlight during the non-breeding season did reduce the activity.

ROOST:
van der Merwe (1973b: 380) reports "*M. schreibersi natalensis*" to occur in colonies of hundreds or thousands of animals occupying a wide range of caves. At Peppercorn's cave and at Sandspruit Cave No. 1 clusters of 50,000 and 100,000 individuals were reported.

van der Merwe (1973a: 133) found that the bats preferred caves with lower temperature for hibernation. Norton and van der Merwe (1978: 220) also found that temperatures in the Long One Cave were probably too high and variable for prolonged hibernation, which resulted in fluctuating numbers of bats. By the end of the winter, however, temperatures decreased and the proportion of *M. natalensis* bats staying in the cave increased.

Bernard and Bester (1988: 921) describe the annual movements of "*M. schreibersi*" between three roosts in the Eastern Cape region (RSA). The maternity roost was warmer than the hibernation site. One of the sites was used as maternity and hibernaculum, but as these functions were at different times of the year, the temperatures were also different. The higher temperature at the maternity roost might increase prenatal and postnatal development rates.

Brown (1999: 171) reported the mean temperature in tunnel roosts is on average 19.5°C in summer (max: 22°C) and 14°C in winter. Czenze *et al.* (2021: 3) confirmed that these bats roost in sites where the maximum temperature is much lower than 30* C and where the maximum temperature was at least 10*C lower than outside.

MIGRATION:
Pretorius *et al.* (2020a: 1110) investigated potential migratory least-cost paths (LCPs) between maternity sites and winter hibernacula in South Africa. Most of the involved caves were

not located in formal protected areas, and the most prominent threat factors were onshore wind energy facilities and human settlements.

Markotter *et al.* (2023: 200) report on a wing-tattooed *M. natalensis* bat that was recaptured 200 km away from the site where it was originally marked.

DIET:
At the Umbilo River (KwaZulu Natal, RSA), Naidoo *et al.* (2011: 26) found the following percentage volume diet composition: Lepidoptera (35.7 ± 10.3), Coleoptera (11 ± 9.1), Hemiptera (28.3 ± 12.9), and Trichoptera (25.0 ± 13.9). No data were provided for the winter.

Schoeman and Jacobs (2002: 157) reported the following volume percentages found in 20 faecal pellets from one "*M. schreibersii*" from the Algeria Forestry Station (RSA): Diptera (49), Hemiptera (33), Lepidoptera (6), Coleoptera (6), and Trichoptera (6).

For 21 "*M. schreibersii*" specimens from Sudwala (RSA), Jacobs (2000: 201) reported the following prey proportions: Lepidoptera (23.1 ± 31.2), Coleoptera (4.5 ± 16.7), Isoptera (70.8 ± 32.2), Diptera (0.6 ± 2.3), Hemiptera (0.6 ± 2.3), and Mantodea (0.4 ± 0.3).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 90 minutes, and the digestibility rate about 78.3 %.

PREDATORS:
Avery *et al.* (2005: 1054) found this species (reported as *M. schreibersii*) to be present in pellets from *Tyto alba* (Scopoli, 1769) in South Africa. van der Merwe (1980a: 15) already reported the barn owl as a predator, but indicated that these bats do not rank high on its diet, although there was an increase when other terrestrial and subterrestrial preys are decreasing in availability. Swartz *et al.* (2025: 1) confirmed that the owl's selection of these bats was more determined by prey abundance than by preference.

Malan *et al.* (2022: 167) reported one individual found in a pellet from a bat hawk (*Macheiramphus alcinus* Bonaparte, 1850 in the RSA.

POPULATION:
Structure and Density
This species can be found in colonies of more than 2,500 animals (Jacobs *et al.*, 2008aj; IUCN, 2009; Monadjem *et al.*, 2017bg). Mason *et al.* (2010: 165) observed that the number of bats in the De Hoop maternity chamber increased from a few hundred to several thousand from 18th August to the 25 September 2006.

Trend
2016: Unknown (Monadjem *et al.*, 2017bg).
2008: Unknown (Jacobs *et al.*, 2008aj; IUCN, 2009).

LIFESPAN:
Based on mark-recapture techniques, van der Merwe (1989b: 87) determined the maximum life expectancy for this species in the wild to be 13 years.

REPRODUCTION AND ONTOGENY:
Delayed implantation, insemination, ovulation and fertilization occur in the autumn (April to May in South Africa, see Bernard *et al.* (1991: 31), as *M. schreibersii*). Embryogenesis proceeds to the blastocyst stage and development is then retarded until arousal in spring, when the blastocyst implants and embryogenisis resumes (van der Merwe, 1980b). van der Merwe (1982b: 319) also mentions that implantation is centric and superficial in the right uterine horn, as was already noticed by Ginther (1967: 580) and van der Merwe (1996: 154), who also indicated [referring to Matthews (1941)], that the implantation occurs in the uterine horn opposite to the ovary containing the corpus luteum. van der Merwe (1979a: 17) and Bernard (1980a: 55) indicated that the delayed implantation period for "*M. schreibersi natalensis*" lasted for four months (120 days), which is as long as the active foetal growth period, giving a gestation period of 240 days. van der Merwe (1981: 172) presented the following formula to calculate the embryo's age in days (t) based on its body mass (W): $t = W^{1/3}/0.0145 + 144$.

Bernard and Davison (1996: 218) investigated the relation between calcium availability (from the poor source that insects are) and the reproduction of "*M. schreibersii*" and found that seasonal changes in insect abundance could not explain the delayed implantation, but that lactating females nevertheless had the lowest bone calcium concentrations. This is probably the reason why parturition occurs in seasons with maximum insect availability.

Mason *et al.* (2010: 165) found at De Hoop that in mid-August 2006 the bats sampled were either not pregnant or at a very early stage of pregnancy and no embryos were present. However, on the 8th September the first bat sampled was pregnant and carried an embryo at the limb bud stage (CS13), this is found

approximately the same time of year as those of the KwaZulu Natal and Eastern Cape populations. No twins were observed, and pregnant bats collected on the same day never had embryos from only one stage of development (Mason *et al.*, 2010). Mason *et al.* (2010: 168) found that the period of early to mid-embryonic development (CS11 to CS21) occurred over a period of about two weeks in both years sampled, however this period appeared to occur about two weeks later in 2008 than in 2006, this delay in pregnancy may be due to environmental factors. Also the embryonic stages were not the same among individuals sampled on the same day, indicating that although reproductive events may be synchronous (within the period of a month) in this species, exact developmental events were not highly synchronized between individuals.

At the Gatkop cave (RSA), Dietrich *et al.* (2018b: 4) were only able to trap non-scrotal males in September 2015. In November 2015, 90 % of the females they trapped had given birth very recently, and in January 2016, large amounts of juveniles were present, together with post-lactating females.

The mass of pregnant females varied greatly and was not correlated to the developmental stage of the embryos that they carried (Mason *et al.*, 2010: 165). Pretorius *et al.* (2019: 319), however, found that lactating females with sclerotized nipples were 6 % heavier than non-reproductive females and pregnant females were 25 % heavier than non-reproductive females, a difference - which at least in part - was attributed to foetus mass. Over three successive years (2015 - 2017), the proportion of active breeding females was found to be 31 %, 33 % and 70 %.

Pretorius *et al.* (2021a: 1) investigated the seasonal variation in body mass and found that varied significantly between the two sexes and by reproductive category. Scrotal males had a higher body mass in summer compared to autumn, which was not the case nin non-scrotal males. The summer body mass of nonpregnant and post-lactating females was not significantly higher than the autumn body mass of nonpregnant females, indicating that females do not seem to store extra fat during the summer and before their migration.

Mason *et al.* (2015) studied the embryological development of the fore- and hindlimbs, and found that that the transcription factor *Meis2* has a significantly higher expression in bat forelimb autopods compared to hindlimbs. Eckalbar *et al.* (2016: 528) found over 7,000 genes and noncoding RNAs (incl. Tbx5-as1 and Hottip), that were differentially expressed between forelimb and hindlimb, and across different stages of development.

MATING:

van der Merwe (1973b: 384) reported that the period of mating was still uncertain, although he assumed that it occurred at the wintering caves prior to hibernation.

PARASITES:

BACTERIA

Dietrich *et al.* (2016b: 3) tested 17 bats from Irene (RSA) and found two testing positive for *Bartonella* and one for *Rickettsia*. Five out of 8 bats from Vanderkloof Dam (RSA) also tested positive for *Bartonella*.

Dietrich *et al.* (2015a: 3) reported the presence of the Enterobacteria *Hafnia* and *Nitrococcus*. They also found *Leptospira* in the urine sample, and *Bartonella* in urine and saliva samples. Dietrich *et al.* (2018a: 4;2018b: 4) reported the presence of bacteria related to *Leptospira borgpetersenii* and a second group closely related to *L. interrogans* and *L. kirschneri*.

Clément *et al.* (2019a: 5) reported on 97 southern African *M. natalensis* specimens of which 12 were infected by either *Trypanosoma* sp. 1_AF (2), *Trypanosoma* sp. 2_A (2), *Trypanosoma* sp. 2_B (3), *Trypanosoma dionisii*_AF1-AF4 (4) and *Trypanosoma* cf. *livingstonei*_likeH_G1 (1).

Federici *et al.* (2022: 5) [referring to Dietrich *et al.* (2016a)] mentions Proteobacteria *Burkholderia, Helicobacter* and *Bartonella*.

HAEMOSPORIDA

Minozzo *et al.* (2021: 7) refer to Lutz *et al.* (2016) to report the presence of *Polychromophilus* in *Miniopterus natalensis* (see also Chumnandee *et al.*, 2020: Suppl.; Lutz *et al.*, 2021: Suppl.). Bajić *et al.* (2023: Suppl.) and Ceballos-Pérez *et al.* (2024: 3) mention the parasites as *Polychromophilus melanipherus* (Dionisi, 1899). However, the bats referred to by Lutz *et al.* (2021) are most probably representatives of *Miniopterus arenarius*.

Gastro-intestinal Helminthes - See Ortlepp (1932) and Junker *et al.* (2008a).

NEMATODA

Genov *et al.* (1992) reported *Molinostrongylus omatus* (Mönnig, 1927) from *M. natalensis* from South Africa. Ramasindrazana *et al.* (2016: 2) indicate that *Litomosa chiropterorum* Ortlepp, 1932 (Onchocercidae) was redescribed from a *M. natalensis* population from South Africa. This

Nematode was already reported from a bat from Katanga (DRC) by Durette-Desset and Chabaud (1975: 304).

Krasnov *et al.* (2020: Suppl.) examined 96 *Miniopterus natalensis* specimens from the RSA and found the following Nematoda: *Aonchotheca* sp., *Molinostrongylus ornatus* (Mönnig, 1927), two unclassified *Molinostrongylus* species, *Litomosa chiropterorum* Ortlepp, 1932 and *Physaloptera* sp.

PLATYHELMINTHES

Krasnov *et al.* (2020: Suppl.) found the Trematodes *Anchitrema sanguineum* (Sonsino, 1894), *Paralecithodendrium khalili* (Saoud & Ramadan, 1977) and *Paralecithodenrium pyramidum* (Looss, 1896) as well as Cestoda belonging to the Hymenolepididae in bats from the RSA.

ARACHNIDA

Argasidae

Argas vespertilionis (Latreille, 1802) from a "*M. schreibersi*" from Pretoria (see Howard, 1908: 168).

Dermanyssidae

Zumpt and Till (1954: 49) report *Steatonyssus natalensis* Zumpt and Patterson, 1951 from bats from Natal. Zumpt (1950: 92) found a new mite of the genus *Bdellonyssus*.

Ixodidae

Krasnov *et al.* (2020: Suppl.) found *Ixodes simplex* Neumann, 1906 on bats in the RSA.

Macronyssidae

Zumpt (1950: 89) described *Hirstesia transvaalensis* from bats from the Sterkfontein cave (RSA). Krasnov *et al.* (2020: Suppl.) reported the presence of *Ichoronyssus miniopteri* (Zumpt & Patterson, 1952) as well as four unclassified species of *Macronyssus* and two of *Steatonyssus*.

Myobiidae

Uchikawa (1985a: 19) also reported that the type specimens of *Miniopterus breyeri*, *M. dasythrix*, and *M. scotinus* harboured the "atypical" form of *Calcarmyobia congoensis* Uchikawa, 1982, and he also (Uchikawa, 1985a: 22) mentioned *Calcarmyobia kenyaensis* Uchikawa, 1982 on "*Miniopterus schreibersi*" from Belgian Congo. Uchikawa (1985c: 110) furthermore reported on the presence of *Pteracarus miniopteri* Uchikawa, 1978 on bats from South Africa, Zambia, Namibia (as *M. schreibersi natalensis* or *M. smitianus*). *Calcarmyobia rhinolophia* (Radford, 1940) (see Krasnov *et al.*, 2020: Suppl.).

Myobia miniopterus Womersley, 1941 (see Zumpt, 1950: 92).

Rosensteiniidae

Fain (1979: 124) reported *Nycteriglyphus miniopteri* Fain, 1963 from a "*Miniopterus schreibersii natalensis*".

Spinturnicidae

Spinturnix semilunaris De Meillon and Lavoipierre, 1944 (see Zumpt, 1950: 92; Krasnov *et al.*, 2020: Suppl.; Orlova *et al.* (2024: 153).

Trombiculidae

Stekolnikov (2018a: 147) mentioned *Microtrombicula armata* Vercammen-Grandjean, 1965 from a South African "*M. schreibersi*". Zajkowska *et al.* (2018: 116) indicated that the host species was originally given as "*M. schreibersii natalensis*".

DIPTERA

Nycteribiidae

Nycteribia capensis Karaman, 1939 from the Cape and Pietermaritzburg, South Africa (Haeselbarth *et al.*, 1966: 108). *Nycteribia latiterga* Theodor, 1957 from Mt. Menengai, Kenya (Haeselbarth *et al.*, 1966: 108). *Nycteribia schmidlii* Schiner, 1853 (Zumpt, 1950: 97; Haeselbarth *et al.*, 1966: 108; Blackwell, 1980: 146 - infected by the fungus *Arthrorhynchus eucampsipodae* Thaxter, 1901 [see also Haelewaters *et al.*, 2018: 794; Szentiványi *et al.*, 2019a: Suppl.], de Groot *et al.*, 2020: Suppl.), *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966: 114; Blackwell (1980: 144 - infected by the fungus *Arthrorhynchus nycteribiae* (Peyritsch) Thaxter [see also Haelewaters *et al.*, 2018: 794; Szentiványi *et al.*, 2019a: Suppl.], de Groot *et al.*, 2020: Suppl.).

Szentiványi *et al.* (2020: 3) reported on *Nycteribia schmidlii scotti* Falcoz, 1923 on bats from the RSA (on average 1.4 ± 0.7 bat flies per bat).

Streblidae

Ascodipteron africanum Jobling, 1939 from Kapretwa and Mt. Kenya, Kenya, other records referred to this species are misidentification (Haeselbarth *et al.*, 1966: 106). *Ascodipteron theodori* Maa 1965 from Rooiberg, South Africa (Haeselbarth *et al.*, 1966: 106). Krasnov *et al.* (2020: Suppl.) also mentioned *Ascodipteron* sp. and *Brachytarsina* sp parasites from the RSA.

Raymondi waterstoni Jobling 1931 which may be accidental (Haeselbarth *et al.*, 1966: 104) (see also Shapiro *et al.*, 2016: 256).

HEMIPTERA
Cimicidae
Kock *et al.* (1998b: 236) mentioned the presence of *Cacodmus villosus* (Stål, 1855) on bats from South Africa.

SIPHONAPTERA
Ischnopsyllidae
Oxyparius isomalus (Waterston, 1915) known from several localities in southern Africa (Transvaal, Natal of South Africa, Botswana and Namibia) (Haeselbarth *et al.*, 1966: 188; Krasnov *et al.*, 2020: Suppl.).

VIRUSES:
In a limited study in Kenya (three caves), Kamau *et al.* (2022: 5) found Astroviridae, Circoviridae, Dicistroviridae and Retroviridae.

Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)
Oelofsen and Van der Ryst (1999) tested [as *M. schreibersi*] 49 individuals from one locality in the Free State Province, South Africa for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested [as *M. schreibersi*] between 1986 and 1999, for antibody to SARS-CoV in sera in one individual from Limpopo Province, South Africa, none were tested positive (0/1). Tong *et al.* (2009) tested 1 bat collected in Kenya during 2006 positive for the presence of coronavirus RNA in a faecal sample. Nine out of 53 (17 %) Kenyan bats tested by Tao *et al.* (2017: Suppl.) was positive for CoV. One out of 14 specimens tested by Geldenhuys *et al.* (2013: 517) from Irene Caves, Gauteng, RSA tested positive for CoV.

Paramyxoviridae
Conrardy *et al.* (2014) detected a paramyxovirus sequence in one of eight bats sampled in Kenya. This virus does not group with the known paramyxoviruses and remains an unclassified paramyxovirus.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Duvenhage
van der Merwe (1982a) implicated *Miniopterus schreibersii*, as an isolate of the virus but the bat was never positively identified. This record was also referred to by Hayman *et al.* (2011a: 88), who indicated that the bas was possibly a *M. natalensis*.

Rabies
Oelofsen and Smith (1993) tested [as *M. schreibersi*] 137 individual brains, from 5 localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

Coertse *et al.* (2020: 3057) reported a new lyssavirus (distantly related to West Caucasian Bat Virus) from two bats from Matlapitsi and Madimatle caves in Limpopo, RSA. This virus was called Matlo Bat Lyssavirus (MBLV) and its entire genome sequence was given by Grobler *et al.* (2021).

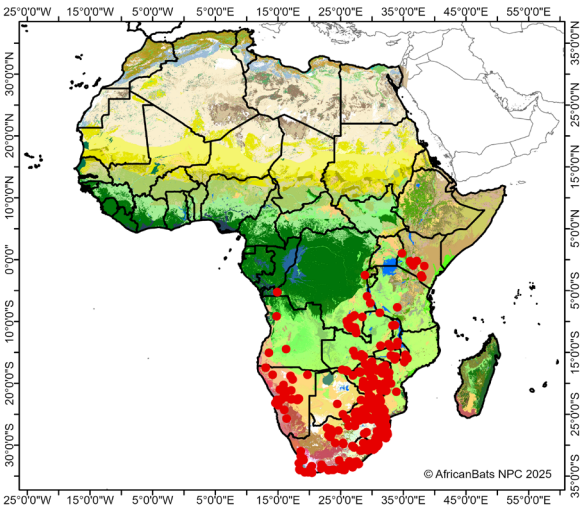

Figure 244. Distribution of *Miniopterus natalensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Congo (Democratic Republic of the), Eswatini, Kenya, Lesotho, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe.

Miniopterus newtoni Bocage, 1889

*1889. *Miniopterus Newtoni* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (3): 198. Publication date: December 1889. Type locality: São Tomé and Príncipe: São Tomé Island. [Goto Description]. Neotype: EBD 17350M: ad ♂, skull and alcoholic. Collected by: Javier Juste and Carlos J. Ibáñez Uargui; collection date: 4 April 1988. São Tomé Island, Santa Catarina, in a cave near the seashore (00 16 N 06 29 E), designated as neotype by Juste and Ibáñez (1992: 361). (Current Combination).
? *Miniopterus newtoni:* (Current Spelling).

TAXONOMY:
Recognised as a synonym (Koopman, 1993a: 231) or a subspecies (Simmons, 2005: 521) of *M. minor* Peters, 1867. Removed from *minor* by Juste [B.] *et al.* (2007: 33), based on mtDNA analyses. Juste and Ibáñez (1992: 361) designated a neotype for *newtoni* Bocage, 1889.

COMMON NAMES:
Czech: létavec tomášský. English: Sao Thome Long-fingered bat. French: Minioptère de São Tomé. German: Sao Thome Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Juste, 2008b; IUCN, 2009; Juste, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Juste, 2019b). 2008: DD ver 3.1 (2001) (Juste, 2008b; IUCN, 2009).

Regional
São Tomé: NT due to a probable decline in the number of individuals and locations because of the destruction and/or disturbance of underground roosts (Rainho *et al.*, 2022: 609).

MAJOR THREATS:
The threats to this species are not well known (Juste, 2008b; IUCN, 2009; Juste, 2019b).

CONSERVATION ACTIONS:
Juste (2008b) [in IUCN (2009)] and Juste (2019b) reports that it is not known if the species is present in any protected areas. Further studies are needed into the natural history and threats to this species.

GENERAL DISTRIBUTION:
Miniopterus newtoni is endemic to the island of São Tomé (São Tomé and Príncipe) where it is widespread (Juste [B.] *et al.*, 2007).

Native: São Tomé and Príncipe (Koopman, 1993a: 231 [as *minor*]; Simmons, 2005: 521 [as *minor*]; Juste [B.] *et al.*, 2007; Rainho *et al.*, 2010a: 33).

ECHOLOCATION:
Rainho *et al.* (2010a: 21) and Rainho *et al.* (2022: 605) reported the calls of 14 individuals from São Tomé with the following characteristics: F_{min}: 50.3 ± 1.3 (47.8 - 52.2) kHz, F_{max}; 101.7 ± 16.7 (69.6 - 119.0) kHz, F_{maxE}: 55.9 ± 2.7 (53.2 - 61.0) kHz, duration: 4.8 ± 2.1 (2.3 - 7.8) ms and interpulse interval: 61.4 ± 23.6 (31.8 - 105.7) ms.

HABITAT:
On Sáo Tomé, Castro-Fernandes *et al.* (2024: 1, 2) reported this bat to be an edge-forager, most active in oil palm plantations.

POPULATION:
Structure and Density
It is a common species (Juste B. and Ibáñez, 1994b; Juste, 2008b; IUCN, 2009; Juste, 2019b).

Trend
2018: Unknown (Juste, 2019b). 2008: Unknown (Juste, 2008b; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Araújo-Fernandes *et al.* (2025: 830) reported that the activity pattern of *Miniopterus newtoni* in rural areas shows two peaks: one at dusk and a second at dawn, whereas the activity in urban areas is continuous during the night. But it is not clear whether this is due to a higher light tolerance or to a limited availability of prey or to the activity patterns of the prey (p. 832).

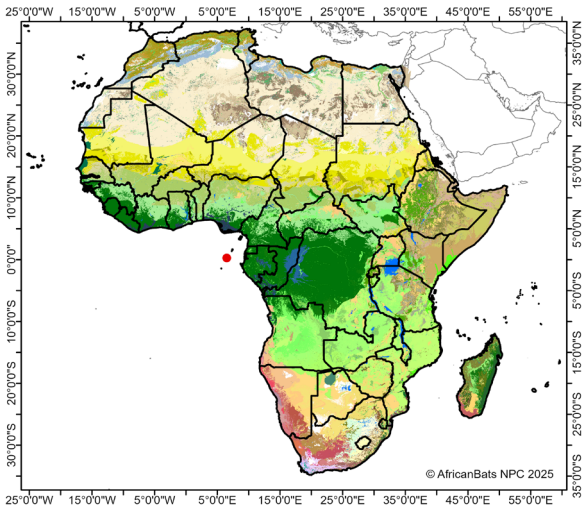

Figure 245. Distribution of *Miniopterus newtoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
São Tomé and Príncipe.

Miniopterus nimbae Monadjem, Shapiro, Richards, Karabulut, Crawley, Nielsen, Hansen, Bohmann and Mourier, 2020

*2020. *Miniopterus nimbae* Monadjem, Shapiro, Richards, Karabulut, Crawley, Nielsen, Hansen, Bohmann and Mourier, Acta Chiropt., 21 (2): 239, 245, figs 6, 7A, 8, 9A. Type locality: Liberia: Nimba county: Mount Gangra:

10 km W Mount Nimba [07 33 16 N 08 37 44 W, 720 m]. Holotype: DNSM 12621: ad ♂, skull and alcoholic. Collected by: Dr. Ara Monadjem; collection date: 18 December 2010; original number: AM2010_12_18_1. Presented/Donated by: Dr. Ara Monadjem. Paratype: DNSM 12614: ad ♀. Collected by: Dr. Ara Monadjem; collection date: 17 December 2010. Presented/Donated by: Dr. Ara Monadjem. - Etymology: Referring to the type locality on Mount Nimba. (Current Combination).

COMMON NAMES:
English: Nimba long-fingered bat

CONSERVATION STATUS:
Monadjem *et al.* (2020e: 252) suggest this species might be assigned to the IUCN category Vulnerable or even Endangered.

GENERAL DISTRIBUTION:
Only known from Liberia (Mount Nimba and surrounding uplands, Wonegizi mountains) and Guinea (Mount Béro) (see Monadjem *et al.*, 2020e: 247).

ECHOLOCATION:
Monadjem *et al.* (2020e: 248) found that the knee frequency of the echolocation calls from four hand-released *M. nimbae* specimens ranged between 47.2 and 48.9 kHz (average 48.4 kHz).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

REPRODUCTION AND ONTOGENY:
Monadjem *et al.* (2020e: 248) found that five out of 13 females captured between late December and the end of March were pregnant, and three out of 10 males had scrotal testes.

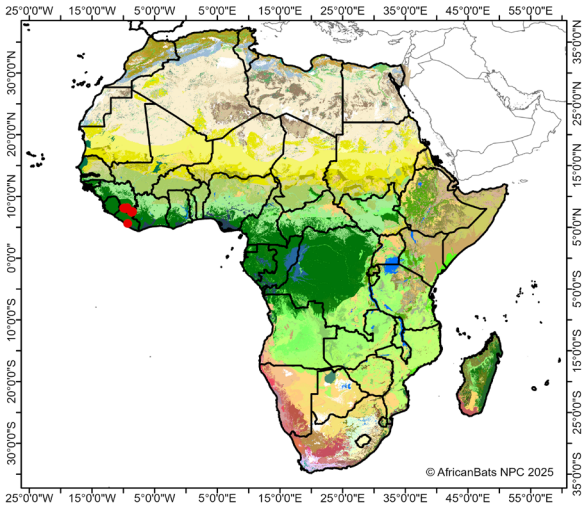

Figure 246. Distribution of *Miniopterus nimbae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Guinea, Liberia.

Miniopterus petersoni Goodman, Bradman, Maminirina, Ryan, Christidis & Appleton, 2008

2007. *Miniopterus cf. sororculus:* Goodman, Ryan, Maminirina, Fahr, Christidis and Appleton, J. Mamm., 88 (5): 1229.
2008. *Miniopterus cf. petersoni:* Goodman, Bradman, Maminirina, Ryan, Christidis and Appleton, Mamm. biol., 73: 202.
*2008. *Miniopterus petersoni* Goodman, Bradman, Maminirina, Ryan, Christidis and Appleton, Mamm. biol., 73: 199, 200, 201, figs 2 - 5. Type locality: Madagascar: Province de Toliara: Cascade de Manantantely: Tolagnaro, 5.2km NW [2459.343S 4655.370E, 65m]. Holotype: FMNH 194136: ad ♂. Collected by: Steven M. Goodman; collection date: 20 February 2007; original number: SMG 15833. Paratype: USNM 577096. Paratype: USNM 577097. Paratype: USNM 577098: Collected by: G. Kenneth Creighton and E. Raholimavo; collection date: 19-30 October 1990. Paratype: USNM 577099. Paratype: USNM 577100. Paratype: USNM 577101. - Etymology: The name *petersoni* is a patronym in honour of Randolph L. Peterson of the Royal Ontario Museum, Toronto, Canada, who made pioneering contributions to the study of Malagasy bats, based on a 1967 collecting trip to the island, as well as other fields in mammalogy (Eger and Mitchell, 1990; Goodman *et al.*, 2008a). (Current Combination).

TAXONOMY:
See Goodman *et al.* (2008a).

COMMON NAMES:
Czech: létavec Petersonův. English: Peterson's Long-fingered Bat, Peterson's Bent-winged Bat. French: Minioptère de Peterson. German: Petersons Langflügelfledermaus.

SIMILAR SPECIES:
See Goodman *et al.* (2008a).

CONSERVATION STATUS:
Global Justification
This species is listed as Data Deficient (DD ver 3.1 (2001)) because although it appears to have a restricted range in the southeast of Madagascar and is associated with forest, there is taxonomic uncertainty about specimens from the north of Madagascar (which if proved valid would greatly extend the known range). There is also limited information on the population status and threats to this species (Jenkins and Rakotoarivelo,

2008b; IUCN, 2009; Jenkins and Rakotoarivelo, 2019).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) (Jenkins and Rakotoarivelo, 2019). 2008: DD ver 3.1 (2001) (Jenkins and Rakotoarivelo, 2008b; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Although robust data are lacking and there are still some taxonomic uncertainties of specimens from the north of Madagascar, the information on *M. petersoni* from the southeast suggests that this species is closely associated with natural forest formations and is therefore threatened by the loss or degradation of these habitats (Goodman *et al.*, 2008a). Threats to roosting colonies have not yet been documented (Jenkins and Rakotoarivelo, 2008b; IUCN, 2009; Jenkins and Rakotoarivelo, 2019).

CONSERVATION ACTIONS:
Jenkins and Rakotoarivelo (2008b) [in IUCN (2009)] and Jenkins and Rakotoarivelo (2019) report that none of the known collecting localities for verified specimens of this species are from within protected areas (Goodman *et al.*, 2008a). The taxonomic status of specimens from north Madagascar requires further study.

GENERAL DISTRIBUTION:
Miniopterus petersoni is endemic to the island of Madagascar and appears to be restricted to lowland (< 550 m elevation) habitats in the south-east (Goodman *et al.*, 2008a).

Schoeman *et al.* (2014: 28, 31) found the most suitable area for this species to be located in the southeastern part of the island, but reaching along the coast to the northeast, where the suitability seems to increase again (eastern humid forest or lowland forest region - humid).

The taxonomic status of specimens from the north of Madagascar remain unresolved (Goodman *et al.*, 2008a).

Native: Madagascar (Goodman *et al.*, 2008a).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Goodman *et al.* (2008a).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2008a).

ECHOLOCATION:
Low-duty cycle, frequency modulated/quasi constant (FM/QCF) echolocation call, with a peak frequency of 53.2 kHz (52.0 - 53.9 kHz) and a duration of 2.9 ms (2.5 - 3.3 ms) (Goodman *et al.*, 2011: 9).

Ramasindrazana *et al.* (2011: 294) recorded 6 calls from 1 *Miniopterus petersoni* specimen, and found the following echolocation call values: Frequency of maximum energy: 53.2 ± 0.75 (52.0 - 53.9) kHz, Maximum frequency: 106.5 ± 6.66 (95.0 - 115.0) kHz, Minimum frequency: 49.0 ± 0.63 (48.0 - 50.0) kHz, Call duration: 2.9 ± 0.32 (2.5 - 3.3) ms, Inter pulse interval: 71.0 ± 4.63 (63.8 - 76.7) ms.

MOLECULAR BIOLOGY:
Genetics
See Goodman *et al.* (2008a).

HABITAT:
See Goodman *et al.*, 2008a).

HABITS:
See Goodman *et al.* (2008a).

ROOST:
See Goodman *et al.* (2008a).

MIGRATION:
May be involved in seasonal migrations between cave roost sites (Goodman *et al.*, 2008a).

POPULATION:
Structure and Density
This species was only formally described in 2008 and there is no information on its population (Goodman *et al.*, 2008a).

Trend
2018: Unknown (Jenkins and Rakotoarivelo, 2019). 2008: Unknown (Jenkins and Rakotoarivelo, 2008b; IUCN, 2009).

PARASITES:
Tortosa *et al.* (2013: 4) and Ramasindrazana *et al.* (2017: Suppl.) reported the presence of the Nycteribiid bat flies *Nycteribia stylidiopsis* and *Penicillidia leptothrinax*. The latter is also reported by Wilkinson *et al.* (2016), and was found to be carrying *Rickettsia* bacteria Szentiványi *et al.*, 2019a: Suppl.).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

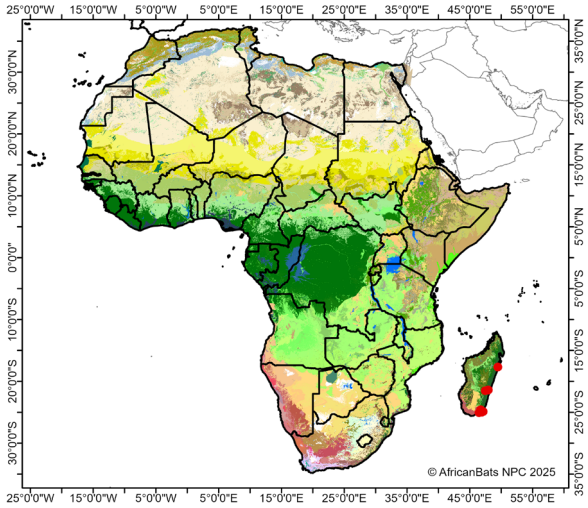

Figure 247. Distribution of *Miniopterus petersoni*.

Miniopterus schreibersii (Kuhl, 1817)

*1817. *Vespertilio schreibersii* Kuhl, Die Deutschen Fledermäuse, Hanau, 14. Type locality: Romania: S Ban(n)at Mnts, near Coronini, left bank Danube: Kolumbács Cave [=Kulmbazer cave] [ca. 44 37 N 21 40 E]. - Comments: Turni and Kock (2008) mention that the type and three "doublets" should have been present in the NMW, but are no longer found. - Etymology: In honour of Karl Franz Anton, Ritter von Schreibers (1775 - 1852), then director of the Vienna Museum (Flannery, 1995a: 378; 1995b: 452; Kozhurina, 2002: 17). - Phonetics: shrie'-berz-ee-ee, shribe'-er-zee-ee.
1827. *Vespertilio Screbersii:* Lesson, Manuel de Mammalogie, 89. (Lapsus).
1855. *V[espertilio] Schreibersi:* Giebel, Die Säugethiere, 950. (Name Combination).
1953. *Miniopterus schrebersii:* Harrison, Durban Mus. Novit., 4 (5): 65. Publication date: 30 June 1953. (Lapsus).
1995. *M[iniopterus] screibersi:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 119. (Lapsus).
2013. *Miniopterus schreibersiias:* Shi, Sci. China Life Sci., 56 (8): 679. (Lapsus).
? *Miniopterus schreibersi schreibersi:* (Name Combination).
? *Miniopterus schreibersii dasythrix:* (Name Combination).
? *Miniopterus schreibersii schreibersii:* (Name Combination).
? *Miniopterus schreibersii villiersi:* (Name Combination).
? *Miniopterus schreibersii:* (Name Combination, Current Combination).

TAXONOMY:
Molecular systematics and biogeography are discussed by Appleton *et al.* (2004: 436 - 437), who indicate that based on their data *M. schreibersii* would be restricted to Europe and North Africa; the Ethiopian representatives would belong to a second species and the Oriental-Australian a third (see also Stadelmann *et al.*, 2004b: 188). Tian *et al.* (2004: 303) confirm the views presented by Appleton *et al.* (2004), and suggest *M. schreibersii* for the European specimens, *M. fuliginosus* for the Asian representatives and *M. oceanensis* for the Australian ones (which was already suggested by Maeda (1982), although he separated the specimens from Hainan from the other Asian representatives, which is no longer supported by Appleton *et al.* (2004).

Reviewed by Crucitti (1976) and Hill (1983).

If *Miniopterus schreibersii* is restricted to northern Africa, then *Miniopterus inflatus villiersi* Aellen, 1956 should possibly be assigned to *Miniopterus natalensis*, but as already indicated by Fahr *et al.* (2006a: 74) and Monadjem *et al.* (2016y: 371), *villiersi* represents a distinct species, restricted to the Upper Guinea forest zone.

COMMON NAMES:
Afrikaans: Schreibers se grotvlermuis, Schreiber-grotvlermuis. Albanian: Miniopteri i Schreibers-it, Lakuriq nate I Schreiber-it. Arabian: Khaffash. Armenian: Սովորական երկարաթև չղջիկ. Azerbaijani: Adi uzunqanad yarasa. Basque: Schreibers saguzar, Schreiber saguzarra. Belarusian: Даўгакрыл звычайны. Bosnian: Šrajberov šišmiš, Dugokrili slijepi miš. Breton: Miniopter Schreibers. Bulgarian: Пещерен дългокрил. Castilian (Spain): Murciélago de cueva. Catalan (Spain): Ratpenat de cova, Rat penat de cova, Ratapinyada de cova. Croatian: Dugokrili pršnjak, Šrajberov šišmiš. Czech:

Létavec stěhovavý, nedopír širokouchý. Danish: Schreibers' langfingerflagermus. Dutch: Langvleugelvleermuis, Schreibers' vleermuis, Grote Schreiber's vleermuis. English: Schreiber's Bent-winged Bat, Schreiber's Bat, Long-wing Bat, Schreibers's Long-fingered Bat, Common Bent-winged Bat, Greater Bent-winged Bat, Large Bentwing Bat, Bent-winged bat, Common Long-fingered Bat, large bent-winged bat. Estonian: Euroopa pikktiib. Finnish: Pitkäsiipiyökkö. French: Minioptère de Schreibers, Minioptère à longues ailes, Chauve-souris de Schreiber, Minioptère. Frisian: Schreibers'langwjukflearmûs. Galician (Spain): Morcego das covas. Georgian: ჩვეულებრივი ფრთაგრძელი. German: Langflügelfledermaus, Gemeine Langflügelfledermaus, Schreibers Langflügelfledermaus, Europäische Sackfledermaus, Schreibers Fledermaus. Greek: Πτερυγονυχτερίδα. Hebrew: ﬠנפן, Kanfan. Hungarian: Európai hosszúszárnyú-denevér, Törpe denevér, Hosszúszárnyú denevér, Nycteris i macropterys. Indonesian: Kelelawar mini schreiber, Tomosu Biasa, Kelelawar mini biasa. Irish Gaelic: Ialtóg mhéarfhada Schreiber. Italian: Miniottero, Miniòttero di Schrèibers, Miniòptero di Schrèibers. Latvian: Šreibersa siksparnis. Lithuanian: Šreiberio ilgapirštis. Luxembourgish: Laangflillekefliedermaus. Macedonian: Долгокрилест лилјак, Dolgokrilest Liljak. Maltese: Farfett il-Lejl ta' Xrajber. Montenegrin: Dugorili prstenjak. Nepali: Bange Chamero. Norwegian: Middelhavslangvinge. Polish: Podkasaniec Schreibersa. Portuguese: Morcego-de-peluche, Morcego de schreiber. Rhaeto-Romance: Miniopter da l'ala lunga, Minopter ad ala lunga. Romanian: Liliacul cu aripi lungi, Liliac-cu-aripi-lungi. Russian: Длиннокрыл обыкновенный, Обыкновенный длиннокрыл [= Obyknovennyj dlinnokryl]. Serbian: Европски дугокрилаш. Serbian Latin: Evropski dugokrilaš. Scottish Gaelic: Ialtag mheur-fhada Schreiber. Sinhalese: Schreibersge dik-angeli wawula. Slovak: Lietavec sťahovavý. Slovenian: Dolgokrili netopir. Swedish: Europeisk vikvinge. Tamil: Sraipars-ṉ Nīṇṭa Viraluḷḷa Veḷavāl, ஸ்ரைப ர்ஸ்-ன் நீண்ட விரலுள்ள வெளவால். Turkish: Uzunkanatlı Yarasa. Ukrainian: Довгокрил звичайний. Welsh: Ystlum adain-gam Schreiber.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Gunnell *et al.* (2015a: 22) report skeletal remains from a Pleistocene deposit at Olduvai Gorge (Tanzania), which they assigned to *Miniopterus* cf. *M. schreibersi*.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened NT ver 3.1 (2001). Significant population declines and range contractions have been recorded in a number of range states and although it is stable in the Balkans and Turkey, overall the rate of population decline may approach 30 % (almost qualifies as VU under A2a) (Hutson *et al.*, 2008c; IUCN, 2009; Benda and Paunović, 2019).

Assessment History
Global
2016: NT ver 3.1 (2001) (Benda and Paunović, 2019). 2008: NT ver 3.1 (2001) (Hutson *et al.*, 2008c; IUCN, 2009). 2004: LC ver 3.1 (2001) [included *natalensis*] (Schlitter, 2004i; IUCN, 2004). 1996: LR/nt [included *M. natalensis*] (Baillie and Groombridge, 1996).

Regional
Mediterranean:- 2008: NT ver 3.1 (2001) (IUCN, 2009).

MAJOR THREATS:
The main threat in Africa is disturbance in roosts. In Europe, the disturbance and loss of underground habitats and pesticide use may threaten this species. In the Caucasus, disturbance caused by tourism in caves is a problem (K. Tsytsulina *pers. comm.,* 2005).

The cause of recent mass mortality events is unknown. In 2002 mass mortalities of this species were reported for populations in France, Spain and Portugal. There are also historical records for such mortalities in Italy, Australia and a possible incidence in Iran. A meeting was held at the 9th European Bat Research Symposium to discuss these incidents. Veterinary investigations in Spain did not identify any disease as the cause of the die offs, and there is increasing belief that the die offs are caused by bad weather in late winter/early spring (Hutson *et al.*, 2008c; IUCN, 2009).

The species' small range, cave/tree roosting and aerial hawking feeding style are believed to be the most important risk factors in view of climatic change (Sherwin *et al.*, 2012: 174).

CONSERVATION ACTIONS:
Hutson *et al.* (2008c) [in IUCN (2009)] and Benda and Paunović (2019) report that in Europe, it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in parts of the range where these apply. It is included in Annex II (and IV) of the EU Habitats and Species Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. There is some habitat protection through Natura

2000, and some roosts are already protected by national legislation. There have been a number of LIFEfunded projects for this species in Spain, Italy, Romania and Germany.

The species is found in many protected areas throughout its range.

Care is required when fencing caves to minimise mortality. Further research is required into the causes of the recent mass mortality events.

GENERAL DISTRIBUTION:
Miniopterus schreibersii occurs from south-western Europe and North and West Africa through Anatolia and the Middle East to the Caucasus. In Africa it is known from records in North Africa (Morocco, Algeria, Tunisia, Libya), and West Africa (Guinea, Sierra Leone, Liberia, Nigeria, Cameroon). It is patchily distributed over its range in some huge and vulnerable colonies. It typically occurs at altitudes of up to 1,400 m asl (commuting up to 2,600 m asl).

Based on cyt b sequences from GenBank, Derouiche *et al.* (2024: 23) conclude that *Miniopterus schreibersii* is the only *Miniopterus* species occurring in Algeria, although *M. maghrebensis* is probably present too (p. 34).

Native: Afghanistan; Albania; Algeria; Armenia; Azerbaijan; Bosnia and Herzegovina; Bulgaria; Cameroon; Cape Verdian Islands (Borloti *et al.*, 2020: 2); Croatia; Cyprus; France [Corse]; Georgia; Gibraltar; Greece [East Aegean Islands; Kriti]; Holy See [Vatican City State]; Hungary; Israel; Italy [Sardinia, Sicily]; Jordan; Lebanon; Liberia; Macedonia, the former Yugoslav Republic of; Malta; Monaco; Montenegro; Morocco (Benda *et al.*, 2010a: 158; El Ibrahimi and Rguibi Idrissi, 2015: 364; Dbiba *et al.*, 2025: 7); Nigeria; Palestinian Territory, Occupied; Portugal; Romania; Russian Federation; San Marino; Serbia; Sierra Leone; Slovakia; Slovenia; Spain [Baleares]; Switzerland; Syrian Arab Republic; Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26); Turkey.

Possibly extinct: Austria.

Regionally extinct: Germany; Ukraine.

Presence uncertain: Libyan Arab Jamahiriya.

DETAILED MORPHOLOGY:
Bhide (1979: 1) described the anatomy, histology and histochemistry of this bat's stomach

In Korea, three types of lingual papillae were on the tongue by Park and Lee (2009: 267): filiform, fungiform, and circumvallate.

Cebesoy and Karakas (2013: 382) report on the muscle fiber types in primary flight muscles of specimens from Turkey, where they recognized three types: I, IIa, and IIb, which respectively make up 14 %, 70 % and 16 % of the *serratus ventralis*. In their study on take-off performance, Gardiner *et al.* (2014: 1059) determined a wing beat frequency of 11.95 ± 0.17 Hz.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 10.2 Pa, aspect ratio 7.0 and tip shape index of 1.03 for a wingspan of 31 cm and a wing area of 137 cm^2 and a body mass of 14 g.

ECHOLOCATION:
The data for 61 animals from Greece are the following: F_{start}: 93.0 ± 11.84 kHz, F_{end}: 50.8 ± 1.16 kHz, F_{peak}: 54.9 ± 5.32 kHz, bandwidth: 17.8 ± 14.30 kHz, duration: 6.7 ± 1.29 ms and interpulse interval: 94.1 ± 35.73 ms (Papadatou *et al.*, 2008b: 133). Walters *et al.* (2012: suppl.) report the following figures for 31 calls from France, Greece, Italy and Switzerland: duration: 6.37 ± 2.89 ms, F_{max}: 73.24 ± 12.13 kHz, F_{min}: 49.75 ± 1.33 kHz, bandwidth: 23.49 ± 11.29, F_{peak}: 52.02 ± 1.68 kHz. Davies *et al.* (2013b: Table S8) report a peak frequency of 56.07 kHz and a range between 52.1 and 85.2 kHz.

From Morocco, Disca *et al.* (2014: 226) indicate that the type of call is FM-QFC, with the following parameters: F_{start}: 97.3 ± 11.3 kHz, F_{end}: 50.6 ± 1.4 kHz, F_{peak}: 53.4 ± 1.2 kHz, $F_{QFC\text{-}peak}$: 52.3 ± 1.1 kHz, bandwidth: 43.2 ± 11.4 kHz, duration: 6.2 ± 1.2 ms.

Ait-Abdesselam *et al.* (2025: 40) reported an F_{max} value of 56.51 ± 0.6 kHz for Algerian bats.

For 3 calls from the Kalahari Desert, the characteristics were: F_{char}: 47.6 ± 6.5 kHz, F_{max}: 76.7 ± 7.7 kHz, F_{min}: 53.2 ± 4.9 kHz, duration: 2.6 ± 0.4 ms (Adams and Kwiecinski, 2018: 4).

Luo *et al.* (2019a: Supp.) reported the following data (from 2 calls): F_{peak}: 54.9, 54.2 kHz, F_{start}: 93, 85.2 kHz, F_{end}: 50.8, 52.1 kHz, Band width: 42.2, 33.1 kHz, and duration: 6.7, 5.8 ms.

MOLECULAR BIOLOGY:
Karyotype
Matthey and Bovey (1948) and Bovey (1949) described the karyotype from Switzerland as having a diploid number of $2n$ = 46, aFN = 48, X

= submetacentric, Y = acrocentric. Rushton (1970: 463) reported 2*n* = 46, FN = 50, X = metacentric, Y = minute. Capanna and Civitelli (1965 - Italy), Baker *et al.* (1974 - Tunisia), Bickham and Hafner, 1978 - Yugoslavia), Zima (1978 - Czechoslovakia), Pérez-Suárez *et al.* (1991 - Spain), Albayrak (2006 - Turkey) found the fundamental number to be aFN = 50, and X = metacentric for Zima (1978). The autosomal chromosomes contain two large metacentrics, one medium-sized metacentric, 17 acrocentric and two dot-like pairs (one of these pairs may be bi-armed) (Arslan and Zima, 2014: 14). In Turkey, Aşan Baydemir (2015: 350) found Nucleolus Organising Regions (NORs) on the secondary constriction in 2 pairs of chromosomes (pairs 18 and 20). Capanna and Civitelli (1965: 546) mention 22 pairs of autosomes, of which 3 are metacentric, 17 acrocentric, and two very small; the X chromosome is a medium sized metacentric and the Y chromosome is a very small one. Capanna and Manfredi Romanini (1971: 474) mention 2*n* = 45, aFN = 50, 2 pairs of metacentrics, 1 pair of submetacentrics, 19 pairs of acrocentrics.

Genetics
Barragán *et al.* (2002), Appleton *et al.* (2004), Tian *et al.* (2004), Bilgin *et al.* (2006, 2008).

Gürün *et al.* (2014: 73) confirmed the pattern of local differentiation previously detected in mitochondrial DNA as they also found significant differences in the nuclear DNA between bats from North Africa, Lebanon, Cyprus, Anatolia, Russia, Thrace-Balkans, Slovakia, Italy, France, and Iberia. Gürün *et al.* (2019: 1866), however, could not confirm the mitochondrial differences in the microsatellite markers they examined, which would suggest a male-biased dispersal.

HABITS:
In southern France, Vincent *et al.* (2011: 57) found that during pregnancy and lactation, females might switch roosts within a 30 km radius around the maternity colony. During the night, the females travelled between 4.1 and 29.2 km to their foraging areas. They also estimated the individual home-ranges for pregnant females to be 10,837 ha, and for lactating females 22,318 ha.

DIET:
Presetnik and Aulagnier (2013: 297) investigated the diet of *M. schreibersii* in Slovenia and found this to consist primarily of Lepidoptera (79 % by volume). Neuroptera (mostly Chrysopidae) accounted for 9.2 %), Diptera for 7.4 %, Trichoptera for 2.2 %, and Coleoptera for 1.4 %. This seems to indicate that *M. schreibersii* is an aerial hawker. Gardiner *et al.* (2014: 1058) assessed its foraging strategy as "high altitude fast aerial hawking".

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Rihane *et al.* (2024: 223) indicate that Miniopterus schreibersii was the most frequently captured prey (22.1 %) of a Moroccan Magreb Owl (*Strix mauritanica* (Witherby, 1905)).

POPULATION:
Structure and Density
See Hutson *et al.* (2008c) [in IUCN (2009)] and Benda and Paunović (2019) for information of populations outside Africa.

Trend
2016: Decreasing (Benda and Paunović, 2019).
2008: Decreasing (Hutson *et al.*, 2008c; IUCN, 2009).

LIFESPAN:
Szekely *et al.* (2015: Supp.) and Lagunas-Rangel (2019: 2) reports a maximum longevity of 22 years.

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 122) indicate that both sexes need about 16 months to attain sexual maturity.

Kurta and Kunz (1987: 82) report that, at birth, the young weights about 20.4 % of the mother's body mass (3.4 g versus 20.4 g), and that its forearm length is 35.5 % of its mother's (16.7 versus 47.0 mm).

Szekely *et al.* (2015: Suppl.) report that males become sexually mature after 730 days (24 months) and females after 577 days (19 months). The young is born after a gestation period of 100 days with a weight of 2.8 g (22 % of the adult). After weaning (66 days), its weight is increased to 12.8 g.

In central Tunisia, females can be gravid until mid-June (Dalhoumi *et al.*, 2019a: 160). In Malawi, births occurred early in the wet season (Happold and Happold, 1990b: 568).

Chari and Gopalakrishna (1984: 464) describe the development of the foetal membranes and the changes in the structure of the placenta in the Indian *Miniopterus schreibersii fuliginosus*, and they indicate that this bat has some unique embryological features.

MATING:
This species has a polygynandrous mating system (Webber *et al.*, 2017: Suppl.)

POSTNATAL DEVELOPMENT:
In Iran, Sharifi and Vaissi (2013: 1) found that new-borns had a mass of 3.74 ± 0.09 g and forearm length of 24.3 ± 0.31 mm. Both of these increased linearly over the first two weeks (at about 0.54 g/day and 1.39 mm/day), after which they remained rather stable. The epiphyseal gap of the fourth metacarpal phalangeal joint increased until the thirteenth day, then decreased linearly until the 70th day and thereafter fused. The eyes opened during the first week and the ears became erect. The pups also began to move by that time. At 21 days, their ability to fly improved, and they started to fly freely in the cave. At that time their average body mass was 11.32 g (91.6 % of adult weight).

PARASITES:
Lei and Olival (2014: Suppl.) mention this species to be a host for *Bartonella* bacteria.

Landau *et al.* (2012: 142) mention the Heamosporidians *Polychromophilus melaniferus* (Dionisi, 1899) and *Polychromophilus corradetti* Landau *et al.*, 1980.

In Europe, Genov *et al.* (1992) reported the following Nematodes: *Molinostrongylus panousei* Dollfus, 1954, *M. skrjabini* Skarbilovitch, 1934, *M. alatus* (Ortlepp, 1932), and *M. ornatus* (Mönning, 1927).

Uchikawa (1985a: 22) proposed the new name *Calcarmyobia dusbabeki* (Acari: Myobiidae) for a mite found on *Miniopterus schreibersii* from amongst others Tunisia and Algeria. The Spinturnicid mites *Spinturnix psi* (Kolenati, 1856) and *Spinturnix myoti* (Kolenati, 1856) were reported by Postawa and Furman (2014: 390) from Central Anatolia and the Levant.

Calcarmyobia ? parenzani Lombardini, 1956 was found on a *M. schreibersii* from Ras el Qued cave, Morocco.

Aellen (1955b) reported on the occurrence of the following nycteribid flies on *M. schreibersii* bats from Morocco and Algeria: *Nycteribia (Nycteribia) latreillei* (Leach, 1817), *Nycteribia (Nycteribia) schmidli* Schiner, 1853, *Nycteribia (Acrocholidia) vexata* Westwood, 1835, *Penicillidia dufouri* (Westwood, 1835), and *Penicillidia conspicua* Speiser, 1901.

Rhipicephalus sanguineus (Latreille, 1806) (Arachnidae: Ixodida: Ixodidae) were reported from Algerian bats by Bendjeddou *et al.* (2013: 325). Bendjeddou *et al.* (2017: 15), Bendjoudi *et al.* (2019: 71) and Khelfaoui *et al.* (2018: 67) reported the following ectoparasites from Algeria: Nycteribiidae: *Nycteribia (Nycteribia) pedicularia* Latreille, 1805, *Nycteribia schmidlii* Schiner, 1853, *Penicillidia (Penicillidia) dufourii* Westwood, 1835 and *Phthiridium biarticulatum* Hermann, 1804; Streblidae: *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851; and Siphonaptera: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes vespertilionis* Koch, 1844.

Khelfaoui *et al.* (2018: 69) also mentioned that *Nycteribia latreillii* (Leach, 1817) had been found earlier on bats from Morocco and Tunisia.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes simplex* Neumann, 1906, *Ixodes vespertilionis* Koch, 1844; Spinturnicidae: *Spinturnix psi* (Kolenati, 1856); Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, *Nycteribia vexata* Westwood, 1835, *Penicillidia conspicua* Speiser, 1901, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851.

In their key, Sun *et al.* (2022: 7) mention that the streblid flies *Ascodipteron minor* Theodor, 1973 and *Ascodipteron theodori* Maa, 1965 have been found on African *M. schreibersii*.

In Italy, Voyron *et al.* (2011: 193) reported the following fungal entities from *M. schreibersii* carcasses: *Aspergillus* sp., *Chrysosporium merdarium*, *Fusarium equiseti*, Ophiostomatacea, *Thielavia* sp., *Mucor hiemalis f. hiemalis*.

Ševčík *et al.* (2012: 35) report on the presence of the bat flies *Nycteribia schmidlii schmidlii* Schiner, 1853 and *Penicillidia conspicua* Speiser, 1901 on bats from Crete and Cyprus. These bat flies are vector hosts for the malaria parasite *Polychromophilus melanipherus* (see Witsenburg *et al.*, 2013: 169). Haelewaters *et al.* (2017: 1) furthermore reported *Nycteribia kolenati* Theodor & Moscona, 1954 from Hungary.

Additionally, Tortosa *et al.* (2013: 6) also reported the Nycteribiid bat fly *Penicillidia oceanica* (Bigot, 1885).

The bat flies *Nycteribia schmidlii* Schiner, 1853, *Penicillidia dufourii* (Westwood, 1834), and *Penicillidia conspicua* Speiser, 1901 were reported by Postawa and Furman (2014: 390) from Central Anatolia and the Levant. Haelewaters *et al.* (2018: 794) additionally reported the flies *Nycteribia parvula, Penicillidia indica, P. jenynsii*, and *P. oceanica* from non-specified areas.

In Europe, the tick *Ixodes simplex* Neumann, 1906 is highly specialized to *M. schreibersii* (see Hornok *et al.*, 2014: 1).

In Spain, Estrada-Peña and Serra-Cobo (1991: 346) found the following Acari: *Ixodes (Pomerantzevella) simplex* Neumann, 1906, *Ixodes (Eschatocephalus) vespertilionis* Koch, 1844, *Macronyssus longimanus* (Kolenati, 1856), *Macronyssus granulosus* (Kolenati, 1856), *Macronyssus cyclaspis* (Oudemans, 1906), *Macronyssus rhinolophi* (Oudemans, 1902), *Macronyssus diversipilis* (Vitzthum, 1920), *Macronyssus ellipticus* (Kolenati, 1857), *Spinturnix psi* (Kolenati, 1856), *Eyndhovenia euryalis euryalis* (Canestrini, 1884); and the bat flies *Nycteribia schmidlii* Schiner, 1853 and *Penicillidia dufouri* (Westwood, 1835).

VIRUSES:

Astroviridae

Luis *et al.* (2013: suppl.) mention the presence of an unassigned bat astrovirus.

Coronaviridae - Coronaviruses

Luis *et al.* (2013: suppl.) report the occurrence of various Coronaviruses (e.g., BatCoV HKU7, Miniopterus bat coronavirus 1, Miniopterus bat coronavirus HKU8).

Alphacoronavirus

Kohl and Kurth (2014: 3112) report this virus from Spain and Germany.

Betacoronavirus

Kohl and Kurth (2014: 3112) report this virus from Bulgaria and Germany.

Filoviridae - Filoviruses

Cuevavirus

Reported from Spain by Kohl and Kurth (2014: 3113).

Negredo *et al.* (2011: 1) described a new virus (Lloviu virus [LLOV]) from *M. schreibersii* in Spain.

Flaviviridae

Flavivirus

de Jong *et al.* (2011: 10), Luis *et al.* (2013: suppl.) report Japanese encephalitis virus. Luis *et al.* (2013) also mentions Kyasanur Forest disease virus and Yokose virus.

Orthomyxoviridae

Despite sampling and testing of 2 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

Papillomaviridae

Dyolambda

A new papillomavirus (*Miniopterus schreibersii* papillomavirus type 1 [MscPV1]) was described by Tse *et al.* (2012: 5) from Hong Kong as the first member of the novel Dyolambda-papillomavirus genus.

Phenuiviridae

Phlebovirus - Rift Valley fever virus

de Jong *et al.* (2011: 11), Luis *et al.* (2013: suppl.) report the occurrence of Rift Valley fever virus.

Picornaviridae

Zeghbib *et al.* (2019: 3) reported a new *Mischivirus* from a bat from Algeria.

Rhabdoviridiae

Lyssavirus - Rabies related viruses

de Jong *et al.* (2011: 9) report the presence of West Caucasian bat virus.

van Eeden *et al.* (2011: 67) report an unconfirmed, but possible occurrence of Duvenhage virus in a specimen from the Limpopo province, South Africa.

In Algeria, Serra-Cobo *et al.* (2018: 2) found seven bats out of 63 testing seropositive for European bat lyssavirus 1.

"Various European bat lyssaviruses" were reported by Kohl and Kurth (2014: 3114) from a variety of European countries.

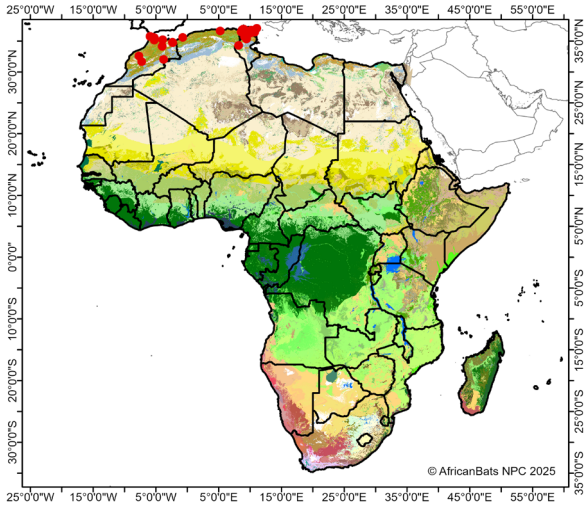

Figure 248. Distribution of *Miniopterus schreibersii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Algeria, Morocco, Tunisia.

Miniopterus sororculus Goodman, Ryan, Maminirina, Fahr, Christidis and Appleton, 2007

*2007. *Miniopterus sororculus* Goodman, Ryan, Maminirina, Fahr, Christidis and Appleton, J. Mamm., 88 (5): 1219, figs 2 - 6. Type locality: Madagascar: Province de Fianarantsoa: unnamed cave: Ambatofinandrahana, 3 km S [2034.321S 4648.530E, 1450 m]. Holotype: FMNH 177259: ad ♀, skull and alcoholic. Collected by: Steven M. Goodman; collection date: 23 March 2003; original number: SMG 13560. Paratype: FMNH 177255: Collected by: Steven M. Goodman; collection date: 23 March 2003. Paratype: FMNH 177256: Collected by: Steven M. Goodman; collection date: 23 March 2003. Paratype: FMNH 177257: Collected by: Steven M. Goodman; collection date: 23 March 2003. Paratype: FMNH 177258: Collected by: Steven M. Goodman; collection date: 23 March 2003. Paratype: FMNH 177260: Collected by: Steven M. Goodman; collection date: 23 March 2003. - Etymology: The name *sororculus* is derived from the Latin ("*sororcula*") and means "small sister" (Goodman *et al.*, 2007b: 1222). This epithet was chosen to contrast this taxon with its African counterpart *fraterculus*, which means "little brother", as well as this animal being slightly smaller than *M. majori* (Goodman *et al.*, 2007b: 1222). (Current Combination).

2017. *Miniopterus sorculus:* Yohe, Abubakar, Giordano, Dumont, Sears, Rossiter and Dávalos, Evolution, 71 (4): Suppl. Publication date: 7 March 2017. (Lapsus).

2018. *Miniopterus soroculus:* Kemp, López-Baucells, Rocha, Wangensteen, Andriatafika, Nair and Cabeza, Agric. Ecosyst. Environ., 369: 90 (for 2019). Publication date: 1 October 2018. (Lapsus).

? *Miniopterus sororculus fraterculus:* (Name Combination).

TAXONOMY:
Specimens from Madagascar assigned to *M. fraterculus* by Peterson *et al.* (1995) and Simmons (2005) are now considered to be a distinct species (Goodman *et al.*, 2007b).

COMMON NAMES:
Czech: létavec sesterský. English: Sororculus Long-fingered Bat, Sororcula Long-fingered Bat, Small sister Long-fingered Bat, Sororcula Bent-winged Bat. French: Minioptère petite soeur. German: Madagaskar-Langflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) as the species appears to have a broad distribution in the central highlands with a relatively wide elevational range. There are no obvious major threats, and based on current records seems to be at least somewhat adaptable to disturbed habitats (Jenkins *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017t)).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017t).
2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008f; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
There are no known threats to this species and it exists in areas some distance from native forest (Goodman *et al.*, 2007b; Jenkins *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017t).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008f) [in IUCN (2009)] and Monadjem *et al.* (2017t) report that at present, there are no known records from protected areas. This is a recently described taxon that does not appear to rely on large tracts of intact forest for its survival (Goodman *et al.*, 2007b). Further studies

are needed to understand its adaptation to high elevations and extreme climate (Goodman *et al.*, 2007b).

GENERAL DISTRIBUTION:
Miniopterus sororculus is endemic to Madagascar where it has mainly been recorded from sites above 900 m elevation (Goodman *et al.*, 2007b) although there are a few records from sites at elevations < 50 m (Goodman *et al.*, 2008a). It is known from < 10 m confirmed localities ranging in elevation from 40 to 2,200 m above sea level. It is presumed to have a broad distribution spanning various portions of the Central Highlands (Goodman *et al.*, 2007b).

Schoeman *et al.* (2014: 28; 31) found the most suitable area for this species to be located in the central highland part of the island (higher elevations of the Central Highlands - sub-humid region).

Native: Madagascar (Goodman *et al.*, 2007b; Goodman *et al.*, 2008a).

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls as *Miniopterus majori/sororculus*, which produced broadband FM/QCF echolocation calls at low duty cycle, but with a lower maximum energy, at about 48.5 kHz. The fundamental being most intense with short duration pulses of about 4.5 ms.

Ramasindrazana *et al.* (2011: 294) recorded 20 calls from 7 *Miniopterus sororculus* specimens, and found the following echolocation call values: Frequency of maximum energy: 55.3 ± 0.92 (53.9 - 56.6) kHz, Maximum frequency: 103.2 ± 9.04 (83.0 - 121.0) kHz, Minimum frequency: 51.7 ± 1.08 (50.0 - 53.0) kHz, Call duration: 3.3 ± 0.29 (2.7 - 3.9) ms, Inter pulse interval: 79.3 ± 13.06 (50.8 - 99.8) ms.

HABITAT:
The holotype of *M. sororculus* was collected in a small limestone cave surrounded by pseudosteppe at 1,450 m (Goodman *et al.*, 2007b). This species is known to use rock crevices and deeper caves as day roosts (Goodman *et al.*, 2007b). At Antsampandrano, this species was found occupying a day roost in the attic of a building occupied by people. Further, it has been obtained in open dry savanna in the central west of Madagascar (Goodman *et al.*, 2007b).

ROOST:
Wilkinson *et al.* (2012: 160) mention that caves are the typical roosting sites for this species on Madagascar, although it is also found in rocky crevices (Garbutt, 2022: 108).

DIET:
Garbutt (2022: 108) states it presumably feeds on small insects like moths (Lepidoptera), bugs (Hemiptera) and beetles (Coleoptera).

POPULATION:
Structure and Density
There is no information available on the population status of this recently described endemic species (Jenkins *et al.*, 2008f; IUCN, 2009; Monadjem *et al.*, 2017t).

Trend
2016: Unknown (Monadjem *et al.*, 2017t). 2008: Unknown (Jenkins *et al.*, 2008f; IUCN, 2009).

PARASITES:
Dietrich *et al.* (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of spirochaetes of the genus *Leptospira*, which Dietrich *et al.* (2018a: 3) identified as *L. borgpetersenii*.

Ramasindrazana *et al.* (2016: 6) recovered *Litomosa* Clade 1 and 2 (Nematoda: Onchocercidae) from this species.

Tortosa *et al.* (2013: 4) reported the presence of *Penicillidia leptothrinax*, a Nycteribiid bat fly. Ramasindrazana *et al.* (2017: Suppl.) mentioned the bat fly *Nycteribia stylidiopsis* (but the specimen on which this was found - UADBA 43264 - is here considered to be a *M. majori*).

Minozzo *et al.* (2021:7) refer to Ramasindrazana *et al.* (2018) to report the presence o the haemosporidian *Polychromophilus* in this bat species.

VIRUSES:
Astroviridae
Hoarau *et al.* (2021: Suppl.) reported these viruses in organs of bats from Madagascar.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 1 individuals from the Mauritius using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 1 positive results for viral nucleic acids.

2 out of 22 Madagascan specimens tested by Mélade *et al.* (2016b: 4) were positive for paramyxoviruses.

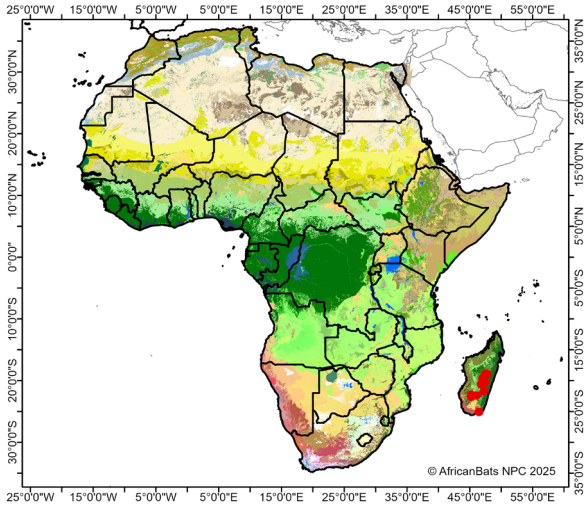

Figure 249. Distribution of *Miniopterus sororculus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Miniopterus villiersi Aellen, 1956

1956. *Miniopterus inflatus villiersi* Aellen, Bull. IFAN, (A) 18: 890. Type locality: Guinea: Dalaba: Grotte du Marché [10 42 N 12 15 W]. [Goto Description]. Holotype: MHNG IFAN 54-1-1: ad ♂. Collected by: Prof. André Villiers; collection date: 16 April 1954; original number: 2839. Former number IFAN: 54-1-1. Paratype: MHNG 983.044: ♂, alcoholic (skull not removed). Collected by: Prof. André Villiers; collection date: 16 April 1954. Paratype: MHNG 983.045: ♀, alcoholic (skull not removed). Collected by: Prof. André Villiers; collection date: 16 April 1954. - Comments: Considered a valid subspecies by Fahr and Ebigbo (2003: 128; 2004: 73), Fahr (2007a: 104). Aellen (1956a: 891) mentions 2 ♂♂ and 5 ♀♀ paratypes.

1965. *Miniopterus schreibersii villiersi:* Koopman, Am. Mus. Novit., 2219: 19. Publication date: 22 June 1965. (Name Combination).

2006. *Miniopterus (schreibersii) villiersi:* Fahr, Djossa and Vierhaus, Rapid assessment of bats (Chiroptera) in Déré, Diécké and Mt. Béro classified forests, southeastern Guinea; including a review of the distribution of bats in Guinée Forestière, 40: 74. (Name Combination).

2006. *Miniopterus villiersi:* Fahr, Djossa and Vierhaus, Rapid assessment of bats (Chiroptera) in Déré, Diécké and Mt. Béro classified forests, southeastern Guinea; including a review of the distribution of bats in Guinée Forestière: 74. (Current Combination).

2017. *Miniopterus screibersii villiersi:* Reardon and Schoeman, Acta Chiropt., 19 (2): Suppl. Publication date: December 2017. (Lapsus).

? *Miniopterus fraterculus villiersi:*

TAXONOMY:
For a long time, *villiersi* was considered to be a synonym or a subspecies of either *M. inflatus*, *M. schreibersii* or *M. natalensis*. Fahr *et al.* (2006a: 74), Weber and Fahr (2006: "4"), Jacobs *et al.* (2008x: 74) and Monadjem *et al.* (2016y: 371) indicated that *villiersi* represents a separate species (restricted to the Upper-Guinea forest zone), a view which is currently gaining support as detailed genetic analyses indicate the presence of multiple taxa in West Africa, and is confirmed by Monadjem *et al.* (2020e: 237, 248).

COMMON NAMES:
German: Lanflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Probably restricted to the Upper-Guinea forest zone, including Guinea (Decher *et al.*, 2016: 274).

ECHOLOCATION:
Monadjem *et al.* (2020e: 248) found that the knee frequency of the echolocation calls from five hand-released *M. villiersi* specimens ranged between 51.1 and 52.4 kHz (average 51.6 kHz).

HABITAT:
Monadjem *et al.* (2016y: 371) recorded *M. (schreibersii) villiersi* from altitudes between 460 and 900m in the Mount Nimba area.

ROOST:
Monadjem *et al.* (2016y: 371) found *Miniopterus (schreibersii) villiersi* roosting in old mine adits in the Mount Nimba area.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
HAEMOSPORIDA
Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Polychromophilus* in three out of 12 investigated *M. villiersi* specimens from West Africa. Rosskopf *et al.* (2018: Suppl.) and Arnuphapprasert *et al.* (2020: Suppl.) also reported *Polychromophilus* sp. in bats from Guinea. Sándor *et al.* (2021b: 7) identified this parasite as *P. melanipherus* Dionisi, 1899 (see also Bajić *et al.*, 2023: Suppl.).

ACARI
Uchikawa (1985a: 19) indicates that *Miniopterus villiersi* is one of the true hosts of "typical" *Calcarmyobia congoensis* Uchikawa, 1982 (Acari: Myobiidae).

DIPTERA
Nycteribiidae
Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Miniopterus* cf. *viliersi* bats from the Mwaluganje Community Elephant Sanctuary: *Nycteribia schmidlii scotti* Falcoz, 1923 and *Penicillidia (Penicillidia) fulvida* (Bigot, 1885). However, given that these records are from Kenya, they most probably do not reprsent true *M. villiersi*.

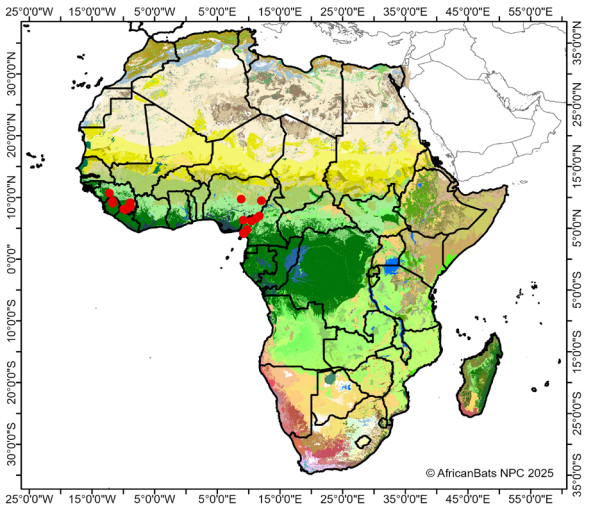

Figure 250. Distribution of *Miniopterus villiersi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Guinea, Liberia, Nigeria, Sierra Leone.

Miniopterus wilsoni Monadjem, Guyton, Naskrecki, Richards, Kropff and Dalton, 2020

*2020. *Miniopterus wilsoni* Monadjem, Guyton, Naskrecki, Richards, Kropff and Dalton, Acta Chiropt., 22 (1): 7, figs 5, 6, 7. Publication date: 3 September 2020. Type locality: Mozambique: Mount Gorongosa [18 28 59 S 034 02 41 E, 920 m]. Holotype: EOWL JAG444: ad ♂, skull and alcoholic. Collected by: Jennifer ("Jen") Anna Guyton; collection date: 22 April 2018. Paratype: EOWL JAG445: ad ♀. Collection date: 22 April 2018. - Etymology: In honour of Edward O. Wilson who has supported and facilitated biodiversity research at Gorongosa National Park over the past decade (Monadjem *et al.*, 2020b: 9).. (Current Combination).

COMMON NAMES:
English: Wilson's Long-fingered Bat

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Based on genetically confirmed specimens, Monadjem *et al.* (2020b: 10) restricted the range of this species to Mount Gorongosa (central Mozambique), but morphologically similar specimens were also recorded from northern Mozambique and southern Malawi. All of the localities are situated on mountains above 1,600 m.

ECHOLOCATION:
Monadjem *et al.* (2020b: 10) reported a F_{peak} of 56.8 ± 0.96 (56 - 58 kHz) for four calls recorded at the type locality and believed to be from this species.

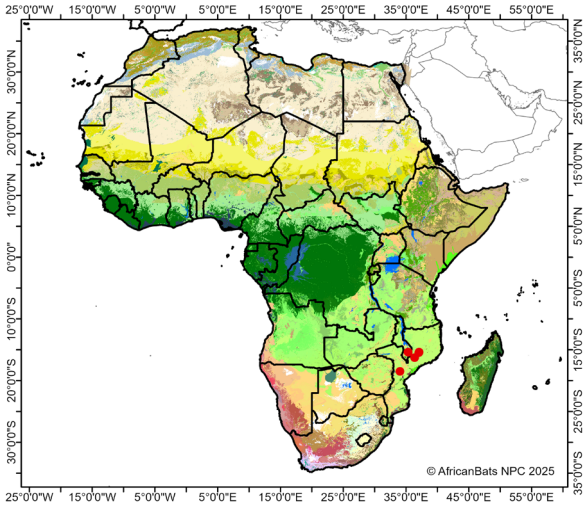

Figure 251. Distribution of *Miniopterus wilsoni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Malawi, Mozambique.

Family MYZOPODIDAE Thomas, 1904

*1904. *Myzopodidae* Thomas, Proc. zool. Soc. Lond., 1904, II, I: 5. Publication date: 1 October 1904. - Comments: Type genus: *Myzopoda* A. Milne-Edwards and A. Grandidier, 1878. (Current Combination).

TAXONOMY:
Although they are currently assigned to different superfamilies, karyotypic data suggest that the closest relatives of the Myzopodidae are the Nycteridae Volleth *et al.* (2020a: 279). Kruskop and Artyushin (2021: 119) assigned the Nycteridae to the Emballonuroidea and the Myzopodidae to an undefined (incertae sedis) superfamily.

Hao *et al.* (2023: 1) suggest that the Myzopodidae should be considered a basal lineage within the Emballonuroidea, having a sister relationship with the Nycteridae and the Emballonuridae.

The analysis of fossil material led Jones *et al.* (2024: 12) to conclude that the Myzopodidae occupy the basal extant branch of the Vespertilionoidea. This is based on three synapomorphies: myotodont lower molars, a tall entocristid on m1-2, and an m3 entocristid that is parallel to the long axis of the tooth.

Currently (Simmons and Cirranello, 2024a) recognized extant genus: ***Myzopoda*** A. Milne-Edwards and A. Grandidier, 1878.
Additionally, there is one extinct genus: †***Phasmatonycteris*** Gunnell, Simmons and Seiffert, 2014.

COMMON NAMES:
Czech: přísavkovcovití, myzopodovití, netopýrkové ušatí. Dutch: Madagassische hechtschijfvleermuizen. English: Sucker-footed Bats. French: Myzopodidés, Vespertilions dorés. German: Madagassische Haftscheibenfledermaus, Madagaskar-Haftscheibenfledermäuse. Norwegian: Sugeskålflaggermus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Butler (1978: 67) suggests that the Myzopodidae are probably of African mainland origin but survive only in Madagascar.

Simmons *et al.* (2013: 146) indicate that one fossil species is known in this family. (Currently three species are known, see below).

The family-level stem and crown ages were calculated by Shi and Rabosky (2015: 1537) as 54.1 and 1.1 mya, respectively.

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) mention a 2*n* value of 26 for the two species in this family.

Genus ***Myzopoda*** Milne-Edwards and A. Grandidier, 1878

*1878. *Myzopoda* A. Milne-Edwards and A. Grandidier, Bull. Sci. Soc. Philom. Paris, sér 7, 2: 220. Publication date: 22 June 1878. - Comments: Type species: *Myzopoda aurita* A. Milne-Edwards and A. Grandidier, 1878. -

Etymology: From the Greek "*μύξάω*", meaning to suck (not from "*μύξα*", meaning mucus) and "*πούς*", meaning foot, referring to the sectional disk on the thumbs and feet (see Palmer, 1904: 446). (Current Combination).

1879. *Myxopoda:* Dobson, Proc. zool. Soc. Lond., 1878, IV: 871. Publication date: April 1879. - Comments: Lapsus (see Allen, 1939a: 82; Schliemann and Maas, 1978: 1) or emendation (see Palmer, 1904: 445). - Etymology: From the Greek "*μύξα*", meaning mucus, and "*πούς*", meaning foot, referring to the sectional disk on the thumbs and feet (see Dobson, 1879a: 281; Palmer, 1904: 445). (Lapsus).

TAXONOMY:

Currently Simmons and Cirranello, 2023b) recognized species of the genus *Myzopoda*: ***aurita*** A. Milne-Edwards and A. Grandidier, 1878; ***schliemanni*** Goodman, Rakotondraparany and Kofoky, 2007.

COMMON NAMES:

Czech: přísavkovci, myzopody. English: Sucker-footed Bats. French: Chauves-souris à ventouses. German: Madagaskar-Haftscheibenfledermäuse.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Butler (1978) found a *Myzopoda* sp. at Olduvai, Kenya, in deposits of early Pleistocene age.

Goodman *et al.* (2022: 1903) indicate that fossils have been identified from the late Eocene and early Oligocene of Egypt, and from the early Pleistocene of Tanzania.

CONSERVATION STATUS:

Assessment History

Global

Assessed as *M. aurita* VU (World Conservation Monitoring Centre, 1993); LC ver 3.1 (2001) (Jenkins *et al.*, 2008h; IUCN, 2009).

Russell *et al.* (2008b: 219) suggests that *Myzopoda* sp. may be among the few Malagasy vertebrate species to benefit from rapid deforestation, due to the species utilizing *Ravenala* as a day roost. *Ravenala* is a dominating pioneering species, and dense stands are found in areas of primary lowland forest which have been cleared (Goodman *et al.*, 2007a).

BIOGEOGRAPHY:

Russell *et al.* (2008b) using coalescent analysis places the time of divergence of *M. aurita* and *M. schliemanni* at approximately 73,500 years ago.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:

A special feature in *Myzopoda* is the presence of adhesive organs on the ventral side of the thumb and the sole. These are flat, diskshaped sessile skin accessories becoming thinner distally and laterally. These pads work by wet adhesion, facilitated by a continuous glandular secretion (Ralisata *et al.* (2022: 1918, 1919)

DENTAL FORMULA:

The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^3/_3$, $M^3/_3$ = 38 (Ralisata *et al.* (2022: 1917).

DETAILED MORPHOLOGY:

Reproductive system

Carter and Enders (2016: 284) found *Myzopoda* sp. to have a smooth chorioallantois, suggesting that this genus belongs in the emballonurid clade.

†***Myzopoda africana*** Gunnell, Butler, Greenwood and Simmons, 2015

*2015. *Myzopoda africana* Gunnell, Butler, Greenwood and Simmons, Am. Mus. Novit., 3846: 1, 3, figs 2A, 2C, 3. Publication date: 16 December 2015. Type locality: Tanzania: Arusha province: Olduvai Gorge: Bed I, FLK NI, Layer 123. - Etymology: The name refers to the African continent as it is the only representative of the genus *Myzopoda* that is found on continental Africa.

SIMILAR SPECIES:

M. africana's humeri are on average 21 % larger than those of its living congeners (Gunnell *et al.*, 2015a: 5).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Timeframe:

Pleistocene (Brown *et al.*, 2019: Suppl.).

Myzopoda aurita Milne-Edwards and A. Grandidier, 1878

*1878. *Myzopoda aurita* A. Milne-Edwards and A. Grandidier, Bull. Sci. Soc. Philom. Paris, sér 7, 2: 220. Publication date: 22 June 1878. Type locality: Madagascar: "Madagascar". Holotype: MNHN ZM-MO-1997-770: alcoholic (skull not removed). Number 223 in Rode (1941); see Peterson *et al.* (1995: 139). (Current Combination).

1879. *Myxopoda aurita:* Dobson, Proc. zool. Soc. Lond., 1878, IV: 879. Publication date: April 1879. (Lapsus).

TAXONOMY:
See Schliemann and Maas (1978: 116).

COMMON NAMES:
Czech: přísavkovec ušatý, netopýrek ušatý, myzopoda ušatá. English: Golden Bat, Old World Sucker-footed Bat, Sucker-footed Bat, Madagascar Sucker-footed Bat, Eastern Sucker-footed Bat. French: Chauve-souris malgache à pieds à ventouses, Chauve-souris à pieds à ventouses de Madagascar, Vespertilion Doré, Myzopoda oreillard, Chauves-souris à ventouses de Madagascar. German: Östliche Haftscheibenfledermaus.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) because it is widespread, thought to be locally common in areas of anthropogenic disturbance, and there are no obvious major threats (Jenkins *et al.*, 2008h; IUCN, 2009; Monadjem *et al.*, 2017p).

Ralisata *et al.* (2010) refute the suggestion that this species is rare (Hutson *et al.*, 2001).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017p). 2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008h; IUCN, 2009). 1996: VU A2c ver 2.3 (1994). 1994: VU (Groombridge, 1994). 1990: VU (IUCN, 1990).

Regional
None known.

MAJOR THREATS:
There are no known major threats to this species. It is occasionally eaten by people when harvesting *Ravenala madagascariensis* plants (Jenkins *et al.*, 2008h; IUCN, 2009; Monadjem *et al.*, 2017p). However, Ralisata *et al.* (2015: 95) do point out that this harvesting itself might lead to a loss of roosts, and as such has a negative impact on the bats.

CONSERVATION ACTIONS:
Jenkins *et al.* (2008h) [in IUCN (2009)] and Monadjem *et al.* (2017p) reported that *M. aurita* has only been recorded from a few protected areas: Parc National de Marojejy (Pont and Armstrong, 1990), Tampolo littoral forest (Ifticene *et al.*, 2005) and near to Parc National de Masoala (Russ and Bennet, 1999) and Réserve Spéciale d'Analamazaotra (Russ and Bennet, 1999). Additional study is needed to develop an understanding of local population densities and precise habitat requirements.

Ralisata *et al.* (2010) indicate that it used disturbed patches of vegetation and is not therefore threatened by deforestation, although it may be affected by loss of roosts for building materials.

GENERAL DISTRIBUTION:
Myzopoda aurita is endemic to the island of Madagascar (Goodman *et al.*, 2007a). It is found in the humid zone of eastern and north-eastern Madagascar and appears to be most common at elevations lower than 500 m (Schliemann and Goodman, 2003) although it has been recorded at Andasibe (ca. 970 m).

Garbutt (2022: 90) also indicated that these bats are found where there are large stands of Traveller's Tree (*Ravenala madagascariensis* - Strelitziaceae) and *Typhonodorum* spp. (Araceae). These trees are generally found in areas where deforestation is acute.

Native: Madagascar.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
For details, see a.o. Thomas (1904g).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_4$, $C^1/_1$, $PM^3/_3$, $M^3/_3$ (see Dobson, 1879a: 872).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 59) described the baculum from two specimens as being a small structure, triangular in shape, without a central shaft (length: 0.21, 0.26 mm; width: 0.15, 0.16 mm). In a third specimen they found a trace of a circular bone structure.

FUNCTIONAL MORPHOLOGY:
Schliemann (1970: 397; 1971; 78) and Schliemann and Goodman (2011: 313) studied the adhesive organs of *Myzopoda*, which are flat, disc-shaped skin duplications, primarily consisting of adipose tissue. He concluded that the static friction between these organs and a vertical surface is sufficient to enable the animals to hold on to this surface.

ECHOLOCATION:
Göpfert and Wasserthal (1995: 2 - 4) reported that this bat uses a complex frequency modulated (FM) echolocation call, consisting of two to four distinct elements of increasing amplitudes and long duration. The second harmonic decreases from 42 to 24 kHz with a shallow FM sweep of about 0.6 to 0.9 kHz/ms during the first three elements and a steeper sweep (2 kHz/ms) during the final element. The duration of the calls varied

between 12 and 23 ms, and call intervals were between 11 and 108 ms.

Altringham (2011: 95) mentioned that the functional value of such a complex call design is unknown.

MOLECULAR BIOLOGY:
Karyotype
Richards *et al.* (2010) examined two females showing a 2*n*=26 and a Fna=48, with all chromosomes being bi-armed. FISH with *Myotis* probes revealed a X-autosome translocation. However, the autosome translocated to the X chromosome has not been counted for the Fna. The number of autosomal arms would then be 50 instead of 48.

Genetics
See Hoofer and Van Den Bussche (2003) and Russell *et al.* (2008b).

HABITAT:
Myzopoda aurita is widespread in intact to degraded and fragmented forests, marshes, agricultural areas, and rice paddies at low to mid elevations in eastern Madagascar (Crowley and Goodman, 2025: 4).

HABITS:
Compositional analysis revealed that *M. aurita* males selected coffee plantations, degraded humid forest and wooded grasslands more than other habitats (Ralisata *et al.*, 2010).

ROOST:
Ralisata *et al.* (2010) found 133 roosts consisting of the partially unfurled leaves of *Ravenala madagascarensis* (Sonn, 1782) and housing between nine and 51 individuals, which changed roosts every 1 - 5 days. Ralisata *et al.* (2015: 95) found that the leaves of the tree became available as roost between one and 19 days after the unfurling started and were inhabited between one and 12 days. Males and females roost separately (Garbutt, 2022: 91).

Ralisata *et al.* (2022: 1921) report roosting groups of between 1 and 36 bats.

DIET:
Göpfert and Wasserthal (1995) noted that *M. aurita* - based on the analysis of faecal pellets of a single individual from north of Tolagnaro, southeast Madagascar - fed on smaller moths ("microlepidoptera"). Ralisata *et al.* (2010) found the diet comprised mainly of Lepidoptera and Coleoptera. The latter was confirmed by Rasoanoro *et al.* (2015: 64), who mention the following volume percentages: Aranea: 15.4 ± 2.38, Coleoptera: 26.7 ± 4.60, Diptera: 3.6 ± 3.59, Homoptera: 0.3 ± 0.33, Hymenoptera: 8.4 ± 3.58, Lepidoptera: 40.1 ± 7.31, and Neuroptera: 5.5 ± 5.07.

Ramasindrazana *et al.* (2009: 161) reported the following percentage frequency / percentage volume: Lepidoptera (100 / 60.4 ± 9.54), Coleoptera (54.5 / 19.4 ± 8.44), Blattaria (54.5 / 19.0 ± 6.32) and Aranea (9.1 / 1.2 ± 1.21).

POPULATION:
Structure
See Russell *et al.* (2008b: 219).

Density
Russell *et al.* (2008b) estimated an effective population size of between 100,054 and 132,742 individuals. In some areas, *M. aurita* is locally common (P. A. Racey, *pers. comm.*), but it is rarely trapped in large numbers during surveys (Russ and Bennet, 1999; Ifticene *et al.*, 2005; Rakotondraparany and Medard, 2005; Jenkins *et al.*, 2007b). Ralisata *et al.* (2010) caught on average of 5.7 (0 - 15) individuals per mist net night, at Kianjavato, where a total of 138 individiuals were captured on 24 nights of netting.

Trend
2016: Unknown (Monadjem *et al.*, 2017p). 2008: Unknown (Jenkins *et al.*, 2008h; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Ralisata *et al.* (2010) found that the foraging areas used by male bats varied between 7 and 108 ha (100 % minimum convex polygon), where the bats foraged close to the roost for the first hour after emergence, then travelled up to 1.8 km away and returned after 03h00.

REPRODUCTION AND ONTOGENY:
See Carter *et al.* (2008).
Ralisata *et al.* (2010) suggest that juvenile males leave their mothers after weaning and join adult males. During October-November, the testes of males appeared larger than at other times of the year, although seasonal variation was not pronounced (Ralisata *et al.*, 2010). Juveniles were caught in February-March and October-November (Garbutt, 2022: 91).

PARASITES:
Ralisata *et al.* (2010) did not observe any parasties on the 138 individual males captured.

UTILISATION:
In the area around Tampolo forest, people collecting leaves of the Traveller's palm (*Ravenala madagascariensis*) for housing materials often encounter *M. aurita* roosting in the

leaves, although no evidence that the bats were deliberately sought, they were collected and taken back to the village where they were cooked and eaten (Jenkins and Racey, 2008).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

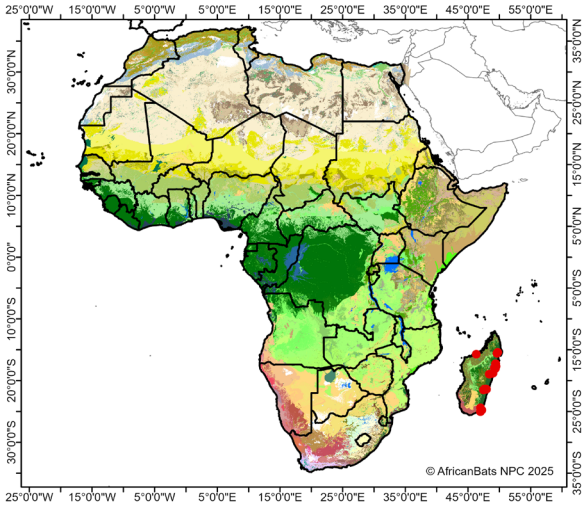

Figure 252. Distribution of *Myzopoda aurita*.

Myzopoda schliemanni Goodman, Rakotondraparany and Kofoky, 2007

*2007. *Myzopoda schliemanni* Goodman, Rakotondraparany and Kofoky, Mamm. biol., 72 (2): 65, 68, figs 2 - 5. Publication date: 26 March 2007. Type locality: Madagascar: Mahajanga province: Parc National d'Anarafantsika: Ampijoroa, forestry station: Jardin Botanique A [16 19.4 S 46 48.4 E, 160 m]. Holotype: FMNH 177327: ad ♂, skin and skeleton and skull and tissue. Collected by: Steven M. Goodman; collection date: 18 April 2003; original number: SMG-13624. 3 male and 4 female paratypes listed. - Etymology: The species name was chosen to honour Professer Dr. Harald Schliemann, University of Hamburg, in recognition of his long interest in sucker-footed bats, including several important anatomical studies (e.g. Schliemann, 1971; 2003). (Current Combination).

2016. *Myz[opoda] schleimanni:* Cardiff and Jenkins, Less. Conserv., 6: 90. Publication date: January 2016. (Lapsus).

2016. *Myzopoda scliemanni:* Amador, Moyers Arévalo, Almeida, Catalano and Giannini, J. mamm. Evolut., 25 (1): Suppl (for 2018). (Lapsus).

TAXONOMY:
Described by Goodman *et al.* (2007a) using external measurements and pelage coloration and supported by population genetics (Russell *et al.*, 2008b).

COMMON NAMES:
Czech: přísavkovec bělobřichý. English: Schliemann's Sucker-footed Bat. French: Chauve-souris à ventouses de Schliemann. German: Schliemanns Haftscheibenfledermaus.

ETYMOLOGY OF COMMON NAME:
The species name was chosen to honour Professor Dr. Harald Schliemann, University of Hamburg, in recognition of his long interest in sucker-footed bats, including several important anatomical studies (e.g., Schliemann, 1970, 1971).

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) as it has a relatively large geographic range and population size, and like other *Myzopoda* is thought to do well in highly modified habitats. It is unlikely to have been negatively impacted by deforestation (Jenkins *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017q). However, it will be important to obtain information on the local abundance of this species (Monadjem *et al.*, 2017q).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017q). 2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008l; IUCN, 2009). 2004: Not assessed but see Goodman *et al.* (2007a), who discuss the possible conservation status.

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known because of a lack of information on habitat preferences (Jenkins *et al.*, 2008l; IUCN, 2009). Russell *et al.* (2008b) consider bats of the genus *Myzopoda* to benefit from deforestation.

CONSERVATION ACTIONS:
Myzopoda schliemanni has been trapped in Parc National de Namoroka and Parc National

d'Ankarafantsika (Goodman *et al.*, 2007a) as well as a recently created protected area in the Lac Kinkony - Mahavay area (Rakotoarivelo and Randrianandrianina, 2007). Based on current information this is a restricted-range species for which there are few data on natural history or ecology and basic field research is clearly needed to obtain information on the local abundance of this species (Jenkins *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017q).

It was not found during surveys of Parc National du Tsingy de Bemaraha (Kofoky *et al.*, 2007), Parc National de Kirindy-Mité (Goodman *et al.*, 2005a; Andriafidison *et al.*, 2006a) or Kirindy CFPF (Goodman *et al.*, 2005a).

GENERAL DISTRIBUTION:
Myzopoda schliemanni is known from central western Madagascar in lowland areas from Ankaboka in the north (Goodman *et al.*, 2007a) to Andranomanintsy in the south (Russell *et al.*, 2008b). Goodman *et al.* (2007a) suggested that the distribution of range of *M. schliemanni* is broader than currently known and may extend north as far as Ambanja. They are found at altitudes of up to 200 m and in marshes dominated by *Bismarckia* palms (Garbutt, 2022: 92).

Native: Madagascar.

GEOGRAPHIC VARIATION:
See Goodman *et al.* (2007a).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Goodman *et al.* (2007a).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2007a).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 59) found in four specimens a triangular-shaped baculum, which was slightly more elongated than in *M. aurita* (length: 0.26 ± 0.078 mm, width: 0.12 ± 0.017 mm) and in a fifth specimen, the baculum was morphologically similar to that of the latter species.

Other
For a description of the crania, teeth, postcranial skeleton, ears and tragus see Goodman *et al.* (2007a).

SEXUAL DIMORPHISM:
Goodman *et al.* (2007a) found there is no sexual dimorphism in *M. schliemanni*.

MOLECULAR BIOLOGY:
Genetics
Russell *et al.* (2008b).

HABITAT:
There are few accounts of its foraging habitats, although Rakotoarivelo and Randrianandrianina (2007) mist-netted 16 individuals in relatively disturbed forest.

HABITS:
See Goodman *et al.* (2007a).

ROOST:
Kofoky *et al.* (2006) observed *M. schliemanni* roosting in a cave. There are no other published observations of this species' roosting preferences, although it is assumed to also use broad-leaved plants such as *Ravenala madagascariensis* (Strelitziaceae) (Goodman *et al.*, 2007a; Russell *et al.*, 2008b). Garbutt (2022: 92) mention they primarily roost in furled fronds of Bismarck Palms (*Bismarckia nobilis*), and frequently change roosts. Each palm tree can house 1 to 12 bats.

Ralisata *et al.* (2022: 1921) mention roosting groups of between 1 and 32 individuals.

DIET:
Rajemison and Goodman (2007) collected feacal samples from 18 individuals during mid-October from Andranomanitsy Forest, western Madagascar, where they reported four different insect orders. Prey belonging to the orders Lepidoptera and Blattaria were the most common in the samples and were more or less equally represented (Rajemison and Goodman, 2007).

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of one individual in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

POPULATION:
Structure
In Andranomanintsy forest, 8 of the 18 bats captured were males indicating a sex ratio of 1 : 1.25 (Goodman *et al.*, 2007a: 312).

Density
Estimated effective population size using demographic models from two sites was between 61,453 and 134,630 individuals (Russell *et al.*, 2008b). A roosting colony of 4 individuals was reported from a cave in Parc National de Namoroka (Kofoky *et al.*, 2006).

Trend
2016: Unknown (Monadjem *et al.*, 2017q). 2008: Unknown (Jenkins *et al.*, 2008l; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Rajemison and Goodman (2007) suggest that *M. schliemanni* is capable of gleaning prey from vegetation (see Diet).

REPRODUCTION AND ONTOGENY:
See Goodman *et al.* (2007a) and Carter *et al.* (2008).

Pregnant females were captured between late October and mid December, and births occurred between late November and early December (Garbutt, 2022: 92).

PARASITES:
Ralisata *et al.* (2022: 1921) mention the presence of unidentified bat flies.

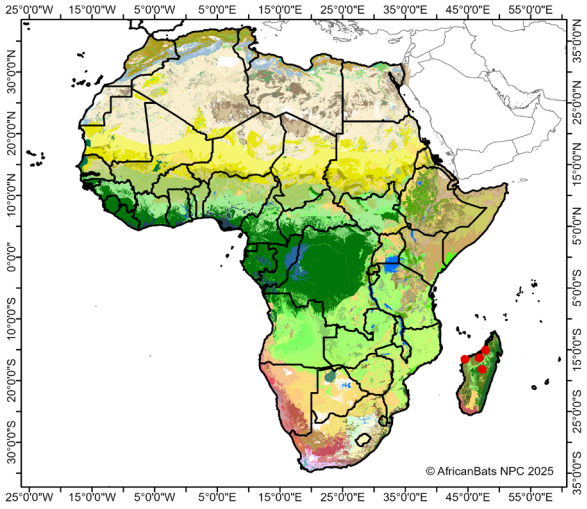

Figure 253. Distribution of *Myzopoda schliemanni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

†Genus ***Phasmatonycteris*** Gunnell, Simmons and Seiffert, 2014

*2014. *Phasmatonycteris* Gunnell, Simmons and Seiffert, PLoS ONE, 9 (2): e86712: 6. Publication date: 4 February 2014. - Etymology: From the Greek "Phasma(to)" for apparition or spectre, in reference to the long ghost lineage connecting Fayum myzopodids with extant forms, and the Greek "Nykteris" for bat (see Gunnell *et al.*, 2014: 7). - ZooBank: 693EEE77-DD52-408B-B404-B689A43706AC. (Current Combination).

TAXONOMY:
Currently recognized species of the genus *Phasmatonycteris*: ***†butleri*** Gunnell, Simmons and Seiffert, 2014. ***†phiomensis*** Gunnell, Simmons and Seiffert, 2014.

†***Phasmatonycteris butleri*** Gunnell, Simmons and Seiffert, 2014

*2014. *Phasmatonycteris butleri* Gunnell, Simmons and Seiffert, PLoS ONE, 9 (2): e86712: 1, 7, figs 3A, 4. Publication date: 4 February 2014. Type locality: Egypt: Western Desert: Fayum Depression: Birket Qarun Formation: Fayum Quarry BQ-2 (23 metre level). - Etymology: In honour of Percy Butler, in recognition of his work on fossil bats from Africa and of his 75 year publishing career (see Gunnell *et al.*, 2014: 7). - ZooBank: E6B5FFD8-5250-4C2A-B83F-CC469DD32557. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
The type specimen was found in the 23 metre level layer at Fayum Quarry BQ-2. This layer is about 37 million year old (Late Eocene, Priabonian - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Native: Egypt.

†***Phasmatonycteris phiomensis*** Gunnell, Simmons and Seiffert, 2014

*2014. *Phasmatonycteris phiomensis* Gunnell, Simmons and Seiffert, PLoS ONE, 9 (2): e86712: 1, 6, figs 2A–D, 3C, E–G. Publication date: 4 February 2014. Type locality: Egypt: Western Desert: Fayum Depression: Fayum Quarry I (242 m level). - Etymology: From "Phiom," Greek for the Fayum Region of Egypt's Western Desert (see Gunnell *et al.*, 2014: 7). - ZooBank: 94812861-7911-438E-BD80-AB849541605B. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
The type material was found in the 242 meter level Fayum Quarry I, in a layer of about 30 million years old (Early Oligocene, Rupelian - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Egypt.

†Family PHILISIDAE Sigé, 1985

1985. *Philisidae* Sigé, 19: ?.

TAXONOMY:
Ravel *et al.* (2014) confirmed the family status of the Philisidae within the superfamily Vespertilionoidae based on a cladistic assessment of the dental data, and that they represent the earliest offshoot of this superfamily (p. 698).

Sigé (1985) [in Ravel *et al.* (2014: 696)] concluded that the Philisidae could have originated in Late or Middle Eocene from a generalized Vespertilionidae after the divergence between the Molossidae and the Vespertilionidae *sensu lato*.

Ravel *et al.* (2012) suggested that *Philisis* and *Dizzya* were probably split of from the third genus of the family (*Witwatia*) in the Early Eocene. Ravel *et al.* (2012: 699), however, doubt the close relationship between the two former genera.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
According to Ravel *et al.* (2014: 691), Philisids were among the most common African bats in the Palaeogene (66 to 23.03 mya). They were found in the Late Eocene - Early Oligocene deposits of the Fayum Depression in Egypt, together with extant bat families, such as Rhinopomatidae, Megadermatidae, Emballonuridae and Myzopodidae (Sigé, 1985; Gunnell *et al.*, 2008, 2014).

†Genus ***Dizzya*** Sigé, 1991

*1991. *Dizzya* Sigé, N. Jb. Geol. Paläont. Abh., 182: ?. - Comments: Type species - *Dizzya exultans* Sigé, 1991.

TAXONOMY:
Currently recognized species of *Dizzya*: ***†exsultans*** Sigé 1991.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Early. Eocene.

DENTAL FORMULA:
Ravel *et al.* (2011: 402) indicate that *Dizzya* differs from the other Philisidae in showing a nyctalodont molar structure.

†***Dizzya exsultans*** Sigé, 1991

*1991. *Dizzya exsultans* Sigé, N. Jb. Geol. Paläont. Abh., 182: ?. Type locality: Tunisia: Chambi. - Comments: Marandat (1994: 62) mentions the holotype to consist of a right M^1 or M^2.

. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Eocene (Ypresian - Brown *et al.*, 2019: Suppl.).

DETAILED MORPHOLOGY:
Ravel *et al.* (2014: 694) indicate that *Dizzya exsultans* is the smallest representative of the Philisidae. Together with *Witwatia sigei*, it is also the oldest. Based on data from Gunnell *et al.* (2009), Ravel *et al.* (2014: 702) estimated the body weight for this bat to be about 8.6 to 9.1 g.

†Genus ***Khonsunycteris*** Gunnell, Simons and Seiffert, 2008

*2008. *Khonsunycteris* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 8. - Comments: Type species - *Khonsunycteris aegypticus* Gunnell, Simons and Seiffert, 2008. - Etymology: Khonsu, Egyptian God of the Moon, in reference to the nocturnal habits of vesper bats (Gunnell *et al.*, 2008).

TAXONOMY:
See Gunnell *et al.* (2008).

Jones *et al.* (2024: 14) transferred this genus from the Vespertilionidae to the Philisidae based on synapomorphies (with *Witwatia*) including a lower

† Phasmatonycteris phiomensis

canine lacking a posterobasal cusp, myotodont lower molars, and m1-2 with large hypoconulids. However, they also point out that this genus' position within either the Philisidae, Vespertilioinidae (or wherever within the Chiroptera) will need additional material, including the upper molars.

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Gunnell *et al.* (2017: 9) indicate that *Khonsunycteris* might be the earliest known myotine bat.

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

DENTAL FORMULA:
Jones *et al.* (2024: 14) mention that *Khonsunycteris* possesses myotodont lower molars and three premolars, including a large, single-rooted p2 and reduced, double-rooted p3.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

†***Khonsunycteris aegypticus*** Gunnell, Simons and Seiffert, 2008

*2008. *Khonsunycteris aegypticus* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 8, fig 8. Type locality: Egypt: Fayum Depression: Quarry L-41: Lower Sequence, Jebel Qatrani Formation. Holotype: CGM 83673. Left dentary c1-m2. - Comments: latest Eocene, Priabonian. - Etymology: Name for Egypt (Gunnell *et al.*, 2008). (Current Combination).
2016. *Khonsunycteris aegyptiacus:* Hand, Sigé, Archer and Black, Palaeovert., 40 (2) e2: 7. Publication date: 1 August 2016. (Lapsus).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Late Eocene (Priabonian - 37.97 - 33.23 - Brown *et al.*, 2019: Suppl.).

GENERAL DISTRIBUTION:
Native: Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

†Genus ***Philisis*** Sigé, 1985

*1985. *Philisis* Sigé, Geol. Palaeontol., 19: ?. - Comments: Type species - *Philisis sphingis* Sigé, 1985. (Current Combination).

TAXONOMY:
May be a junior synonym of *Provampyrus*.

Ravel *et al.* (2014: 699) indicate that the genus might be paraphyletic.

Currently recognized species of *Philisis*: †*sevketi* Sigé, Thomas, Sen, Gheerbrant, Roger & Al-Sulaimani 1994 - Oman; †***sphingis*** Sigé 1985.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Ravel *et al.* (2014: 699) indicate that fossils of this genus were only found in deposits dating from the Early Oligocene.

†***Philisis sphingis*** Sigé, 1985

*1985. *Philisis sphingis* Sigé, Geologica et Palaeontologica, 19: ?. Holotype: YPM MAM 034488. Right maxilla (P^4-M^3): see Gunnell *et al.* (2008: 2). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Oligocene (Rupelian - 32.46 - 29 mya) (see Brown *et al.*, 2019: Suppl.).

DETAILED MORPHOLOGY:
Based on data from Gunnell *et al.* (2009), Ravel *et al.* (2014: 702) estimated the body weight for this bat to be between 36 to 74 g.

†Genus ***Witwatia*** Gunnell, Simons and Seiffert, 2008

*2008. *Witwatia* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 2. - Comments: Type species - *Witwatia schlosseri* Gunnell, Simons and Seiffert, 2008. - Etymology: *Wit Wat*, Egyptian Arabic for large, flapping wings (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

Ravel *et al.* (2014: 702) mention that the differences between *W. schlosseri* and *W. eremicus* (both found in the same locality: BQ2, Fayum, Egypt), might be attributed to the presence of a sexual dimorphism, where the former might represent the larger female and he latter the smaller male. But they also indicate that this is currently speculative.

Jones *et al.* (2024: 17) indicate that there might still be some uncertainty to its association with the Philisidae

Currently recognized species of the genus *Witwatia*: †***eremicus*** Gunnell, Simons and Seiffert, 2008; †***schlosseri*** Gunnell, Simons and Seiffert, 2008; †***sigei*** Ravel, Marivaux, Tabuce, Bel Haj Ali, Essid, and Vianey-Liaud, 2012.

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe - Ravel *et al.* (2014: 699) indicate that fossils were found dating back between the early and latest Eocene.

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Simmons and Jones (2024: 16) estimated that some members of this genus might have attained a weight between 40 and 116 g.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

DIET:
Simmons and Jones (2024: 16) [referring to Ravel *et al.* (2011,2014)] indicate that Witwatia species could possibly have fed on small vertebrates, at least opportunistic. Similarly, they might have consumed fruits too.

†***Witwatia eremicus*** Gunnell, Simons and Seiffert, 2008

*2008. *Witwatia eremicus* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 3, 4, 5. Type locality: Egypt: Fayum Depression: Quarry BQ-2: Umm Rigl Member of the Birket Qurun Formation. - Etymology: *Eremikos*, Greek for solitude, in reference to the vast solitude of the Egyptian Western Desert (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Earliest Late Eocene (Priabonian - Brown *et al.*, 2019: Suppl.), Umm Rigl Member of the Birket Qarum formation.

GENERAL DISTRIBUTION:
Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

DETAILED MORPHOLOGY:
Based on data from Gunnell *et al.* (2009), Ravel *et al.* (2014: 702) estimated the body weight for this bat to be about 40 to 98 g.

†*Witwatia schlosseri* Gunnell, Simons and Seiffert, 2008

*2008. *Witwatia schlosseri* Gunnell, Simons and Seiffert, J. Vert. Paleont., 28 (1): 2, 3, fig 3D. Type locality: Egypt: Fayum Depression: Quarry BQ-2: Umm Rigl Member of the Birket Qarun Formation. Holotype: CGM 83668. Left dentary (c1-m3): see Gunnell *et al.* (2008: 3). - Etymology: Specific name for Max Schlosser who described the first fossil bat from the Fayum (Gunnell *et al.*, 2008). (Current Combination).

TAXONOMY:
See Gunnell *et al.* (2008).

SIMILAR SPECIES:
See Gunnell *et al.* (2008).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
See Gunnell *et al.* (2008).

Timeframe:
Earliest Late Eocene (Priabonian - Brown *et al.*, 2019: Suppl.), Umm Rigl Member of the Birket Qarum formation.

GENERAL DISTRIBUTION:
Native: Egypt (Gunnell *et al.*, 2008).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Gunnell *et al.* (2008).

DETAILED MORPHOLOGY:
Based on data from Gunnell *et al.* (2009), Ravel *et al.* (2014: 702) estimated the body weight for this bat to be between 57 and 116 g.

†*Witwatia sigei* Ravel, Marivaux, Tabuce, Bel Haj Ali, Essid and Vianey-Liaud, 2012

*2012. *Witwatia sigei* Ravel, Marivaux, Tabuce, Bel Haj Ali, Essid and Vianey-Liaud, Palaeontology, 55 (5): 1035, 1036, fig 2. Publication date: 18 September 2012. Type locality: Tunisia: Kasserine area: Chambi. Holotype: ONM CB1-230: unknown / no information. Left upper molar (M2), see Ravel *et al.* (2012: 1036). - Etymology: In honour of Bernard Sigé, who first extensively described Paleogene bats remains, including those from Chambi (see Ravel *et al.*, 2012: 1036). (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Eocene (Ypresian - Brown *et al.*, 2019: Suppl.).

DETAILED MORPHOLOGY:
Based on data from Gunnell *et al.* (2009), Ravel *et al.* (2014: 702) estimated the body weight for this bat to be about 100 g.

Family VESPERTILIONIDAE J. E. Gray, 1821

1815. *Vespertilia* Rafinesque, Analyse de la Nature, 54. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Conserved by Direction 98 (IUCN , 1958), which also corrected the name to Vespertilionidae. Originally included the subfamilies Lophinia (Rafinesque, 1815) [including the genera *Rhinolophus* Lacépède, 1799; *Phyllostoma* G. Cuvier, 1800 [= *Phyllostomus* Lacépède, 1799]; *Vampyrum* Rafinesque, 1815; and *Megaderma* É. Geoffroy, 1810]; and Nycteria (Rafinesque, 1815) [including the genera *Pteropus* Brisson, 1762; *Eidolon* Rafinesque, 1815; *Pteronotus* Rafinesque, 1815; *Cephalotes* É. Geoffroy, 1810 [= *Nyctimene* Borkhausen, 1797]; *Tadaris* [sic = *Tadarida*] Rafinesque, 1814; *Vespertilio* Linnaeus, 1758; *Nycterus* [sic = *Nycteris*] É. Geoffroy and G. Cuvier, 1795; *Noctilio* Linnaeus, 1766; *Molossus* É. Geoffroy, 1805; and *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825: 36]] (see Jackson and Groves, 2015: 264).

*1821. *Vespertilionidæ* J. E. Gray, London Med. Repos., 15: 299. Publication date: 1 April 1821. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Dobson (1878: 167) refers to Dobson, 1875 (p. 347), indicating that Gray's (1866) definition includes genera beloning to very distinct families. Originally included the genera *Megadermes* [sic = *Megaderma*] É. Geoffroy, 1810; *Rhynolophus* [sic = *Rhinolophus*] Lacépède, 1799; *Nycterus* [sic = *Nycteris*] É. Geoffroy and G. Cuvier, 1795; *Rhynopoma* [sic = *Rhinopoma*] É. Geoffroy, 1818; *Thaphosores* [sic = *Taphozous*] É. Geoffroy, 1818; *Vespertilio* Linnaeus, 1758; *Pecotus* [sic = *Plecotus*] É. Geoffroy, 1818; and *Barbastella* J. Gray, 1821 (see Jackson and Groves, 2015: 264). The name was conserved by Direction 98 (ICZN, 1958: 131). (Current Combination).

1825. *Vespertilionina* J. E. Gray, Ann. Philos., 10 (5): 339. Publication date: November 1825. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Originally include the genera *Vespertilio* Linnaeus, 1758; *Plecotus* É. Geoffroy, 1818; *Barbastellus* J. Gray, 1825 [= *Barbastella* J. Gray, 1821]; *Proboscidea* Spix, 1823 [= *Rhynchonycteris* Peters, 1867; *Thyroptera* Spix, 1823; and *Caelano* [sic = *Celaeno*] Leach, 1821 [= *Noctilio* Linnaeus, 1766: 88] (see Jackson and Groves, 2015: 264).

1843. *Gymnorhina* Wagner.

1855. *Nycticeina* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool, ???. Publication date: 23 July 1856.

1866. *Nyctophilina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 91. Publication date: 1 February 1866.

1866. *Plecotina* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 91. Publication date: 1 February 1866.

1866. *Romiciana* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 90. Publication date: 1 February 1866.

1866. *Vespertiliones* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 524. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Originally included the genera *Synotus* Keyserling & Blasius, 1839 [= *Barbastella* J. Gray, 1821]; *Plecotus* É. Geoffroy, 1818; *Histiotus* Gervais, 1855; *Otonycteris* Peters, 1859; *Miniopterus* Bonaparte, 1837; *Vespertilio* Linnaeus, 1758; *Vesperugo* Keyserling and Blasius, 1839 [= *Vespertilio* Linnaeus, 1758]; *Vesperus* Keyserling and Blasius, 1839 [= *Vespertilio* Linnaeus, 1758]; *Murina* J. Gray, 1842; *Harpiocephalus* J. Gray, 1842; *Nycticejus* [sic = *Nycticeius*] Rafinesque, 1819]; *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825]; *Thyroptera* Spix, 1823; and *Antrozous* H. Allen, 1862 (see Jackson and Groves, 2015: 265). Jackson and Groves (2015: 227) consider this (family) name a homonym of Vespertiliones Pallas, 1767, and indicated that it covers the Vespertionidae family, rather than the Vespertilioninae subfamily. Not Vespertiliones Dobson, 1878, a group name for the subfamily Vespertilioninae.

1869. *Gymnorhinidæ* Fatio, Faune des Vertébrés de la Suisse.

1872. *Vespertilionidae:* Gill, Smiths. Misc. Coll., 11 (1): 17. Publication date: November 1872. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Originally included the subfamilies Vespertilioninae J. Gray, 1821 and Nycticejinae Gill, 1872 (see Jackson and Groves, 2015: 265).

1893. *Nycteridae:* Schulze. - Comments: Not of Van der Hoeven, 1855. Not of Dobson, 1875 (see Pavlinov *et al.*, 1995: 93).

1893. *Vespertilionini:* Winge, Samling af Afhandlinger. E Museo Lundii, 2 (1): 24. - Comments: Introduced as tribe (?). Jackson and Groves (2015: 265) (erroneously?) mention *Emballonura* Temminck, 1838 as type genus. Originally included the genera *Vespertilio* Linnaeus, 1758 [including the subgenera *Kerivoula* J. Gray, 1842; *Natalus* J. Gray, 1838; and *Nyctiellus* Gervais, 1855]; *Plecotus* É. Geoffroy, 1818; *Minyopterus* Agassiz, 1846 [= *Miniopterus* Bonaparte, 1837]; *Lasionycteris* Peters, 1865; *Vesperugo* Keyserling and Blasius, 1839 [= *Vespertilio* Linnaeus, 1758]; *Harpyiocephalus* J. Gray, 1866 [= *Harpiocephalus* J. Gray, 1842]; *Synotus* Keyserling & Blasius, 1839 [= *Barbastella* Gray, 1821]; *Chalinolobus* Peters, 1865; *Otonycteris* Peters, 1859; *Nyctophilus* Leach, 1821; *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825]; and *Antrozous* H. Allen, 1862 (see Jackson and Groves, 2015: 265).

1907. *Nyctophilinæ* Miller, Bull. U.S. natl. Mus., 57: xi, *234*. Publication date: 29 June 1907. - Comments: Type genus: *Nyctophilus* Leach, 1821. Originally included the genera *Antrozous* H. Allen, 1862 and *Nyctophilus* Leach (see Jackson and Groves, 2015: 270).

1942. *Myotini* Tate, Bull. Am. Mus. Nat. Hist., 80 (7): 221, 229. Publication date: 27 November 1942. - Comments: Type genus: *Myotis* Kaup, 1829. Introduced as tribe, and originally included the genera *Myotis* Kaup, 1829; *Lasionycteris* Peters, 1865; *Plecotus* É. Geoffroy, 1818; *Corynorhinus* H. Allen, 1865; *Idionycteris* Anthony, 1923; and *Euderma* H. Allen, 1891 (see Jackson and Groves, 2015: 280).

2008. *Vespertolionidae:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Lapsus).

2018. *Vespertilionnidae:* Malekani, Musaba, Gembu, Bugentho, Toengaho, Badjedjea, Ngabu, Mutombo, Laudisoit, Ewango, Van Cakenberghe, Verheyen, Asimonyo, Masudi, Bongo and Ngbolua, Nat. Conserv. Res., 3 (1): 67. Publication date: January 2018. (Lapsus).

2024. *Vespertlionidae:* Rihane, Nahli, Laghzaoui, Dbiba, Radi, Dakki, El Mouden and El Hamoumi, Ostrich, 95 (3): 224. Publication date: 11 October 2024. (Lapsus).

2025. *Vespertiliondae:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: 1. Publication date: 18 July 2025. (Lapsus).

? *Vespertilioninae sp.:*

TAXONOMY:

Systematicians have long recognized that Vespertilionidae as so defined, is diagnosed by few if any apomorphies, and some data have been cited as evidence that the family is not monophyletic. For example, *Tomopeas ravus* (the only member of the subfamily Tomopeatinae) shares immunological affinities and several derived morphological and molecular traits with molossidis (Miller, 1907; Davis, 1970; Barkley, 1984; Pierson, 1986; Sudman *et al.* (1994). Miniopterines, which differ from other vespertilionids in several aspects of foetal development and adult morphology, show immunological affinity with molossids (Mein and Tupinier, 1977; Gopalakrishna and Chari, 1983; Pierson, 1986). Kerivoulines share derived morphological traits with Natalidae, Thyropteridae, Furipteridae, and Myzopodidae (Sigé, 1974; Van Valen, 1979). These patterns have lead various workers to suggest removal of one or more subfamilies from Vespertilionidae (Davis, 1970; Sigé, 1974; Mein and Tupinier, 1977; Van Valen, 1979; Gopalakrishna and Chari, 1983; Barkley, 1984; Sudman *et al.*, 1994). Each of the eight vespertilionid subfamilies just listed appears to be monophyletic, with the exception of Vespertilioninae, which may be paraphyletic. In morphology, Vespertilioninae is "perhaps best characterized by absence of the special modifications that distinguish the other groups" (Miller, 1907: 197). Volleth and Heller, 1994) describe several derived karyotype features that diagnose Vespertilioninae (including Nyctophilinae but exclude Myotinae), but their study did not include any members of Antrozoinae or Lasiurini.

Molecular phylogenetics reviewed by Hoofer and Van Den Bussche (2003).

Roehrs *et al.* (2011: 24) suggest the following subdivision in tribes/groups:
Vespertilionini (*Nyctalus, Pipistrellus, Scotoecus, Vespertilio*)
Hypsugine group (*Chalinolobus, Vespadelus, Hypsugo, Nycticeinops, Neoromicia, Laephotis, Tylonycteris*)

Eptesicini / Nycticeiini (*Arielulus, Lasionycteris, Glauconycteris, Nycticeius, Eptesicus, Scotomanes*)
Perimyotine group (*Parastrellus, Perimytois*)
Scotophilini (*Scotophilus*)
Antrozini (*Antrozous, Rhogeessa, Baeodon*)
Lasiurini (*Lasiurus*)
Plecotini (*Corynorhinus, Otonycteris, Barbastella, Plecotus, Idionycteris*).

Known genera in the subfamily Vespertilioninae:
Tribe Eptesicini Volleth and Heller, 1994 - *Arielulus* Hill and Harrison, 1987; ***Eptesicus*** Rafinesque, 1820; *Hesperoptenus* Peters, 1868.
Tribe Lasiurini Tate, 1942 - *Lasiurus* Gray, 1831.
Tribe Nycticeiini Gervais, 1855 - ***Nycticeinops*** Hill and Harrison, 1987; *Nycticeius* Rafinesque, 1819; *Rhogeessa* H. Allen, 1866; *Scoteanax* Troughton, 1943; ***Scotoecus*** Thomas, 1901; *Scotomanes* Dobson, 1875; ***Scotophilus*** Leach, 1821; *Scotorepens* Troughton,1943.
Tribe Nyctophilini Peters,1865 - *Nyctophilus* Leach, 1821; *Pharotis* Thomas, 1914.
Tribe Pipistrellini Tate, 1942 - *Glischropus* Dobson, 1875; *Nyctalus* Bowditch, 1825; ***Pipistrellus*** Kaup, 1829; *Scotozous* Dobson, 1875.
Tribe Plecotini Gray, 1866 - *Barbastella* Gray, 1821; *Corynorhinus* H. Allen, 1865; *Euderma* H. Allen, 1892; *Idionycteris* Anthony, 1923; ***Otonycteris*** Peters, 1859; ***Plecotus*** E. Geoffroy Saint-Hilaire, 1818.
Tribe Vespertilionini Gray, 1821 - *Chalinolobus* Peters, 1867; *Eudiscopus* Conisbee, 1953; *Falsistrellus* Troughton, 1943; ***Glauconycteris*** Dobson, 1875; *Histiotus* Gervais, 1856; ***Hypsugo*** Kolenati, 1856; *Ia* Thomas, 1902; ***Laephotis*** Thomas, 1901; ***Mimetillus*** Thomas, 1904; ***Neoromicia*** Roberts, 1926; *Philetor* Thomas, 1902; *Tylonycteris* Peters, 1872; *Vespadelus* Troughton, 1943; *Vespertilio* Linnaeus, 1758.

Currently, Simmons and Cirranello (2024a) do not recognize subdivision (subfamilies/tribes) of the family Vespertionidae, but they do recognize the following genera:
- Kerivoulinae Miller, 1907: ***Kerivoula*** Gray, 1842; *Phoniscus* Miller, 1905.
- Murininae Miller, 1907: *Harpiocephalus* Gray, 1842; *Harpiola* Thomas, 1915; *Murina* Gray, 1842.
- Myotinae Tate, 1942: *Eudiscopus* Conisbee, 1953; ***Myotis*** Kaup, 1829; *Submyotodon* Ziegler, 2003.
- Scotophilinae Leach, 1821: ***Scotophilus*** Leach, 1821.
- Vespertilioninae Gray, 1821:
Antrozoini Miller, 1897: *Antrozous* H. Allen, 1863; *Baeodon* Miller, 1906; *Bauerus* Van Gelder, 1959; *Rhogeessa* H. Allen, 1866.
Lasiurini Tate, 1942: *Lasiurus* Gray, 1831.
Nycticeiini Gervais, 1866: *Arielulus* Hill and Harrison, 1987; ***Cnephaeus*** Kaup, 1829; *Eptesicus* Rafinesque, 1820; ***Glauconycteris*** Dobson, 1875; *Hesperoptenus* Peters, 1869; *Histiotus* P. Gervais, 1855; *Ia* Thomas, 1902; *Lasionycteris* Peters, 1866; *Neoeptesicus* Cláudio, Novaes, Gardner, Nogueira, Wilson, Maldonado, Oliveira and Moratelli6, 2023 [described after Simmons and Cirranello (2023b)]; *Nycticeius* Rafinesque, 1819; *Scoteanax* Troughton, 1944; *Scotomanes* Dobson, 1875; *Scotorepens* Troughton, 1944; *Thainycteris* Kock and Storch, 1996.
Pipistrellini (Tate, 1842): *Glischropus* Dobson, 1875; ***Nyctalus*** Bowdich, 1825; ***Pipistrellus*** Kaup, 1829; ***Scotoecus*** Thomas, 1901; *Scotozous* Dobson, 1875, ***Vansonia*** Roberts, 1946.
Plecotini: ***Barbastella*** Gray, 1821; *Corynorhinus* H. Allen, 1865; *Euderma* H. Allen, 1892; *Idionycteris* Anthony, 1923; ***Otonycteris*** Peters, 1860; ***Plecotus*** E. Geoffroy Saint Hilaire, 1818.
Vespertilionini Gray, 1821: ***Afronycteris*** Monadjem, Patterson and Demos, 2020; *Cassistrellus* Ruedi, Eger, Lim and Csorba, 2017; *Chalinolobus* Peters, 1867; *Falsistrellus* Troughton, 1944; ***Hypsugo*** Kolenati, 1856; ***Laephotis*** Thomas, 1901; ***Mimetillus*** Thomas, 1904; *Mirostrellus* Görföl, Kruskop, Tu, Estók, Son and Csorba, 2020; ***Neoromicia*** Roberts, 1926; ***Nycticeinops*** Hill and Harrison, 1987; *Nyctophilus* Leach, 1821; *Pharotis* Thomas, 1914; *Philetor* Thomas, 1902; ***Pseudoromicia*** Monadjem, Patterson, Webala and Demos, 2020; *Tylonycteris* Peters, 1872; *Vespadelus* Troughton, 1944; *Vespertilio* Linnaeus, 1758.
Unassigned to tribe: *Parastrellus* Hoofer, Van Den Bussche and Horáček, 2006; *Perimyotis* Menu, 1984; *Rhyneptesicus* Bianchi, 1917.

Common Names:
Castilian (Spain): Murcielagos chicos, Murciélagos de cola envainada. Czech: netopýrovití, netopýři holonosí. Dutch: Gladneusvleermuizen. English: Evening bats, Vespertilionid bats, Vesper Bats, Plain-faced Bats, Simple-nosed Bats. Finnish: Siipat. French: Vespertilionidés, Chauve-souris vesper. German: Glattnasen, Glattnasen-Fledermäuse. Italian: Vespertiliònidi. Norwegian: Glattneser, Glattneseflaggermus. Polish: mroczkowate. Romanian: Lilieci cu tragus. Russian: Гладконосые. Ukrainian: Лиликові [= Lylykovi]. Vietnamese: Họ dơi muỗi.

Etymology of common name:
Rosevear (1965) uses the colloquial name vesper bats, borrowing it from the name for the family, which is derived from the Latin for a bat,

vespertilio. They are sometimes called 'evening bats' because of their time of activity (Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Shi and Rabosky (2015: 1537) report the family-level stem ages/crown ages for the Vespertilionidae (including Miniopteridae and Cistugidae) to be 52.1 and 51.1 million years ago, respectively.

The oldest African fossil assigned to this family is *Khonsunycteris aegypticus* from the late Eocene (ca. 34 MYA) of the Fayum, Egypt (Hand *et al.*, 2016: 7).

GENERAL DISTRIBUTION:
Luo *et al.* (2019b) investigated the geographic range of 126 vespertilionid bat species (including 20 African) in relation to their wing morphology and found that species with higher wing loading have larger distribution ranges than those with lower wing loading, and that the size of geographic ranges was associated with wing aspect ratio.

DENTAL FORMULA:
Esquivel *et al.* (2021: 1093) found that the Vespertilionidae are one of the families where dental anomalies appear to occur to a greater extent, possibly as they have more complex taxonomic histories and their correct identification heavily depends on dental characters.

MOLECULAR BIOLOGY:
Karyotype
Sotero-Caio *et al.* (2017: 5) indicate that familywide the karyotype has a 2*n* value between 18 and 52.

ROOST:
López-Baucells *et al.* (2018: 30) examined the roost selection by synanthropic bats in rural Madagascar and found that small colonies of vespertilionid bats had a preference for small, traditional houses made of mud and wood, especially if the roof was made from leaves.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention a Vespertiliondae bat taken as prey by a Swamp boubou (*Laniarius bicolor* (Hartlaub, 1857)) in Botswana.

PARASITES:
Fain (1994: 1280) reports that three genera of Myobiidae (Acari) are occurring on members of the Vespertilionidae: *Acanthophthirius*, with 4 subgenera (*Acanthophtirius, Myotimyobia, Chiromyobia, Mimetillobia*) and 47 species, *Pteracarus* with 21 species, and *Calcarmyobia* with 18 species and 8 subspecies. The latter genus is restricted to bats of the genus *Miniopterus*, and since this genus is currently included in a family of its own, this implies that only two genera of Myobiidae parasite on Vespertilionidae.

VIRUSES:
Gutiérrez-Guerrero *et al.* (2020: Suppl. Fig 3A) report that worldwide 33 % of the species belonging to this family are confirmed viral carriers.

A paramyxovirus was detected in one out of nine Vespertilionidae bats sampled in Kirindy in Madagascar (Wilkinson *et al.*, 2014).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Angola, Botswana, Congo (Democratic Republic of the), Ethiopia, Kenya, Morocco, Namibia, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia.

Subfamily Kerivoulinae Miller, 1907

*1907. *Kerivoulinae* Miller, Bull. U.S. natl. Mus., 57: 232. Publication date: 29 June 1907. - Comments: Type genus: *Kerivoula* Gray, 1842. Originally included the genera *Kerivoula* J. Gray, 1842 and *Phoniscus* Miller, 1905 (see Caron *et al.*, 2018: 265).

TAXONOMY:
Known genera in the Kerivoulinae: †***Chamtwaria*** Butler, 1884; ***Kerivoula*** Gray, 1842; *Phoniscus* Miller, 1905.

COMMON NAMES:
Czech: vlnouškové, kerivuly. English: Forest Bats, Woolly bats.

†Genus *Chamtwaria* Butler, 1984

*1984. *Chamtwaria* Butler, Palaeovert., 14 (3): 117, 187. Publication date: 15 November 1984 [Goto Description].

TAXONOMY:
Was assigned to the Vespertilionidae by Beard *et al.* (1992).

Currently recognized species of the genus *Chamtwaria*: †***pickfordi*** Butler, 1984.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe- Early Miocene (Burdigalian).

†***Chamtwaria pickfordi*** Butler, 1984

*1984. *Chamtwaria pickfordi* Butler, Palaeovert., 14 (3): 118, 187, figs 25 A, A'. Publication date: 15 November 1984. Type locality: Kenya: Tinderet (volcano) Region, Songhor, Kapurtay agglomeration: Chamtwara. [Goto Description]. - Etymology: Named after Dr. Martin Pickford. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Miocene (Burdigalian - Brown *et al.*, 2019: Suppl.).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola.

Genus ***Kerivoula*** J. E. Gray, 1842

*1842. *Kerivoula* J. E. Gray, Ann. Mag. nat. Hist., [ser 1], 10 (65): 258. Publication date: 1 December 1842. - Comments: Type species: *Vespertilio pictus* Pallas, 1767. Gray (1842: 258) mentions *Vesp. Hardwickii Horsfield, V. picta* Pallas, *V. tenuis*, G. Gärtneri [and *Kerivoula griseus, Kerivoula Poensis*]. Type species by subsequent designation (Peters, 1867c) (see Corbet and Hill, 1992: 153). Allen (1939a: 100) mentioned *Vespertilio hardwickii* Horsfield as genotype. - Etymology: Rosevear suggested that *Kerivoula* was derived from the Cingalese name for the Painted Bat, kehel vuhla. Flannery (1995a: 369) indicates that it was derived from the Ceylonese for plantain (banana) bat. - Phonetics: ke'-ree-vue'-lah, ke-ree-vool'-ah.

1849. *Kirivoula* Gervais, Dictionnaire Universelle d'Histoire naturelle, 13: 213. Publication date: 1849. - Comments: Emendation (see Meester *et al.*, 1986: 63). (Emendation).

1861. *Nyctophylax* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 42: 390 (for 1860). Publication date: 1861. - Comments: "Apparently based on *Vespertilio tralatitius*, Temminck, 1840 =*V. tralatitius* Horsfield, 1824, an indeterminable name according to Laurie and Hill (1954: 66). According to Palmer (1904), *Nyctophylax* was 'a new name for the barbaric *Kerivoula* Gray, 1842'" (see Corbet and Hill, 1992: 153). Mentioned as a possible synonym (question mark) by Pavlinov *et al.* (1995: 93). - Etymology: From the Greek "*νύξ*" or "*νυκτός*", meaning night and "*φύλαξ*", meaning watcher (see Palmer, 1904: 467).

1870. *Nyctophilax:* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 62 (1): 544. Publication date: November 1870. (Lapsus).

1891. *Cerivoula* Blanford, The fauna of British India, including Ceylon and Burma. Part II, 338. Publication date: 1891. - Comments: Emendation (see Meester *et al.*, 1986: 63). (Emendation).

1904. *Kehelvoulha* Jentink, Notes Leyden Mus., 24 (4): 175 (for 1902). Publication date: 15 Jul 1904. - Comments: *Nomen nudum*. Jentink (1904: 175) suggests that this should be the etymologically correct name, but adds immediately that this name has no taxonomical value whatsoever.

2005. *Keivoula:* Struebig, Rossiter, Bates, Kingston, Sai Sein Lin Oo, Aye Aye Nwe, Moe Moe Aung, Sein Sein Win and Khin Mya Mya, Acta Chiropt., 7 (1): 14. (Lapsus).

? *Kerivoula sp.:*

TAXONOMY:
Phoniscus Miller, 1906, has been included in *Kerivoula* as either a subgenus (Ellerman and Morrison-Scott, 1951; Ellerman *et al.*, 1953) or a synonym (Ryan, 1965). Hill (1965) argues for the generic separation of *Phoniscus* from *Kerivoula*, and this view appears to be widely accepted (Rosevear, 1965; Hayman and Hill, 1971; Corbet and Hill, 1992), but see Koopman (1982).

The species *aerosa* Tomes, 1858, was described from the east coast of South Africa, but Roberts (1951: 76) questions whether the description is not that of an immature *argentata*, although the colour is reminiscent of *lanosa*; Ellerman *et al.* (1953) point out that the type specimen resembles the Oriental species of *Kerivoula* (in which they include *Phoniscus*) rather than *argentata* or *lanosa*; Hill (1965: 553) has shown that *aerosa* should be transferred to the Asiatic *Phoniscus*. Hayman and Hill (1971) question the African origin of *aerosa*, and Corbet and Hill (1980) dubiously place it in Southeast Asia, while Koopman (1982) cite the provenance as 'possibly Africa'. In view of the considerable doubt about the status and origin of this species it is not treated as a member of the southern African fauna.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Kerivoula*: ***africana*** Dobson, 1878; *agnella* Thomas, 1908 – Louisiade Arch., Woodlark and D'Entrecasteaux Isls (Papua New Guinea) (Simmons, 2005: 526);

argentata Tomes, 1861; *crypta* Wroughton and Ryley, 1913 – S India; ***cuprosa*** Thomas, 1912; *depressa* Miller, 1906 – Indochina, India, Burma [=Myanmar]; *dongduongana* Tu, Hassanin, Furey and Csorba, 2018 – Vietnam; ***eriophora*** (Heuglin, 1877); *flora* Thomas, 1914 – Borneo, Lesser Sunda Isls, Bali, Sumbawa and Sumba (Indonesia), Vietnam and Thailand (Simmons, 2005: 526); *furva* Kuo, Soisook, Ho, Csorba, Wang and Rossiter, 2017 – Taiwan, India, Myanmar, China; *hardwickii* (Horsfield, 1824) – India and Sri Lanka, Burma, Laos, Cambodia, Vietnam, Thailand, China, western Malaysia, Borneo, Java, Sumatra, Nusa Penida, Mentawai Isls, Sulawesi, Bali, Lesser Sundas, Kangean Isl and Talaud Isl (Indonesia), Philippines (Simmons, 2005: 526); *intermedia* Hill and Francis, 1984 – Borneo, western Malaysia (Simmons, 2005: 527); *kachinensis* Bates, Struebig, Rossiter, Kingston, Oo and Mya, 2004 – Myanmar, Vietnam, Cambodia; *krauensis* Francis, Kingston and Zubaid, 2007 – Peninsular Malaysia; S Peninsular Thailand; ***lanosa*** (A. Smith, 1847); *lenis* Thomas, 1916 – northeastern and southern India, western Malaysia, Sabah (Simmons, 2005: 527); *malpasi* Thomas, 1916 – India (Calcutta and Tamil Nadu), (Sabah, Sepilok) Malaysia (incl. Sarawak); Indonesia (S Borneo); *minuta* Miller, 1898 – western Malaysia, southern Thailand, Borneo (Simmons, 2005: 527); *muscina* Tate, 1941 – central New Guinea (Simmons, 2005: 527); *myrella* Thomas, 1914 – Bismarck Arch. (Simmons, 2005: 527); *oreias* (Temminck, 1840) – Known only from the type locality in Singapore; *papillosa* (Temminck, 1840) – Thailand, Cambodia, Vietnam, western Malaysia, Sumatra, Java, Sulawesi, Borneo (Simmons, 2005: 527); *pellucida* (G.R. Waterhouse, 1845) – Borneo, Philippines, Java and Sumatra, western Malaysia (Simmons, 2005: 528); ***phalaena*** Thomas, 1912; *picta* (Pallas, 1767) – Sri Lanka; India and Nepal to Vietnam, western Malaysia and southern China, Borneo, Sumatra, Java, Bali, Lombok and Molucca Isls (Simmons, 2005: 528); *pusilla* Thomas, 1894 – Mindanao (Philippines), Sarawak (Borneo); ***smithii*** Thomas, 1880; *titania* Bates, Struebig, Hayes, Furey, Mya, Thong, Tien, Son, Harrison, Francis and Csorba, 2007 – Myanmar, Thailand, Laos, Cambodia, Vietnam; Taiwan; China (Hainan Island); *whiteheadi* Thomas, 1894 – Philippines, Borneo, southern Thailand, western Malaysia (Simmons, 2005: 528).

COMMON NAMES:
Czech: praví vlnouškové. English: Woolly Bats, Trumpet-eared Bats. French: Chauves-souris peintes. German: Wollfledermäuse. Italian: Cherìvoule.

ECHOLOCATION:
Keeley *et al.* (2018: 13) indicate that some *Kerivoula* species have fundamental frequencies up to 295 kHz and bandwidths up to 155 kHz, which they link to the absence of grooves in the external ear.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Tanzania.

Kerivoula africana Dobson, 1878

*1878. *Kerivoula africana* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, p xl, 331, ul 335. Publication date: 15 June 1878. Type locality: Tanzania: Coast opposite Zanzibar Island. [Goto Description]. Holotype: MNHN ZM-MO-1985-1063: ♂, skull and alcoholic. Collected by: Achille Raffray; collection date: 1875. - Comments: Type specimen: MNHN ???, ad ♂, alcoholic. (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: vlnoušek východoafrický, netopýr vlnatý, kerivula africká. English: African Woolly Bat, Tanzanian Woolly Bat. French: Kérivoule de Tanzanie, Chauve-souris peinte de Tanzanie. German: Tanzania-Wollfledermaus.

CONSERVATION STATUS:
Global Justification
MacPhee and Flemming (1999) considered this species to be extinct, followed by Simmons (2005), but it was recently rediscovered, see (Burgess *et al.*, 2000). Listed as Endangered under criterion B2ab(ii, iv) because its area of occupancy is estimated at 16 km^2 (the species has only been captured from four sites). The forests of the region are continuing to decline as it is converted to subsistence agriculture and is harvested as timber and firewood for local use (Cooper-Bohannon *et al.*, 2020a).

Assessment History
Global
2019: EN B2ab(iii, iv) ver 3.1 (2001) (Cooper-Bohannon *et al.*, 2020a). 2008: EN B2ab(iii) ver 3.1 (2001) (Fahr and Jacobs, 2008; IUCN, 2009). 2004: EN B2ab(iii) ver 3.1 (2001) (Fahr and Jacobs, 2004; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996). 1994: Ex (Groombridge, 1994). 1993: Ex (World Conservation Monitoring Centre, 1993). 1990: Ex

(IUCN 1990). 1988: Ex (IUCN Conservation Monitoring Centre 1988).

Regional
None known.

MAJOR THREATS:
It is threatened by the loss of coastal forests, largely through conversion of land to subsistence agriculture and harvesting of timber and firewood for local use (Fahr and Jacobs, 2008; IUCN, 2009; Cooper-Bohannon *et al.*, 2020a).

CONSERVATION ACTIONS:
Fahr and Jacobs (2008) [in IUCN (2009)] and Cooper-Bohannon *et al.* (2020a) report that it has been recorded from Morogoro (presumably within the Morogoro State Forest Reserve) and Genda Genda (possibly in a Forest Reserve). There is a need to prevent further loss of coastal forest habitat. Research is also needed into population size and trends, species' ecology and threats (Cooper-Bohannon *et al.*, 2020a).

GENERAL DISTRIBUTION:
Endemic to eastern Tanzania, where it has only been recorded from Morogoro; the Genda Genda coastal forest; and the Tong'omba coastal forest.

Native: Tanzania (Matschie, 1895; Swynnerton and Hayman, 1951; Cockle *et al.*, 1998; Burgess *et al.*, 2000).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 61 minutes, and the digestibility rate about 82.5 %.

POPULATION:
Structure and Density
Very little is known about the population of this rarely recorded species (Fahr and Jacobs, 2008; IUCN, 2009). It has been recorded at four times [sites], its global population is suspected to be declining due to extensive and continued deforestation (Cooper-Bohannon *et al.*, 2020a).

Trend
2019: Decreasing (Cooper-Bohannon *et al.*, 2020a). 2008: Decreasing (Fahr and Jacobs, 2008; IUCN, 2009).

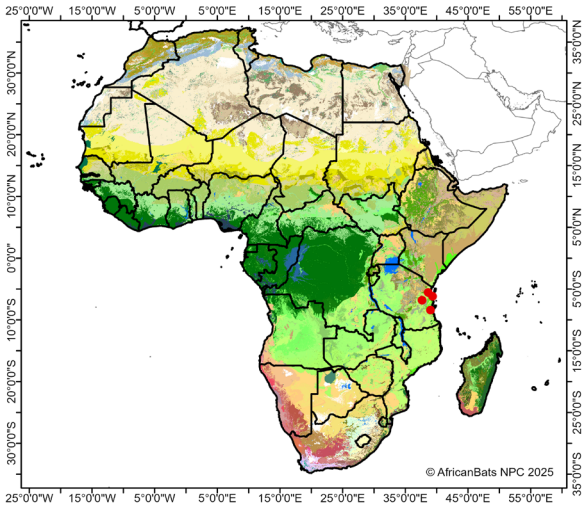

Figure 254. Distribution of *Kerivoula africana*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Tanzania.

Kerivoula argentata Tomes, 1861

*1861. *Kerivoula argentata* Tomes, Proc. zool. Soc. Lond., 1861, I: 31, 32. Publication date: May 1861. Type locality: Namibia: Ovamboland: Otjoro [=Otjihoro] [ca. 17 54 S 15 38 E]. [Goto Description]. Holotype: [Unknown] |TS171|: ♀. Collection date: 1 December 1859. See Tomes (1861b: 33). Holotype: NHMUK 1907.1.1.540: ♀. Collection date: 1 December 1859. - Comments: Ansell and Dowsett (1988: 44) indicate the type locality is probably Otjihoro, according to Shortridge (1934: 70). (Current Combination).

1865. *Nycticejus nidicola* Kirk, Proc. zool. Soc. Lond., 1864, III: 651. Publication date: May 1865. Type locality: Mozambique: Zambesi River: Shupanga [=Chupanga] [18 02 S 35 37 E]. [Goto Description]. Syntype: NHMUK 1864.1.9.37: ad. Collected by: Dr. Kirk. Syntype: NHMUK 1864.1.9.38: ad. Collected by: Dr. Kirk. Syntype: NHMUK 1864.1.9.39: ad. Collected by: Dr. Kirk. - Comments: (1 ad ♂ + 2 ad ♀♀). Considered a valid subspecies by Ansell and Dowsett (1988: 44.

1924. *Kerivoula nidicola zuluensis* Roberts, Ann. Transv. Mus., 10: 61. Publication date: 31 January 1924. Type locality: South Africa: KwaZulu-Natal: White Umfolosi River [28 19 S 31 50 E]. [Goto Description]. Holotype: TM 3025: ad ♂, skin and skull. Collected by: Austin Roberts; collection date: 17 July 1922. Note: In weaver nest with two others. - Comments: Considered a valid subspecies by Taylor (1998: 57).

? *Kerivoula argentata argentata:* (Name Combination).

? *Kerivoula argentata zuluensis:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Afrikaans: Damara-wolhaarvlermuis, Damaralandse Wolhaarvlermuis. Chinese: 银彩蝠. Czech: vlnoušek damarský. English:

Silvery Woolly Bat, Silvered Woolly Bat, Silver Woolly Bat, Damara Woolly Bat. French: Chauve-souris peinte argentée, Chauve-souris laineuse du Damara. German: Bunte Wollfledermaus. Kiluba (DRC): Kasusu. Portuguese: Morcego lanoso da Damaralandia.

ETYMOLOGY OF COMMON NAME:
This species was originally described from a specimen from Damaraland, Namibia (Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
K. argentata may be represented in the late Holocene at Nkupe, South Africa (Avery, 1991: 6).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008k; IUCN, 2009; Monadjem *et al.*, 2017ch).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ch). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008k; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004h; IUCN, 2004). 1996: Lower Risk/least concern (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: NT C2a(i) ver 3.1 (2001) (Monadjem *et al.*, 2016f). 2004: EN B1ab(iii)+2ab(iii) ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Jacobs *et al.*, 2008k; IUCN, 2009; Monadjem *et al.*, 2017ch).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008k) [in IUCN (2009)] and Monadjem *et al.* (2017ch) report that there appear to be no direct conservation measures in place. It has been recorded from the Kambai Forest Reserve in Tanzania by Cunneyworth (1996b), and seems likely to be present in a number of protected areas within its range. Further studies are needed to determine if the species is truly present in Angola.

GENERAL DISTRIBUTION:
Kerivoula argentata is distributed in East Africa and southern Africa, with some records in southern parts of the Democratic Republic of the Congo and possibly northern Angola in Central Africa (records are uncertain from this country). In East Africa it has been recorded from Kenya and Tanzania in the north, through Zambia, Malawi and Mozambique. In southern Africa, it appears to be widespread in Zimbabwe, with additional scattered records from northeastern South Africa and central Namibia.

For southern Africa, Cooper-Bohannon *et al.* (2016: "5") calculated a potential distribution area of 752,853 km^2.

Native: Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 563); Eswatini (Monadjem *et al.*, 2021: 5); Kenya (Aggundey and Schlitter, 1984); Malawi (Happold and Happold, 1997b: 822; Monadjem *et al.*, 2010d: 563); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 563; Monadjem *et al.*, 2010c: 383); Namibia (Monadjem *et al.*, 2010d: 563); Rwanda (Flanders *et al.*, 2022: 3); South Africa (Roberts, 1951; Smithers, 1983; Skinner and Smithers, 1990; Taylor, 2000; Skinner and Chimimba, 2005; Monadjem *et al.*, 2010d: 563); Tanzania, United Republic of (Cunneyworth, 1996b); Zambia (Ansell, 1974; Monadjem *et al.*, 2010d: 563); Zimbabwe (Smithers and Wilson, 1979; Monadjem *et al.*, 2010d: 563).

Presence uncertain: Angola (Hill and Carter, 1941), although Taylor *et al.* (2018b: 63) predict it might occur in that country.

ECHOLOCATION:
See Taylor (1999b).

Schoeman and Waddington (2011: 291) mention a F_{peak}: 99 kHz and a duration: 1.7 ms for a specimen from the Mkuze Game Reserve, South Africa.

Moir (2020: 30) and Moir *et al.* (2021a: 371) reported six calls from one bat from southern KwaZulu-Natal or Eastern Cape (RSA), with the following features: F_{max}: 151.48 ± 6.60 (141.22 - 157.871) kHz, F_{min}: 84.06 ± 4.29 (77.67 - 90.28) kHz, F_{char}: 108.02 ± 12.76 (93.81 - 122.56) kHz, F_{knee}: 104.50 ± 3.69 (100.37 - 110.46) kHz, and duration: 1.55 ± 0.70 (0.70 - 2.54) ms.

28 calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 87.09 ± 10.39 kHz, F_{min}: 75.29 ± 9.80 kHz, F_{knee}: 77.89 ± 6.38 kHz, F_{char}:

77.44 ± 6.73 kHz, slope: 7.86 ± 28.41 OPS, duration: 3.37 ± 1.01 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 35 calls of 11 bats: F_{max}: 159.23 ± 6.03 kHz, F_{min}: 135.12 ± 15.89 kHz, F_{knee}: 142.39 ± 7.02 kHz, F_{char}: 140.26 ± 16.47 kHz, slope: 46.99 ± 7660.2 OPS, duration: 1.98 ± 1.33 ms.

ROOST:
Kerivoula argentata was found to be roosting in nests of weaver birds, but also among clusters of dead leaves, on bark of trees, under eaves of huts or on walls. They roost singly, in twos or in small groups of up to six animals (Happold and Happold, 2023: 139).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 88 minutes, and the digestibility rate about 78.5 %.

POPULATION:
Structure and Density
Although this species is rarely encountered, it is not thought to be especially uncommon (Jacobs *et al.*, 2008k; IUCN, 2009; Monadjem *et al.*, 2017ch).

Trend
2016: Unknown (Monadjem *et al.*, 2017ch). 2008: Unknown (Jacobs *et al.*, 2008k; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Trentin and Rovero (2011: 51) reported two lactating females, captured at Uzungwa Scarp Forest Reserve, Tanzania, at the end of November 2005.

VIRUSES:
Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that the one specimen they examined from South Africa tested positive for *Paramyxovirus* sequences.

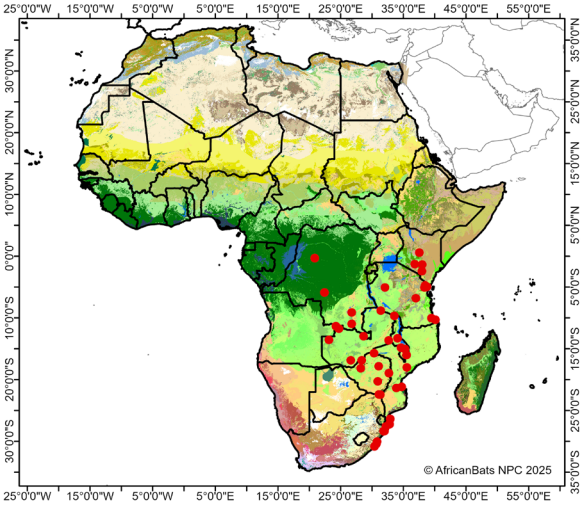

Figure 255. Distribution of *Kerivoula argentata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Kenya, Malawi, Mozambique, Namibia, Senegal, South Africa, Tanzania, Zambia, Zimbabwe.

Kerivoula cuprosa Thomas, 1912

*1912. *Kerivoula cuprosa* Thomas, Ann. Mag. nat. Hist., ser 8, 10 (55): 41. Publication date: 1 July 1912. Type locality: Cameroon: Ja River: Bitye [03 13 N 12 22 E, 2 000 ft]. [Goto Description]. Holotype: NHMUK 1912.10.25.1: ad ♂. Collected by: George Latimer Bates Esq. Collection date: 17 October 1911; original number: 564. (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: vlnoušek bronzový. English: Copper Woolly Bat. French: Chauve-souris laineuse cuivrée, Chauve-souris peinte cuivrée. German: Kupferfarbene Wollfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, ecological requirements and threats (Fahr, 2008b; IUCN, 2009; Fahr, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) (Fahr, 2019a). 2008: DD ver 3.1 (2001) (Fahr, 2008b; IUCN, 2009). 2004: NT ver 3.1 (2001) (Fahr, 2004m; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not well known. In parts of its range it is presumably threatened to some degree by habitat loss resulting from conversion of land to agricultural use, and

harvesting of timber and firewood (Fahr, 2008b; IUCN, 2009; Fahr, 2019a).

CONSERVATION ACTIONS:
Fahr (2008b) [in IUCN (2009)] and Fahr (2019a) reports that it is unclear if this species is present in any protected areas. Additional studies are needed into the taxonomy, distribution, natural history and threats to this little-known bat.

GENERAL DISTRIBUTION:
Scattered records from West and Central Africa. It has apparently been reported from Guinea, Côte d'Ivoire, Liberia, possibly Ghana (see Koopman *et al.*, 1995; Grubb *et al.*, 1998), Cameroon and the Democratic Republic of the Congo (see Hayman and Hill, 1971). It is found up to 600 m asl.

Grubb *et al.* (1998: 92) indicate that records west of Cameroon are erroneous and probably refer to a specimen from Oda, Ghana in the FMNH that was re-identified as *K. lanosa muscilla*. A record of this species from Kenya was based on a specimen subsequently reidentified as *Kerivoula smithii* (J. Fahr *pers. Comm.,* in Simmons, 2005: 526; and also in Fahr (2008b) [in IUCN (2009)]).

Native: Cameroon; Congo (The Democratic Republic of the); Côte d'Ivoire; Guinea (Fahr and Ebigbo, 2004: 69); Kenya (Harrison, 1957b); Liberia (Koopman, 1989b; Koopman *et al.*, 1995); Nigeria (Tanshi *et al.*, 2022a: 317); Uganda (Kityo *et al.*, 2009b: 135).
Presence uncertain: Ghana.

ECHOLOCATION:
Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003669_PWGCLEZAOQ.WAV, https://chirovox.elte.hu/sounds/A003670_BBNOKVNQBS.WAV, https://chirovox.elte.hu/sounds/A003671_QTREJYLLLY.WAV

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 62 minutes, and the digestibility rate about 82.4 %.

POPULATION:
Structure and Density
It appears to be a rare, or rarely recorded, species (Fahr, 2008b; IUCN, 2009; Fahr, 2019a).

Trend
2018: Unknown (Fahr, 2019a). 2008: Unknown (Fahr, 2008b; IUCN, 2009).

PARASITES:
ACARI
Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides kerivoluae* Fain, 1959 on *Kerivoula cuprosa* specimens from the DRC.

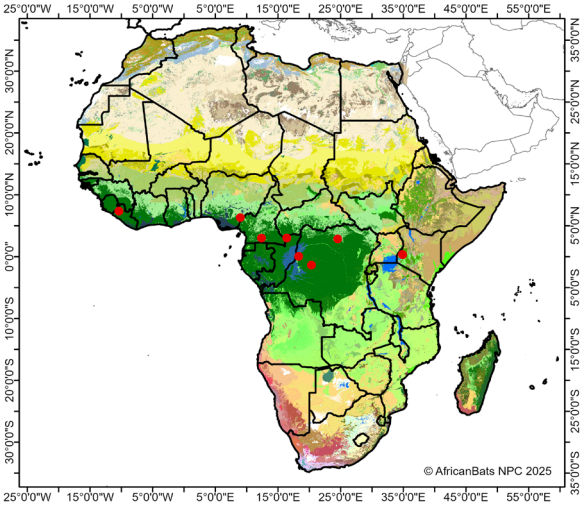

Figure 256. Distribution of *Kerivoula cuprosa*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Kenya, Liberia, Nigeria.

Kerivoula eriophora (Heuglin, 1877)

*1877. *Nycticejus eriophorus* Heuglin, Reise in Nordost Afrika, 2: 34. Publication date: 1877. Type locality: Ethiopia: Begemdir province: Belegaz Valley: Semian and Wogara, between [ca. 12 50 N 38 20 E]. [Goto Description]. - Etymology: From the Greek "*eriophora*" meaning wool-bearing.
? *Kerivoula eriophora:* (Current Combination).

TAXONOMY:
May be conspecific with *africana* which it antedates; see Hayman and Hill (1971: 53) and Simmons (2005: 526).

COMMON NAMES:
Czech: vlnoušek habešský. English: Ethiopian Woolly Bat. French: Chauve-souris laineuse d'Ethiopie, Chauve-souris peinte d'Ethiopie. German: Heuglins Wollfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, ecological requirements and threats (Fahr, 2008c; IUCN, 2009; Fahr, 2019e).

Assessment History
Global
2008: DD ver 3.1 (2001) (Fahr, 2008c; IUCN, 2009). 2004: DD ver 3.1 (2001) (Fahr, 2004p; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Fahr, 2008c; IUCN, 2009; Fahr, 2019e).

CONSERVATION ACTIONS:
Fahr (2008c) [in IUCN (2009)] and Fahr (2019e) reports that it is not known if the species is present in any protected areas. Further research is needed into the systematic status, distribution, natural history and possible threats to this species.

GENERAL DISTRIBUTION:
Kerivoula eriophora has only been recorded at the type locality of 'between Semian and Wogara, Belegaz Valley, Ethiopia'.

Native: Ethiopia (Heuglin, 1877: 34), South Sudan (SMF record)

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 62 minutes, and the digestibility rate about 82.4 %.

POPULATION:
Structure and Density
It is known only from the holotype (Fahr, 2008c; IUCN, 2009; Fahr, 2019e).

Trend
2018: Unknown (Fahr, 2019e). 2008: Unknown (Fahr, 2008c; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Sudan.

Kerivoula lanosa (A. Smith, 1847)

*1847. *Vespertilio lanosus* A. Smith, Illustrated Zoology of South African Mammals, pl 50 and text. Publication date: December 1847. Type locality: South Africa: Cape province: Cape Town, 200 mi (332 km) E. Syntype: NHMUK 1907.1.1.538: ♂. Syntype: NHMUK 1907.1.1.539. - Comments: Thorn *et al.* (2009: 50) indicate that Roberts (1951: 75) designated Knysna as type locality. - Etymology: From the Greek "*lanosa*" meaning woolly.

1878. *Kerivoula brunnea* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, xl, 331, 334. Publication date: 15 June 1878. Type locality: South Africa: "South Africa or Madras". [Goto Description]. Holotype: NHMUK 1852.8.12.9: sad ♂, alcoholic (skull not removed). Presented/Donated by: Sir Andrew Smith. - Comments: Roberts (1951: 75) mentioned "Madras or South Africa as type locality. Sir A. Smith (Obviously the type of Smith's *V. Lanosus*, cf. Roberts, 1913: Knysna)". Meester *et al.* (1986: 64) mention "South Africa or Madras").

1901. *Kerivoula harrisoni* Thomas, Proc. zool. Soc. Lond., 1900, IV: 802, footnote. Publication date: April 1901. Type locality: Ethiopia: between Lakes Zwai and Margherita [=Lake Abaya]: Walamo [c. 07 00 N 38 00 E,, 6 700 ft]. [Goto Description]. Holotype: NHMUK 1900.11.4.1: Collected by: J.J. Harrison; collection date: 21 February 1900. Presented/Donated by: J.J. Harrison.

1906. *Kerivoula muscilla* Thomas, Ann. Mag. nat. Hist., ser 7, 18 (106): 294. Publication date: 1 October 1906. Type locality: Cameroon: Ja River [ca. 03 00 N 13 00 E]. [Goto Description]. Holotype: NHMUK 1908.6.23.10: ad ♂. Collected by: George Latimer Bates Esq. Collection date: 22 December 1905. - Comments: Considered a valid subspecies by Fahr and Ebigbo (2003: 128; 2004: 73).

1920. *Kerivoula lucia* Hinton, Ann. Mag. nat. Hist., ser 9, 6 (32): 240. Publication date: 1 August 1920. Type locality: Zambia: N'dola. [12 58 00 S 28 38 00 E, 1304 m]. [Goto Description]. Holotype: NHMUK 1920.11.3.27: ad ♂. Collected by: Captain Guy Chester Shortridge; collection date: 26 September 1919; original number: 472.

1922. *Kerivoula lueia* Kershaw, Ann. Mag. nat. Hist., ser 9, 10 (55): 99. Publication date: 1 July 1922. - Comments: Erratum (see Meester *et al.*, 1986: 64).

1959. *Kerivoula harrisoni bellula* Aellen, Archs Sci. Genève, 12 (2): 221. Type locality: Côte d'Ivoire: NW of Abidjan: Adiopodoumé [05 19 N 04 08 W, 0 - 30 m]. [Goto Description]. Holotype: MHNG 965.038: ad ♂, alcoholic (skull not removed). Collected by: Dr. Villy Aellen; collection date: 20 July 1953; original number: 622. Paratype: MHNG 965.039: ♀, alcoholic (skull not removed). Collected by: Dr. Villy Aellen; collection date: 21 December 1953; original number: 622.

? *Kerivoula harrisoni lucia:* (Name Combination).

? *Kerivoula lanosa harrisoni:* (Name Combination).

? *Kerivoula lanosa lucia:* (Name Combination).

? *Kerivoula lanosa muscilla:* (Name Combination).

? *Kerivoula lanosa:* (Current Combination).

TAXONOMY:
Includes *harrisoni* and *muscilla*; see Hill (1977b), but see Fahr and Ebigbo (2003: 128; 2004: 73).

COMMON NAMES:
Afrikaans: Klein wolhaarvlermuis. Chinese: 小彩蝠. Czech: vlnoušek malý. English: Lesser Woolly Bat. French: Petite Chauve-souris laineuse, Chauve-souris laineuse. German: Kleine Wollfledermaus. Portuguese: Morcego lamoso Harrison.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017ci).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ci). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008l; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004a; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016g). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017ci).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008l) [in IUCN (2009)] and Monadjem *et al.* (2017ci) report that it is not known if the species is present in any protected areas. Further studies are needed to better understand the taxonomic status of *Kerivoula lanosa*.

GENERAL DISTRIBUTION:
Kerivoula lanosa has been recorded across sub-Saharan Africa, from Liberia and Guinea in the west, to Ethiopia and Kenya in the east, and ranging as far south as southern South Africa. In the latter country, its distribution is mainly affected by temperature seasonality (Babiker Salata, 2012: 49).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 636,522 km^2.

Native: Angola (Monadjem *et al.*, 2010d: 563; Taylor *et al.*, 2018b: 63); Botswana (Monadjem *et al.*, 2010d: 563); Central African Republic; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 563); Côte d'Ivoire; Eswatini (Monadjem *et al.*, 2010d: 563, Monadjem *et al.*, 2021: 5); Ethiopia (Kruskop and Lavrenchenko, 2009: 72 - first record in over a 100 years); Gabon; Ghana; Guinea (Fahr and Ebigbo, 2003: 128); Kenya; Liberia; Malawi (Ansell and Dowsett, 1988; Monadjem *et al.*, 2010d: 563); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 563; Monadjem *et al.*, 2010c: 383); Nigeria (Happold, 1987); South Africa (Roberts, 1951; Smithers, 1983; Skinner and Smithers, 1990; Taylor, 1998; Skinner and Chimimba, 2005; Monadjem *et al.*, 2010d: 563); Tanzania; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 563); Zimbabwe (Cotterill, 1996a; Monadjem *et al.*, 2010d: 563).

Presence uncertain: Namibia (Cotterill, 2004a: 262; Monadjem *et al.*, 2010d: 563).

ECHOLOCATION:
Moir (2020: 30) and Moir *et al.* (2021a: 371) reported 10 calls from one bat from southern KwaZulu-Natal or Eastern Cape (RSA) with the following characteristics: F_{max}: 147.28 ± 5.53 (137.19 - 152.32) kHz, F_{min}: 70.28 ± 2.95 (67.59 - 74.65) kHz, F_{char}: 95.41 ± 3.31 (89.28 - 98.86) kHz, F_{knee}: 95.58 ± 5.68 (90.79 - 107.94) kHz, and duration: 1.22 ± 0.2 (0.66 - 1.60) ms.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 28, FN = 50, BA = 24, a metacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa.

ROOST:
In the southern part of the Kruger Park, Pienaar (1964: 12) indicated that it is said that it often used disused nests of weaver birds, but he could not confirm this without doubt.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 71 minutes, and the digestibility rate about 80.9 %.

POPULATION:
Structure and Density
There appears to be little information available on the population abundance of this species (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017ci).

Trend
2016: Unknown (Monadjem *et al.*, 2017ci). 2008: Unknown (Jacobs *et al.*, 2008l; IUCN, 2009).

PARASITES:
ACARI
Psorergatidae
Cierocka *et al.* (2022: 10) mention the presence of *Psorergatoides kerivoluae* Fain, 1959 on *Kerivoula lanosa* specimens from the DRC (Mentioned as "*Kerivoula harrisoni bellula*" by Fain, 1959a).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mozambique, Namibia, Nigeria, South Africa, Tanzania, Zambia, Zimbabwe.

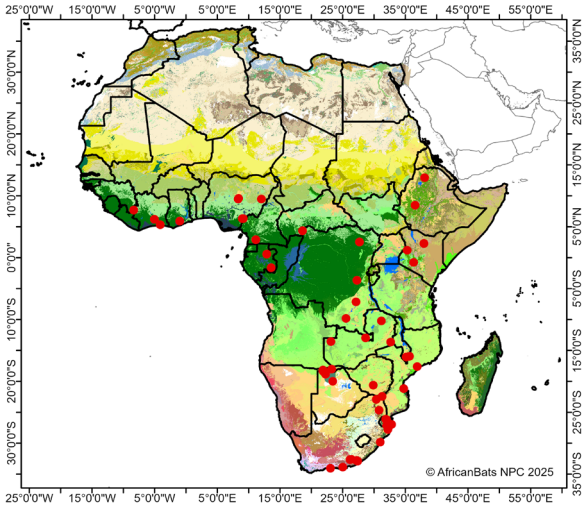

Figure 257. Distribution of *Kerivoula lanosa*.

Kerivoula phalaena Thomas, 1912

*1912. *Kerivoula phalæna* Thomas, Ann. Mag. nat. Hist., ser 8, 10 (57): 281. Publication date: 1 September 1912. Type locality: Ghana: Western province: Inland from Denkwa: Bibianaha [=Bibiani] [06 28 N 02 20 W, 720 ft]. [Goto Description]. Holotype: NHMUK 1912.6.20.3: ad ♀. Collected by: Dr. H.G.F. Spurrell; collection date: 24 April 1912; original number: 224. Presented/Donated by: Dr. H.G.F. Spurrell. - Etymology: From the Greek "*phalaena*" meaning whale. (Current Combination).
1973. *Kerivoula phalaema:* Eisentraut, Bonn. zool. Monogr., 3: 46. (Lapsus).
2010. *Kerivoula cf. phalaena:* Monadjem, Schoeman, Reside, Pio, Stoffberg, Bayliss, Cotterill, Curran, Kopp and Taylor, Acta Chiropt., 12(2): 383.
? *Kerivoula phalaena:* (Current Spelling).

TAXONOMY:
See Simmons (2005: 528).

COMMON NAMES:
Czech: vlnoušek západoafrický. English: Spurrell's Woolly Bat, Spurell trumpet-eared bat. French: Chauve-souris à oreilles en trompette de Spurell, Chauve-souris peinte phalène, Chauve-souris à oreilles en trompette de Spurell. German: Spurrells Wollfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008d; Fahr, 2008d; Monadjem and Fahr, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Fahr, 2017a). 2008: LC ver 3.1 (2001) (Fahr, 2008d; Fahr, 2008d). 2004: NT ver 3.1 (2001) (Fahr, 2004l; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known. Koopman *et al.* (1995) mention that this one of seven bat species from Liberia that have not been recorded from the lowland since 1965, and that it might have declined because of deforestation, although this may instead just indicate vagaries of collection within this country (Fahr, 2008d; IUCN, 2009; Monadjem and Fahr, 2017a).

CONSERVATION ACTIONS:
Fahr (2008d) [in IUCN (2009)] and Monadjem and Fahr (2017a) reports that it is not known if the species is present within any protected areas. Additional studies are needed into the distribution, abundance, natural history and threats to this little known species.

GENERAL DISTRIBUTION:
Recorded from Guinea, Liberia, Côte d'Ivoire and Ghana in West Africa; and from Cameroon, the Democratic Republic of the Congo to western Uganda in Central Africa.

Native: Cameroon; Congo (The Democratic Republic of the); Côte d'Ivoire; Ghana; Guinea (Fahr and Ebigbo, 2004: 69); Liberia (Kuhn, 1965; Koopman *et al.*, 1995); Nigeria (Tanshi *et al.*, 2022a: 317); Rwanda; Uganda.

Presence uncertain: Mozambique (Monadjem *et al.*, 2010c: 383, recorded as *K.* cf. *phalaena*).

HABITAT:
Monadjem *et al.* (2016y: 368) collected this bat in forested habitats in the Mount Nimba area, at altitudes between 450 and 700 m.

POPULATION:
Structure and Density
It appears to be a rare species that is known only from 14 localities (Fahr, 2008d; IUCN, 2009; Monadjem and Fahr, 2017a).

Trend
2016: Unknown (Monadjem and Fahr, 2017a).
2008: Unknown (Fahr, 2008d; IUCN, 2009).

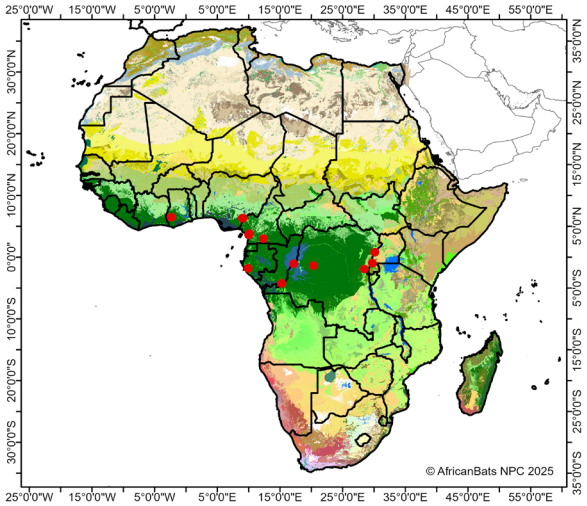

Figure 258. Distribution of *Kerivoula phalaena*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Gabon, Ghana, Liberia, Nigeria, Uganda.

Kerivoula smithii Thomas, 1880

*1880. *Kerivoula Smithii* Thomas, Ann. Mag. nat. Hist., ser 5, 6 (32): 166, text-fig. Publication date: 1 August 1880. Type locality: Nigeria: Eastern region: Old Calabar [04 56 N 08 22 E]. Holotype: NHMUK 1880.7.21.9: Collected by: Dr. A. Robb. Presented/Donated by: Dr. J.A. Smith. - Etymology: In honour of Dr. J.A. Smith, who presented to the type specimen to the British Museum of Natural History. (Current Combination).
? *Kerivoula smithi:* (Alternate Spelling).
? *Kerivoula smithii:* (Current Spelling).

TAXONOMY:
See Simmons (2005: 528).

COMMON NAMES:
Chinese: 史密斯彩蝠. Czech: vlnoušek guinejský. English: Smith's Woolly Bat. French: Chauve-souris peinte de Smith. German: Smith's Wollfledermaus. Italian: Cherìvoula di Smith.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008e; IUCN, 2009; Monadjem and Fahr, 2017b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Fahr, 2017b). 2008: LC ver 3.1 (2001) (Fahr, 2008e; IUCN, 2009). 2004: LC ver 3.1 (2001) (Fahr, 2004a; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species (Fahr, 2008e; IUCN, 2009; Monadjem and Fahr, 2017b).

CONSERVATION ACTIONS:
Fahr (2008e) [in IUCN (2009)] and Monadjem and Fahr (2017b) reports that it is not known if the species is present within any protected areas. Further studies are needed into the distribution, abundance, and general ecology of this apparently rare species.

GENERAL DISTRIBUTION:
Kerivoula smithii is known from scattered records in a distribution band ranging from Nigeria and Cameroon in the west, through the Democratic Republic of the Congo, to Uganda and Kenya in the east. It has been recorded at elevations of 900 to 2,800 m asl.

Fahr (2007a: 105) indicates that the specimens from Liberia mentioned by Happold (1987: 349) and Koopman *et al.* (1995) are actually

representatives of *K. phalaena*. J. Fahr *pers. comm.* [in Simmons (2005: 528)] also suggests that records from Côte d'Ivoire (Happold, 1987: 349) appear to be in error.

Native: Cameroon; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966); Kenya (Harrison, 1963c; Aggundey and Schlitter, 1984) ; Nigeria (Happold, 1987: 77); Uganda.

Presence uncertain: Côte d'Ivoire (Happold, 1987: 349).

ECHOLOCATION:
Eisenring *et al.* (2016: SI 2) reported the following values for 14 calls from the Aberdares Range in Kenya: F_{peak}: 95.9 ± 6.2 (81.5 - 104.9) kHz, F_{max}: 126.3 ± 7.2 (115.6 - 137.2) kHz, F_{min}: 65.3 ± 13.2 (44.9 - 91.8) kHz, duration: 61.0 ± 16.5 (25.1 - 85.5) ms, interpulse interval: 0.2 ± 0.1 (0.1 - 0.6) ms.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 62 minutes, and the digestibility rate about 82.4 %.

POPULATION:
Structure and Density
This species has been very rarely recorded (Happold, 1987: 77; Fahr, 2008e; IUCN, 2009; Monadjem and Fahr, 2017b).

Trend
2016: Unknown (Monadjem and Fahr, 2017b).
2008: Unknown (Fahr, 2008e; IUCN, 2009).

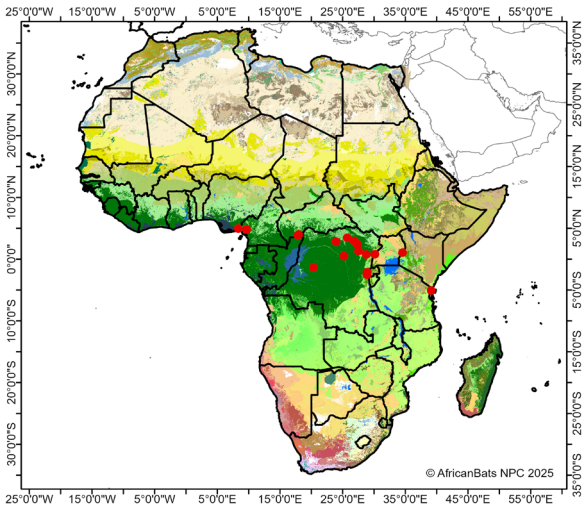

Figure 259. Distribution of *Kerivoula smithii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Congo (Democratic Republic of the), Kenya, Nigeria, Tanzania, Uganda.

Subfamily Myotinae Tate, 1942

*1942. *Myotinae* Tate, Bull. Am. Mus. Nat. Hist., 80 (7): 221, 229. Publication date: 27 November 1942. - Comments: Type genus: *Myotis* Kaup, 1829. (Current Combination).

1942. *Myotini* Tate, Bull. Am. Mus. Nat. Hist., 80 (7): 221, 229. Publication date: 27 November 1942. - Comments: Type genus: *Myotis* Kaup, 1829. Introduced as tribe, and originally included the genera *Myotis* Kaup, 1829; *Lasionycteris* Peters, 1865; *Plecotus* É. Geoffroy, 1818; *Corynorhinus* H. Allen, 1865; *Idionycteris* Anthony, 1923; and *Euderma* H. Allen, 1891 (see Jackson and Groves, 2015: 280).

1987. *Leuconoformes* Menu, Palaeovert., 17 (3): 77, 7312, 133. Publication date: 31 March 1987. - Comments: Type genus: *Leuconöe* Boie, 1830. Introduced with unclear rank, and originally included the genera *Leuconöe* Boie, 1830 [= *Myotis* Kaup, 1829]; *Pizonyx* Miller, 1906 [= *Myotis* Kaup, 1829]; and *Perimyotis* Menu, 1984 (see Jackson and Groves, 2015: 280).

1998. *Myotinae:* Simmons, in: Kunz, T. H.; Racey, P. A., A reappraisal of interfamilial relationships of bats, 12. - Comments: Type genus: *Myotis* Kaup, 1829.

2005. *Myotiinae:* Ramírez-Pulido, Arroyo-Cabrales and Castro-Campillo, Acta Zool. Mex. (ns), 21 (1): 31. - Comments: Ramírez-Pulido *et al.* (2005) refer to Simmons (1998) for Myotiinae, but Simmons (1998: 5) uses the correct spelling (Myotinae). (Lapsus).

TAXONOMY:
Tate (1942: 229) originally named Myotini as a tribe within Vespertilioninae, in which he included the genera *Myotis*, *Lasionycteris*, *Plecotus*, *Corynorhinus*, *Idionycteris* and *Euderma*. Although Tate (1942: 230) noted that the latter four genera might alternatively be referred to their own tribe Plecotini. This suggestion was followed by subsequent authors, and Myotini has been restricted to *Myotis* and *Lasionycteris* in recent classifications (e.g., Hill and Harrison, 1987; Koopman, 1994). Volleth and Heller (1994) described karyological data which indicate that Myotini represents a lineage distinct from Vespertilioninae, and therefore they suggested that Myotini be raised to the rank of subfamily. Despite their suggestion, Volleth and Heller (1994) did not use the name Myotinae in their publication, so formal usage of the name at the subfamily rank dates from Simmons (1998: 3, 5),

who raised it to the subfamily level, and followed in recent classifications (e.g., Bannikova *et al.*, 2002: 722; Hoofer and Van Den Bussche, 2003: 21; Guan *et al.*, 2025: 3).

May not be monophyletlic; see Hoofer and Van Den Bussche (2001), and Simmons (2005). Hoofer and Van Den Bussche (2003: 21) and Roehrs *et al.* (2010: 1081) only include the members of the genus *Myotis*, (not *Lasionycteris* nor *Cistugo*).

Known genera of the subfamily Myotinae: †***Khonsunycteris*** Gunnell, Simons and Seiffert, 2008; ***Myotis*** Kaup, 1829.

COMMON NAMES:
Czech: netopýrcové. Ukrainian: Нічниці [= Nichnytsi]

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Ruedi *et al.* (2013: 446-447) doubt the African origin of the Myotinae as proposed by Gunnell *et al.* (2012), and their molecular phylogeny points to eastern Asia as the cradle of *Myotis* evolution.

Gunnell *et al.* (2017: 14) suggest that the basal myotines (e.g., *Khonsunycteris*) originated in northern Africa in the Late Eocene, followed by the appearance of *Myotis* in the early Oligocene of Europe. The fact that they found a plecotine bat (*Quinetia misonnei*) in the same Belgian location, furthermore, suggests that the vespertilionid subfamilies Vespertilioninae and Myotinae had already diverged by 33.5 MYA.

The discovery of the southernmost and oldest record of *Myotis podlesicensis* Kowalski, 1956 in Europe (Spain; Late Miocene) by Crespo *et al.* (2017: 324) provides support for an African origin of this taxon.

Genus ***Myotis*** Kaup, 1829

*1829. *Myotis* Kaup, Skizzierte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 106. Publication date: 1829. - Comments: Type species: *Vespertilio myotis* Borkhausen, 1797, by subsequent designation by Miller (1912: 167). Kaup (1829: 106) mentioned *Vespertilio murinus*, but for a discussion on the type species, see Jackson and Groves (2015: 280). - Etymology: From the Greek "*μύς*" or "*μυός*", meaning mouse and "*ούς*" or "*ώτός*" meaning ear (see Palmer, 1904: 442). Gardner (2005:184) considers the name to be masculine (My = mouse + ot = ear(ed) + is (Latin third declension ending)). - Phonetics: mie-oh′-tis.

1829. *Nystactes* Kaup, Skizzirte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 108. Publication date: 1829. - Comments: Type species: *Vespertilio bechsteini* Kuhl, 1819. Jackson and Groves (2015: 281) indicate that this name is an objective synonym of *Paramyotis* Bianchi. Not *Nystactes* Gloger, 1827 (Aves, Piciformes, Bucconidae). - Etymology: From the Greek "*νυστακτής*", meaning the one who nods, a sleeper (see Palmer, 1904: 467).

1830. *Leuconoe* Boie, Isis oder Encyclopädische Zeitung von Oken, 256. Publication date: 1830. - Comments: Type species: *Vespertilio daubentonii* Kuhl, 1817. Considered a valid genus based on tooth morphology: see Menu (1985, 1987) in Menu *et al.* (2002: 320).

1841. *Capaccinius* Bonaparte, Iconografia Fauna italiana, 1: Indice Distributivo: 1. - Comments: Type species: *Vespertilio megapodius* Temminck, 1840 [=*Vespertilio capaccinii* Bonaparte, 1837], by tautonomy (see Jackson and Groves, 2015: 281). - Etymology: In honour of Francesco Capaccini, under secretary of state of Rome about 1833-34, and a patron of Bonaparte's "Iconografia della Fauna Italica," published in 1832-1841 (see Palmer, 1904: 49).

1841. *Selysius* Bonaparte, Iconografia Fauna italiana, 1: Mamm, Introd: 3. Publication date: 1841 [Goto Description]. - Comments: Type species: *Vespertilio mystacinus* Kuhl, 1817, by monotypy (see Jackson and Groves, 2015: 281). - Etymology: In honour of Baron Edmond de Selys-Longchamps, 1813 - 1900, an eminent naturalist and statesman, some time president of the Belgian Senate; author of "Etudes de Micromammalogie," 1839, and "Faune Belge," 1844 (see Palmer, 1904: 51).

1842. *Trilatitus* J. E. Gray, Ann. Mag. nat. Hist., [ser 1], 10 (65): 258. Publication date: 1 December 1842. - Comments: type species: *Vespertilio hasseltii* Temminck, 1840, by subsequent designation (see Jackson and Groves, 2015: 281). Included *Vespertilio hasselti* Temminck, *M. macellus* Temminck, and *V. blepotis* Temminck (a *Miniopterus*) (see Hall and Kelson, 1959: 159; Hall, 1981: 183; Corbet and Hill, 1992: 119).

1843. *Vespertilio* J. E. Gray, Cat. specs mamm, xix, 26. Publication date: 13 May 1843. - Comments: Type species: *Vespertilio mystacinus* Kuhl, 1817, by monotypy according to Jackson and Groves (2015: 281). Not iVespertilio Linnaeus, 1758, nor *Vespertilio* Mörch, 1852 (Mollusca, Neogastropoda, Volutidae) (see Jackson and Groves, 2015: 281).

1849. *Tralatitus:* Gervais, Dictionnaire Universelle d'Histoire naturelle, 13: 213. - Comments: A lapsus for *Trilatitus* (see Hall, 1981: 183). Modification of *Trilatitus* (see Ellerman and Morrison-Scott, 1951: 137; Meester *et al.*, 1986: 47). Incorrect subsequent spelling (see Jackson and Groves, 2015: 281). (Lapsus).

1856. *Brachyotus* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Type species: *Vespertilio mystacinus* Kuhl, 1817, by subsequent designation by Ellerman and Morrison-Scott (1951: 137) (see Jackson and Groves, 2015: 281). Preoccupied by *Brachyotus* Gould, 1837 (Aves, Strigiformes, Strigidae) (see Allen, 1939a: 89; Hall, 1981: 183; Corbet and Hill, 1992: 119; Pavlinov *et al.*, 1995: 95; Jackson and Groves, 2015: 281). Based on *V. mystacinus*, *daubentonii* and *dascyneme* (see Allen, 1939a: 89).

1856. *Isotus* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Type species: *Vespertilio nattereri* Kuhl, 1817. Considered a valid subgenus by Pavlinov *et al.* (1995: 95). - Etymology: From the Greek "*ίσος*", meaning equal and "*ούς*" or "*ώτός*", meaning ear (see Palmer, 1904: 354).

1856. *Myotus:* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Incorrect subsequent spelling (see Palmer, 1904: 442; Jackson and Groves, 2015: 282). (Lapsus).
1866. *Tralatitius:* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 90. Publication date: 1 February 1866. - Comments: Lapsus for *Trilatitus* Gray (seeHall, 1981: 183). Modification of *Trilatitus* (see Ellerman and Morrison-Scott, 1951: 137; Meester *et al.*, 1986: 47). (Lapsus).
1867. *Vespertilio (Pternopterus)* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 706. Publication date: 1867. - Comments: Type species: *Vespertilio (Pternopterus) lobipes* Peters, 1867 (=*Vespertilio muricola* Gray, 1846).
1868. *Pternopterus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1867: 706. - Comments: Type species: *Vespertilio (Pternopterus) lobipes* Peters, 1867 [= *Myotis muricola* (J. Gray, 1846)] by monotypy (see Jackson and Groves, 2015: 282).
1870. *Aëorestes* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 62 (1): 427. Publication date: October 1870. - Comments: Based upon *Vespertilio villosissimus* E. Geoffroy, 1806, *albescens* E. Geoffroy, 1806, *laevis* I. Geoffroy, 1824 and *nigricans* Schinz, 1821 (see Allen, 1939a: 90; Hall, 1981: 183 [who excludes *laevis*]). Hill (in litt. In Meester *et al.*, 1986: 48) pointed out that *villosissimus* is a member of *Lasiurus* Gray, 1831, but all others are indeed *Myotis* representatives. If *villosissimus* can be regarded as the type species of *Aeorestes*, it should instead be included in *Lasiurus* (Meester *et al.*, 1986: 48). Hoofer and Van Den Bussche (2003: 25) consider *Aeorestes* a valid subgenus, including all of the New World species.
1870. *Comastes* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 62 (1) 9: 565. Publication date: 1870. - Comments: Type species: *Vespertilio capaccinii* Bonaparte, 1837, by subsequent designation (see Jackson and Groves, 2015: 282). Based upon *Vespertilio capaccinii* Bonaparte, *megapodius*, *dasycneme* Boie, *limnophilus* (see Allen, 1939a: 90). Based upon *Vespertilio capaccinii* and *dasycneme* according to Hall and Kelson (1959: 159) and Hall (1981: 183). Not *Comastes* Jan, 1863 (Reptilia, Squamata, Colubridae) (see Jackson and Groves, 2015: 282). - Etymology: From the Greek "*κωμαστής*", meaning reveler, probably referring to the animal's nocturnal habits (see Palmer, 1904: 197).
1870. *Exochurus* Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 62 (1) 6: 75. Publication date: 1870. - Comments: Type species: *Vespertilio macrodactylus* Temminck, 1840, by subsequent designation (see Jackson and Groves, 2015: 282). Not of Kolenati (1858). Based upon *Vespertilio macrodactylus* Temminck, *V. horsfieldii* Temminck, and *V. macrotarsus* Waterhouse (see Hall, 1981: 183; Corbet and Hill, 1992: 119). Not of Kolenati, 1858: see Cabrera (1914: 91). - Etymology: From the Greek "*εξοχος*", meaning standing out and "*ούρά*", meaning tail (see Palmer, 1904: 284).
1899. *Euvespertilio* Acloque, Faune de France, Mammifères, 38. - Comments: Includes *Vespertilio emarginatus* Geoffroy, *murinus* Schreber =*myotis* Borkhausen, *mystacinus* Kuhl, *nattereri* Kuhl, and *bechsteinii* Kuhl. Hall and Kelson (1959: 159) and Hall (1981: 183) state that *Euvespertilio* includes *emarginatus* and *murinus* in a composite sense.
1906. *Pizonyx* Miller, Proc. Biol. Soc. Wash., 19: 85. Publication date: 4 June 1906. - Comments: Type species: *Myotis vivesi* Menegaux, 1901, by original designation (see Jackson and Groves, 2015: 282). Considered a valid genus by Hall and Kelson (1959), but only as a subgenus of *Myotis* by Hall (1981: 183).
1917. *Dichromyotis* Bianchi, Ann. Mus. zool. Acad. Impér. Sci. St. Petersbourg, 21: lxxviii (for 2016). Publication date: 14 May - 13 Jun 1917. - Comments: Type species: *Vespertilio formosus* Hodgson, 1835, by original designation according to Csorba *et al.* (2014: 668), by monotypy according to Jackson and Groves (2015: 283).
1917. *Megapipistrellus* Bianchi, Ann. Mus. zool. Acad. Impér. Sci. St. Petersbourg, 21: lxxvii (for 2016). Publication date: 14 May - 13 June 1917. - Comments: Type species: *Pipistrellus annectans* Dobson, 1871, by monotypy (see Jackson and Groves, 2015: 282). Considered a valid subgenus by Pavlinov *et al.* (1995: 95).
1917. *Paramyotis* Bianchi, Ann. Mus. zool. Acad. Impér. Sci. St. Petersbourg, 21: lxxix (for 2016). Publication date: 14 May - 13 Jun 1917. - Comments: Type species: *Vespertilio bechsteinii* Kuhl, 1817. New name for *Nystactes* Kaup, 1829, preoccupied (see Hall and Kelson, 1959: 159; Hall, 1981: 183). Considered a valid subgenus by Pavlinov *et al.* (1995: 95).
1917. *Rickettia* Bianchi, Ann. Mus. zool. Acad. Impér. Sci. St. Petersbourg, 21: lxxvii (for 2016). Publication date: 14 May - 13 Jun 1917. - Comments: Type species: *Vespertilio (Leuconoe) ricketti* Thomas, 1894, by monotypy (see Jackson and Groves, 2015: 282). Valid as a subgenus (see Hall and Kelson, 1959: 159; Hall, 1981: 183).
1929. *Anamygdon* Troughton, Rec. Austr. Mus., 17 (2): 87. Publication date: 26 Jun 1929. - Comments: Type species: *Anamygdon solomonis* Troughton, by original designation (see Jackson and Groves, 2015: 283) [=*Vespertilio adversus* Horsfield, 1824 or *Leuconoe moluccarum* Thomas, 1915 ?].
1934. *Brachyotis:* Taylor, Monographs of the Bureau of Science, Manila, 30: 278. (Lapsus).
1958. *Hesperomyotis* Cabrera, Rev. Mus. Arg. Cienc. Nat., Zool., 4: 103. - Comments: Type species: *Myotis simus* Thomas, 1901, by original designation (see Jackson and Groves, 2015: 283).
1982. *Myottis:* Alberico and Orejuela, Cespedesia, 3 (suppl): 103. (Lapsus).
1995. *Capaccinus:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 95. (Lapsus).
1995. *Exochirus:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 95. (Lapsus).
1995. *Selisius:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 99. (Lapsus).
1996. *Myotiz:* Spiewak, Johansson and Wüthrich, Allergologie, 19 (11): 510 - 511. (Lapsus).
? *Loeconoe:* (Alternate Spelling).
? *Myotis sp.:*

TAXONOMY:

Woodman (1993) indicated that the genus name ending on -otis" is female, and therefore the species name should also be female. Benda and Tsytsulina (2000: 335) agree with Woodman (1993), but continue to understand *Myotis* as a masculine name, because it has been used for over 170 years, and hence was conserved in this way. Simmons (2005) follows Pritchard (1994) and retains the masculine names too. Simmons *et al.* (2021: 9) furthermore remarked that both Woodman (1993) and Pritchard (1994)

overlooked a 1958 ruling by the ICZN, which fixed the gender of *Myotis* as masculine and placed the name as such on the Official List of Generic Names in Zoology. See also Gardner (2005: 184) where *Myotis* = My (mouse) + ot (ear[ed]) + is (Latin third declension ending) = masculine (Mammalia).

Bronner *et al.* (2003) state that the genus *Myotis* has been considered to include several subgenera, but the number thereof, and placement of species, varied considerably. Meester *et al.* (1986) listed three subgenera from the Southern African subregion, namely *Cistugo* Thomas, 1912 (for *seabrai* and *lesueuri*), *Chrysopteron* Jentink, 1910 (for *welwitschii*) and *Selysius* Bonaparte, 1841 (for *tricolor* and *bocagei*). Menu (1987) proposed synonymising *Selysius* under the subgenus *Leuconoe* Boie, 1830 on the basis of dental characters. This was endorsed by Koopman (1993a, 1994) who transferred *M. bocagei* to *Leuconoe* but included other *Selysius* and *Chrysopteron* in the subgenus *Myotis*, and also by Godawa-Stormark (1998)'s phenetic analysis of dental variation in the genus. Phylogenetic analysis of mitochondrial DNA sequences, however, do not support the monophyly of the three subgenera (*Selysius, Leuconoe* and *Myotis*) analysed (Ruedi and Mayer, 2001), but *Cistugo* warrants generic separation (N. Simmons in litt.) owing to the distinct wing glands and unique karyotypes (see Rautenbach *et al.*, 1993) found in *seabrai* and *lesueuri* from southern Africa.

Meester *et al.* (1986) state that their synonymy is slightly modified from Ellerman and Morrison-Scott (1951), who include also *Aeorestes* Fitzinger, 1870, a South American group, in the synonymy of *Myotis*, as does Hall (1981). However, J.E. Hill points out (in litt) that of the species included in this genus, the first, *Vespertilio villosissimus* E. Geoffroy, 1806, is a *Lasiurus* Gray, 1831, although the others, *albescens* E. Geoffroy, 1806, *nigricans* Schinz, 1821, and *levis* I. Geoffroy, 1824, belong in *Myotis*. If, as Hill suggests, *villosissimus* can be regarded as the type species of *Aeorestes*, it should instead be included in *Lasiurus*.

Phylogenetic analyses performed by Ruedi *et al.* (2013: 441) confirm that the Ethiopian clade within *Myotis* is highly supported with all methods of reconstruction (see also Stadelmann *et al.*, 2004b). This clade contains all of the sub-Saharan species, the species inhabiting the islands in the Western Indian Ocean, as well as *M. emarginatus* (which occurs circum-Mediterranean) and two Asian forms (*M.* cf. *formosus* and *M. formosus flavus*).

Patterson *et al.* (2019a: "4') made an extensive phylogenetic analysis on the Afrotropical *Myotis* species and found that they were not monophyletic as *M. welwitschii* formed a sister clade with the east Asian *M. rufoniger*, which was separate from all other African species. All African species, together with *M. rufoniger, M. formosus* and *M. emarginatus* appeared to be grouping on a higher level.

Ghazali *et al.* (2016: 475) state that phylogenetic relationships within *Myotis* reflect biogeographic affinities rather than phenotypes. They also suggest that *Myotis* diverged from other bats in the early Miocene, with a subsequent split between Old and New World lineages about 19 MYA, and that ecomorphs ('Leuconoe' [near-water hunters], 'Myotis' [gleaners], 'Selysius' [aerial hawkers]) emerged independently in different lineages of *Myotis*. Their analyses indicate the ancestor of the African (Ethiopian) clade was most likely a *Myotis*, which diverged from the Eurasian clade about 17.0 MYA. Depending on the calibration, Morales *et al.* (2019: 2271) estimated this last split to have occurred at either 27 ± 3.5 mya or at 17.8 ± 3.5 mya.

Bogdanowicz *et al.* (2015: Fig. 2, p. 640) mention Moroccan data for *Myotis nattereri*, but in the supplementary information, these are mentioned as *Myotis* cf. *nattereri*. They also include the Mediterranean coastal areas of Morocco and Algeria in the distribution area of *M. capaccinii*.

Currently (Simmons and Cirranello, 2024a) recognized subgenera and species of the genus *Myotis*:
Subgenus *Pizonyx* Miller, 1906: *albescens* (E. Geoffroy Saint-Hilaire, 1806) – southern Veracruz (Mexico), Guatemala, Honduras, Nicaragua, Panama, Colombia, Venezuela, Guyana, Surinam, Equador, Peru, Brazil, Uruguay, northern Argentina, Paraguay and Bolivia (Simmons, 2005: 501); *arescens* Osgood, 1943 – C Chile; *armiensis* Carrión-Bonilla and Cook, 2020 – Panama; Costa Rica; *atacamensis* (Lataste, 1892) – southern Peru, northern Chile (Simmons, 2005: 502); *attenboroughi* Moratelli, Wilson, Novaes, Helgen and Gutiérrez, 2017 – Tobago Island; *auriculus* Baker and Stains, 1955 – Arizona and New Mexico (USA) to Jalisco and Veracruz (Mexico); Guatemala (Simmons, 2005: 502); auriculus Baker and Stains, 1955: USA (Arizona and New Mexico) to Mexico (Chihuahua, Coahuila, Colima, Durango, Hidalgo, Jalisco, Michoacán, Nayarit, Nuevo Leon, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas); Guatemala; *austroriparius* (Rhoads, 1897) –

southeastern USA including Florida, north to Indiana and North Carolina, west to Texas and southeastern Oklahoma (Simmons, 2005: 502); *bakeri* Moratelli, Novaes, Bonilla and Wilson, 2019 – Known only from two localities in the departments of Lima and Lambayeque, Peru; *barquezi* Novaes, Cláudio, Díaz, Wilson, Weksler and Moratelli, 2022 – Known only from the type locality in Argentina; *brandtii* (Eversmann, 1845) – Britain south to Italy, Greece and Bulgaria, east to Kazakhstan and Mongolia, eastern Siberia, Kamchatka Peninsula and Kurile Islands; Ussuri region (Russia), Korea (Simmons, 2005: 503); *californicus* (Audubon and Bachman, 1842) – southern Alaska Panhandle (USA) to Baja California and higher elevations in the Sonoran and Chihuahuan deserts (Mexico); Guatemala (Simmons, 2005: 504); *carteri* LaVal, 1973 – Mexico (Colima, Jalisco, México, Michoacán, Nayarit); *caucensis* J.A. Allen, 1914 – occurs along the Andes of Colombia, Ecuador, and Peru, including intermontane valleys and adjacent Amazon lowlands of those countries; *chiloensis* (G.R. Waterhouse, 1840) – central and southern Chile; Argentina (Simmons, 2005: 504); *ciliolabrum* (Merriam, 1886) – southern Alberta and Saskatchewan (Canada) south through eastern Colorado and western Kansas (USA) (Simmons, 2005: 505); *clydejonesi* Moratelli, Wilson, Gardner, Fisher and Gutiérrez, 2016 – Only known from the type specimen from Suriname; *cobanensis* Goodwin, 1955 – central Guatemala (Simmons, 2005: 505); *csorbai* Topál, 1997 – Nepal (Simmons, 2005: 505); *diminutus* Moratelli and Wilson, 2010 – Ecuador, Colombia; *dinellii* Thomas, 1902 – Bolivia, Uruguay, Argentina (incl. Entre dos Rios; Patagonia); Brazil; *dominicensis* Miller, 1902 – Dominica, Guadeloupe (Simmons, 2005: 506); *elegans* Hall, 1962 – Mexico to Costa Rica (Simmons, 2005: 506); *evotis* (H. Allen, 1864) – southern British Columbia, southern Alberta, southern Saskatchewan (Canada) to New Mexico (USA) and Baja California (Mexico) (Simmons, 2005: 506); *findleyi* Bogan, 1978 – Trés Marías Isls (Mexico) (Simmons, 2005: 507);*fortidens* Miller and Allen, 1928 – Sonora and Veracruz (Mexico) to Guatemala (Simmons, 2005: 507); *grisescens* A. H. Howell, 1909 – Florida Panhandle to Kentucky, Indiana, Illinois, eastern Kansas and northeastern Oklahoma (USA) (Simmons, 2005: 508); *handleyi* Moratelli, Gardner, de Oliveira and Wilson, 2013 – Known from two cordilleras in northern Venezuela; *izecksohni* Moratelli, Peracchi, Dias and Oliveira, 2011 – Brazil; *keaysi* J. A. Allen, 1914 – Tamaulipas (Mexico) to Bolivia, northern Argentina, Peru, Ecuador, Venezuela and Trinidad (Simmons, 2005: 509); *keenii* (Merriam, 1895) – Alaska Panhandle to W Washington (USA); Mackenzie to Prince Edward Island; British Columbia (Canada), south to Arkansas and Florida Panhandle (USA); *larensis* LaVal, 1973 – mainland South America in northeastern Colombia and northwestern Venezuela; *lavali* Moratelli, Peracchi, Dias and Oliveira, 2011 – Brazil, Paraguay, Argentina; *leibii* (Audubon and Bachman, 1842) – eastern North America from southern Ontario, southern Quebec (Canada) and southern Maine (USA) to southwards to Georgia and western to eastern Oklahoma (USA) (Simmons, 2005: 509); *levis* (I. Geoffroy Saint-Hilaire, 1824) – Bolivia, Argentina, southeastern Brazil, Uruguay (Simmons, 2005: 510); *lucifugus* (Le Conte, 1831) – Alaska (USA) to Labrador and Newfoundland (Canada), south to southern California, northern Arizona, northern New Mexico (USA) (Simmons, 2005: 510); *martiniquensis* LaVal, 1973 – Martinique, Barbados (Lesser Antilles) (Simmons, 2005: 511); *midastactus* Moratelli and Wilson, 2014 – Bolivia, Paraguay; *moratellii* Novaes, Cláudio, Carrión-Bonilla, Abreu, Wilson, Maldonado and Weksler, 2021 – W Ecuador; *nesopolus* Miller, 1900 – northeastern Venezuela; Curaçao and Bonaire (Netherlands Antilles) (Simmons, 2005: 513); *nigricans* (Schinz, 1821) – Nayarit and Tamaulipas (Mexico) to Peru, Bolivia, northern Argentina, Paraguay and southern Brazil; Trinidad and Tobago; St. Martin, Montserrat, Grenada (Lesser Antilles) (Simmons, 2005: 513); *nyctor* LaVal and Schwartz, 1975 – Barbados; Grenada (?); *occultus* Hollister, 1909 – southern California to Arizona, New Mexico and Colorado (USA), south to Distrito Federal (Mexico) (Simmons, 2005: 514); *oxyotus* (Peters, 1867) – Venezuela to Bolivia; Colombia, Ecuador, Panama; Costa Rica; Peru; possibly Guyana; *pampa* Novaes, Wilson and Moratelli, 2021 – Uruguay (Artigas and Tacuarembó provinces); *pilosatibialis* LaVal, 1973 – Colombia; *planiceps* Baker, 1955 – Coahuila, Nuevo León and Zacatecas (Mexico) (Simmons, 2005: 515); *riparius* Handley, 1960 – Honduras south to Uruguay, eastern Brazil, Argentina, Paraguay and Bolivia; Trinidad (Simmons, 2005: 515); *ruber* (E. Geoffroy Saint-Hilaire, 1806) – southeastern Brazil, southeastern Paraguay, northeastern Argentina (Simmons, 2005: 516); *septentrionalis* (Trouessart, 1897) – eastern USA and Canada west to British Columbia, eastern Montana, eastern Wyoming; south to Alabama, Georgia, and Florida Panhandle (Simmons, 2005: 516); *sibiricus* (Kastschenko, 1905) – Southern part of the Russian Far East, S of the Uda river (incl. Sakhalin and Kunashir isls); Korea: Mongolia; *simus* Thomas, 1901 – Colombia, Ecuador, Peru, northern Brazil, Bolivia, northeastern Argentina and Paraguay (Simmons, 2005: 517); *sodalis* Miller and G.M. Allen, 1928 – New Hampshire to Florida Panhandle, west to Wisconsin and

Oklahoma (USA) (Simmons, 2005: 517); *thysanodes* Miller, 1897 – Chiapas (Mexico) to southwestern South Dekota (USA) and south-central British Columbia (Canada) (Simmons, 2005: 517); *velifer* (J. A. Allen, 1890) – Honduras to Kansas and southeastern California (USA) (Simmons, 2005: 517); *vivesi* Menegaux, 1901 – coast of Sonora and Baja California (Mexico), mainly on small islands (Simmons, 2005: 518); *volans* (H. Allen, 1866) – Jalisco to Veracruz (Mexico); Alaska Panhandle (USA) to Baja California (Mexico), east to northern Nuevo León (Mexico), South Dekota (USA) and central Alberta (Canada) (Simmons, 2005: 518); *yumanensis* (H. Allen, 1864) – Hidalgo, Morelos and Baja California (Mexico) north to British Columbia (Canada), east to Montana and western Texas (USA) (Simmons, 2005: 518).

Subgenus *Chrysopteron* Jentink, 1910: ***anjouanensis*** Dorst, 1960; *bartelsi* (Jentink, 1910) – Indonesia (Java and Bali); ***bocagii*** (Peters, 1870); ***dieteri*** M. Happold, 2005; ***emarginatus*** (E. Geoffroy Saint-Hilaire, 1806); *formosus* (Hodgson, 1835) – Afghanistan to northern India, Nepal, Tibet, Kweichow, Kwangsi, Kiangsu and Fukien (China), Taiwan, Korea, Tsushima Isl (Japan), Malaysia, Philippines, Sumatra, Java, Sulawesi and Bali (Simmons, 2005: 507); ***goudotii*** (A.Smith, 1834); *hermani* Thomas, 1923 – Sumatra (Indonesia) (Simmons, 2005: 508); ***morrisi*** Hill, 1971; ***nimbaensis*** Simmons, Flanders, Bakwo Fils, Parker, Suter, Bamba, Douno, Keita, Morales and Frick, 2021; *rufoniger* (Tomes, 1858) – Korea, Japan, China, Taiwan, Laos, Vietnam; *rufopictus* (G.R. Waterhouse, 1845) – Philippines; ***scotti*** Thomas, 1927; ***tricolor*** (Temminck, 1832); *weberi* (Jentink, 1890) – Indonesia (Sulawesi); ***welwitschii*** (Gray, 1866).

Subgenus *Myotis* Kaup, 1829: *adversus* (Horsfield, 1824) – islands in Indonesia, New South Wales, Taiwan, possibly Vietnam and peninsular Malaysia (Simmons, 2005: 500); *alcathoe* von Helversen and Heller, 2001 – Greece, Hungary, France (Simmons, 2005: 501); *altarium* Thomas, 1911 – Szechwan, Kweichow (China), Thailand (Simmons, 2005: 501); *alticraniatus* Osgood, 1932 – Vietnam, Laos; *ancricola* Kruskop, Borisenko, Dudorova and Artyushin, 2018 – Only known from the type locality and the Ngoc Ling mountains in Vietnam; *annatessae* Kruskop and Borisenko, 2013 – Vietnam; Central Laos; *annectans* (Dobson, 1871) – northeastern India to Burma, Thailand, Laos, Cambodia and Vietnam (Simmons, 2005: 502); *ater* (Peters, 1866) – Vietnam, western Sumatra, Peninsular Malaysia, Sulawesi, Togian Isl, northern Borneo, Moluccas, Papua New Guinea (Simmons, 2005: 502); *australis* Dobson, 1878) – New South Wales (Simmons, 2005: 502); *bechsteinii* (Kuhl, 1817) – Europe to Caucasus and Iran; Bulgaria; England; southern Sweden (Simmons, 2005: 503); *blythii* (Tomes, 1857) – Turkey and Israel to Iraq and Iran; northwestern India and the Himalayas; northwestern Altai Mtns; Inner Mongolia and Shensi (China) (Simmons, 2005: 503); *bombinus* Thomas, 1906 – Japan, Korea, southeastern Siberia, northeastern China (Simmons, 2005: 503); *borneoensis* Hill and Francis, 1984 – Sabah (Borneo); *bucharensis* Kuzyakin, 1950 – Uzbekistan, Tajikistan and Afghanistan (Simmons, 2005: 504); ***capaccinii*** (Bonaparte, 1837); *chinensis* (Tomes, 1857) – Szechwan and Yunnan to Kiangsu (China); Hong Kong; northern Thailand; Burma; Vietnam (Simmons, 2005: 505); *crypticus* Ruedi, Ibáñez, Salicini, Juste and Puechmaille, 2019 – Mountain areas of N + C Spain, S France, Italy, SW Austria?, W Switzerland, SE France; *dasycneme* (Boie, 1825) – France and Sweden east to Yenisei River (Russia), south to Ukraine, northwestern Kazakhstan, China (Simmons, 2005: 505); *daubentonii* (Kuhl, 1817) – Europe (including Britain and Ireland; Scandinavia) east to Kamtschatka, Vladivostok, Sakhalin and Kurile Isls (Russia), Japan, Korea, Manchuria, northern and eastern China (including Tibet), Vietnam (Simmons, 2005: 505); *davidii* (Peters, 1869) – northern China (Simmons, 2005: 506); *escalerai* Cabrera, 1904 – France, Spain, Portugal; *federatus* Thomas, 1916 – Peninsular Malaysia; *fimbriatus* (Peters, 1871) – southeastern China (Simmons, 2005: 507); *frater* G. M. Allen, 1923 – eastern Siberia, Ussuri Region, Krasnoyarsk Region (Russia) to Korea, Heilungkiang (China), southeastern China; Japan (Simmons, 2005: 507); *gomantongensis* Francis and Hill, 1998 – Sabah (Borneo, Malaysia) (Simmons, 2005: 508); *hasseltii* (Temminck, 1840) – eastern India, Sri Lanka, Burma, Thailand, Cambodia, Vietnam, western Malaysia, Sumatra, Mentawai Isls, Riau Arch., Java, Borneo (Simmons, 2005: 508); *hayesi* Csorba and Furey, 2022 – Known from the type locality in Cambodja; *horsfieldii* (Temminck, 1840) – India, Andaman Isls, southeastern China, Thailand, Burma, Laos, Vietnam, western Malaysia, Java, Bali, Sulawesi, Borneo, Philippines (Simmons, 2005: 508); *hoveli* Harrison, 1964 – Israel, Lebanon, Syria, Turkey; *hyrcanicus* Benda, Reiter and Vallo, 2012 – Only known from the type locality in Iran; *ikonnikovi* Ognev, 1912 – Ussuri region and North Korea to Lake Baikal (Russia), the Altai Mtns and Mongolia, northeastern China; Sakhalin Isl (Russia) and Honshû and Hokkaido Isls (Japan) (Simmons, 2005: 509); *indochinensis* Son, Görföl, Francis, Motokawa, Estók, Endo, Thong, Dang, Oshida and Csorba, 2013 – Vietnam; *insularum*

(Dobson, 1878) – Samoa (Simmons, 2005: 509); *laniger* (Peters, 1871) – southern China including Tibet, Vietnam, eastern India (Simmons, 2005: 509); *longicaudatus* Ognev, 1927 – E. Siberia, Ussuri region, Korea; Mongolia; *longipes* (Dobson, 1873) – Afghanistan, northeastern India, Nepal (Simmons, 2005: 510); *macrodactylus* (Temminck, 1840) – Japan, Kunashir Isl and Kurile Isls (Russia), southeastern Siberia, Korea (Simmons, 2005: 510); *macropus* (Gould, 1854) – southern Australia (Simmons, 2005: 511); *macrotarsus* (G.R. Waterhouse, 1845) – Philippines, northern Borneo (Simmons, 2005: 511); *moluccarum* (Thomas, 1915) – Ambon and Kai Isls (Moluccas), northern and western Australia, Seram, Waigeo Isl (West Palua, Indonesia), Papua New Guinea, Bismarck Arch., Solomon Isls (Simmons, 2005: 511); *montivagus* (Dobson, 1874) – Yunnan to Fukien and Chihil (China), northeastern India, Burma, Vietnam, Laos, northeastern Thailand, western Malaysia, Borneo (Simmons, 2005: 511); *muricola* (Gray, 1846) – Afghanistan through northern India and Nepal to Taiwan, Vietnam, Malaysia, Indonesia and New Guinea (Simmons, 2005: 512); *myotis* (Borkhausen, 1797) – central and southern Europe, east to Ukraine; southern England, most Mediterranean islands; Asia Minor; Lebanon, Syria and Israel (Simmons, 2005: 512); ***mystacinus*** (Kuhl, 1817); *nattereri* (Kuhl, 1817) – Ireland, Great Britain, Europe (except northern Scandinavia), Morocco, northern Algeria, Turkey, Israel, Jorden, Lebanon, Iraq, Iran, Bulgaria, Crimea and Caucasus to Turkmenistan (Simmons, 2005: 513); *nipalensis* (Dobson, 1871) – Asia from the Caucasus mountains and Caspian Sea to E Turkestan, Tibet, Nepal, Kazakhstan, Mongolia, S Siberia, Turkey, NW Iran. Wiantoro et al. (2012: 272) indicate that *nipalensis* is distributed from Iran, Turkey, and Uzbekistan to Nepal, Mongolia, Tibet, NW China and Siberia. Vietnam?; *nustrale* Ruedi, Beuneux and Puechmaille, 2023 – Endemic to Corsica; *pequinius* Thomas, 1908 – Hong Kong, Hopeh, Shantung, Honan and Kiangsu (China) (Simmons, 2005: 514); *petax* Hollister, 1912 – Kamtschatka, Vladivostok, Sakhalin and Kurile Isls (Russia), Japan, Korea, Manchuria, E and S China Mongolia, Tibet, Vietnam; *peytoni* Wroughton and Ryley, 1913 – S + EC India; *phanluongi* Borisenko, Kruskop and Ivanova, 2009 – Vietnam; *pilosus* (Peters, 1869) – China, Hong Kong, Vietnam, Laos, NE India; *pruinosus* Yoshiyuki, 1971 – Honshu and Shikoku (Japan) (Simmons, 2005: 515); ***punicus*** Felten, Spitzenberger and Storch, 1977; *ridleyi* Thomas, 1898 – western Malaysia, Sumatra, Borneo (Simmons, 2005: 515); *rosseti* (Oey, 1951) – Cambodia, Thailand (Simmons, 2005: 516); *schaubi* Kormos, 1934 – Armenia and western Iran (Simmons, 2005: 516); *secundus* Ruedi, Csorba, Lin and Chou, 2015 – Taiwan; *sicarius* Thomas, 1915 – northeastern India and Nepal (Simmons, 2005: 516); *siligorensis* (Hodgson, 1855) – northern India to southern China, Burma, Vietnam and Laos; south to western Malaysia; Borneo (Simmons, 2005: 516); *soror* Ruedi, Csorba, Lin and Chou, 2015 – Taiwan (only known from the type specimen); *sowerbyi* A.B. Howell, 1926 – China; *stalkeri* Thomas, 1910 – Kai and Gebe Isls (Molucca Isls), Waigeo Isl. (Prov. of Papua, Indonesia) (Simmons, 2005: 517); *tschuliensis* Kusjakin, 1935 – Transcaucasia, Iraq, Turkmenia; *yanbarensis* Maeda and Matsumura, 1998 – Northern Okinawa Isl (Japan) (Simmons, 2005: 518); ***zenatius*** Ibáñez, Juste, Salicini, Puechmaille and Ruedi, 2019.

COMMON NAMES:
Czech: netopýři myší, ouška myší, netopýrcové. English: Mouse-eared Bats, Little Brown Bats, Hairy Bats, Large-footed Bats. French: Murins. German: Mausohr, Mausohren. Polish: nocki. Ukrainian: Нічниця [= Nichnytsya].

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
In Africa *Myotis* sp. have been found deposits of the Plio-Pleistocene, at Bolt's Farm, South Africa (Broom, 1948). Early Pleistocene, at Olduvai (Butler, 1978). Geraads *et al.* (2010: 279) reported the presence of *Myotis* in Late Cenozoic (ca. 2.5 MYA) deposits in Ahl al Oughlam, Morocco.

Molecular dating performed by Ruedi *et al.* (2013: 437-441) suggest an origin of all recent *Myotis* in the early Miocene (about 21 MYA with 95 % highest posterior density interval 23 - 20 MYA).

Shi and Rabosky (2015: 1532) report the approximate fossil date for crown Myotinae to be 27 MYA.

However, a recent study by Gunnell *et al.* (2017) reported on a fossil *Myotis* found in a Belgian Oligocene locality, dating 33 MYA. Morales *et al.* (2019: 2264) find this to be consistent with other fossils of a primitive *Myotis*-like form found in Africa suggest and dating from the late Eocene (37.8 - 33.9 mya), which suggest that the early diversification of the subfamily might have occurred on that continent. However, these authors also indicate that this interpretation depends on the correct identification of the "*Myotis*-like" material. Alternatively, the radiation of *Myotis* could only date from about 18 mya.

The Ethiopian clade (see Taxonomy) would have been separated about 12.33 (15 - 10) MYA.

MOLECULAR BIOLOGY:
Karyotype
Baker *et al.* (1974) recorded the karyotype of *Myotis* as 2*n* = 44, AA = 50, but Dippenaar *et al.* (1983) give it as 2*n* = 50, AA = 48 in both *seabrai* and *lesueuri*.

PREDATORS:
In Algeria, Djilali *et al.* (2016: 159) found the Short-eared owl (*Asio flammeus*) to feed primarily on bats of the genus *Myotis*. They made up 37.8 % of all prey items (195 specimens on 516 prey items). The second one was *Gerbillus nanus* with only 5.4 % of all preys.

PARASITES:
From non-specified *Myotis* specimens, the following nycteribiids were reported by Vermeil (1960) from Tunisia: *Penicillidia conspicua* Speiser, 1900, *Nycteribia vexata vexata* Westwood, 1835, *Nycteribia biarticulata* Hermann, 1804, *Nycteribia latreillii* Leach, 1817, and *Nycteribia schmidlii* Schiner, 1853.

VIRUSES:
Although we cannot find this confirmed, Bonilla-Aldana *et al.* (2020: 5) mention "Multiple studies point at bats of the genus *Myotis* as the main reservoir for Ebola virus given that these bats carry a copy of viral gene VP35, which may hinder human and animal immune responses and thus explaining its high mortality rates."

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Egypt, Ethiopia, Gabon, Kenya, Madagascar, Malawi, Tanzania, Tunisia, Uganda.

Subgenus *Myotis (Chrysopteron)* Jentink, 1910

*1910. *Chrysopteron* Jentink, Notes Leyden Mus., 32: 74. Publication date: January 1910 [Goto Description]. - Comments: Type species: *Chryopteron bartelsii* Jentink, 1910 [=*Vespertilio formosa* Hodgson, 1835]. Considered a valid subgenus by Hall and Kelson (1959: 159), Hall (1981: 183), Corbet and Hill (1992: 121) and Pavlinov *et al.* (1995: 95).
1924. *Epetiscus:* Granvik, Lunds Univ. Arss. N.F., (2) 21 (3): 12. (Lapsus).

Myotis (Chrysopteron) anjouanensis Dorst, 1960

*1960. *Myotis Goudoti anjouanensis* Dorst, Bull. Mus. natn. Hist. nat., Paris, sér 2, 31: 476 (for 1959). Type locality: Comoros: Anjouan Island. [Goto Description]. Holotype: MNHN ZM-MO-1886-1536: ad ♀, skull and alcoholic. Collected by: Léon Humblot. - Etymology: The specific name refers to the island where the type specimen was collected.
? *Myotis (Chrysopteron) anjouanensis:* (Current Combination).
? *Myotis anjouanensis;* (Name Combination).

TAXONOMY:
Considered a synonym of *goudotii* by Koopman (1993a: 211), and a subspecies of *goudotii* by Peterson *et al.* (1995: 89), but a valid species by Simmons (2005).

Csorba *et al.* (2014: 667) and Simmons and Cirranello (2023b: 79) include *anjouanensis* in the subgenus *Chrysopteron*.

COMMON NAMES:
Czech: netopýr anžuánský. English: Anjouan Myotis, Anjouan Mouse-eared Bat. French: Murin d'Anjouan, Vespertilion de l'Ile d'Anjouan. German: Anjouan-Mausohr.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since it has only recently been recognised as a distinct species, and there is still very little information on its extent of occurrence, status, threats and ecological requirements (Jacobs, 2008c; IUCN, 2009; Jacobs, 2019c).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs, 2019c). 2008: DD ver 3.1 (2001) (Jacobs, 2008c; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs, 2004k; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs, 2008c; IUCN, 2009; Jacobs, 2019c).

CONSERVATION ACTIONS:
Jacobs (2008c) [in IUCN (2009)] and Jacobs (2019c) reports that it is not known if the species is present in any protected areas. Further studies are needed into the natural history and possible threats to this little-known species.

GENERAL DISTRIBUTION:
Myotis anjouanensis is endemic to the island of Anjouan in the Comoros Islands.

Native: Comoros.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 77 minutes, and the digestibility rate about 79.9 %.

POPULATION:
Structure and Density
There is currently little information on the abundance of this species (Jacobs, 2008c; IUCN, 2009; Jacobs, 2019c). Specimens were collected by Goodman, 2007) from Anjouan in 2007.

Trend
2018: Unknown (Jacobs, 2019c).

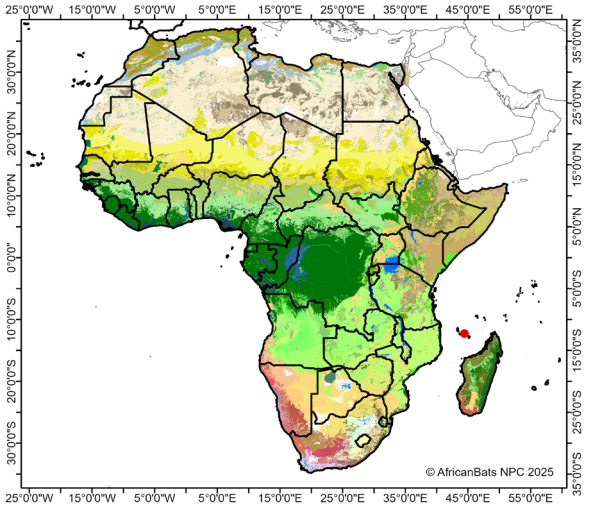

Figure 260. Distribution of *Myotis (Chrysopteron) anjouanensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Comoros.

Myotis (Chrysopteron) bocagii (Peters, 1870)

*1870. *Vespertilio Bocagii* Peters, J. Sci. mat. phys. nat., ser 1, 3 (10): 125. Publication date: December 1870. Type locality: Angola: Duque de Bragança [08 55 S 16 10 E]. Lectotype: ZMB 3973: ad ♂, skull and alcoholic. Presented/Donated by: José Vicente Barboza du Bocage. Lectotype designated by Turni and Kock (2008: 57). - Comments: Turni and Kock (2008: 57) also indicate that Peters did not mention the number of specimens he examined, therefore it might be possible that additional syntypes might have existed in the Lisbon museum, but were destroyed by the fire in 1978. Thorn *et al.* (2009: 51) situate the type locality at 09 23 S 15 53 E. - Etymology: In honour of J.V. Barbosa du Bocage, an eminent Portuguese zoologist, who worked during the nineteenth century, and who named material from the Congo and Angola collected by his Portuguese colleague Snr. M. Jose d'Anchieta (Smithers, 1983: 93).
1976. *Myotis boccagei:* Brosset, Z. Tierpsychol., 42 (1): 50. (Lapsus).
1996. *Myotis bocagi:* Kityo and Kerbis, J. East Afr. Nat. Hist., 85: 63. (Lapsus).
2019. *Myotis bocageii:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).
? *Myotis (Chrysopteron) bocagii:* (Current Combination).
? *Myotis (Selysius) bocagei:* (Name Combination, Alternate Spelling).
? *Myotis bocagei:* (Alternate Spelling).
? *Myotis bocagii:* (Name Combination).

TAXONOMY:
Mentioned as *bocagei* by Corbet (1978: 49), Smithers (1983: 93), Meester *et al.* (1986: 49), Koopman (1993a: 209), Horáček *et al.* (2000: 121) Wilson and Cole (2000: 58), Hutson *et al.* (2001: 28), Fenton and Bogdanowicz (2002: 1008) but as *bocagii* by Ansell and Dowsett (1988: 37), Harrison and Bates (1991: 76), Grubb *et al.* (1998: 82), Stadelmann *et al.* (2004b: 178); and as *bocagi* by Kityo and Kerbis (1996: 63).

Csorba *et al.* (2014: 667) and Simmons and Cirranello (2023b: 79) include *bocagii* in the subgenus *Chrysopteron*, but see Ruedi and Mayer (2001: 436), Ghazali *et al.* (2016: 476) and Patterson *et al.* (2019a: "2") who reject the subgeneric division.

The phylogenetic analyses by Patterson *et al.* (2019a: "5") revealed the presence of two groups within *M. bocagii*: one including a single Senegalese specimen and two all the remainder, including material from Ghana, DRC, Kenya, and Tanzania. These findings do not support the currently accepted division into two subspecies: *bocagii* and *cupreolus*, although the authors stress that no material from Angola (where the type of *bocagii* was collected) was included in the

analyses (p. "9"). As such, it might be possible that two subspecies might still be present, with *bocagii* restricted to Angola. Until this has been resolved, we do retain the two traditionally recognized subspecies. Patterson *et al.* (2019a) also indicated that *M. bocagii* forms a sister group with *M. goudotii* + *M. anjouanensis*, which in turn form a sister group to *M. tricolor* and *M. emarginatus* (based on nuclear genes).

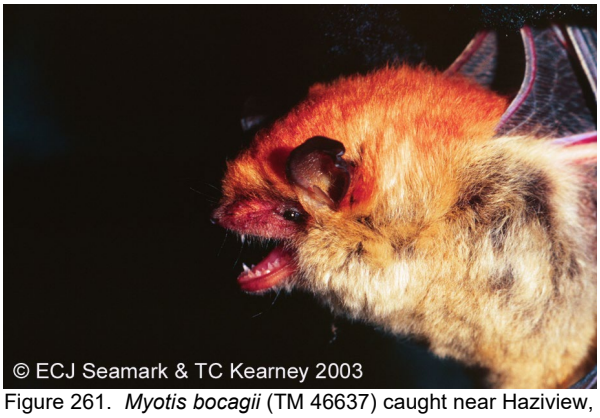

Figure 261. *Myotis bocagii* (TM 46637) caught near Haziview, Mpumalanga, South Africa.

COMMON NAMES:
Afrikaans: Rooi langhaarvlermuis. Castilian (Spain): Murciélago de Orejas de Ratón. Chinese: 棕红鼠耳蝠. Czech: netopýr Bocageův. English: Rufous Mouse-eared bat, Bocage's Mouse-eared Bat, Rufous Mouse-eared Myotis, Rufous Hairy Bat, Bocage Banana Bat, Bocage's Hairy Bat. French: Murin roux, Murin de Du Bocage. German: Kupferfarbenes Mausohr, Bananen-Mausohr. Malawian: Liputiputi, Ndemiya, Namsimsi, Namzeze. Portuguese: Morcego lanudo de Bocage.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs, 2008d; IUCN, 2009; Monadjem and Jacobs, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Jacobs, 2017a). 2008: LC ver 3.1 (2001) (Jacobs, 2008d; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs, 2004f; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016j). 2004: DD ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Jacobs, 2008d; IUCN, 2009; Monadjem and Jacobs, 2017a).

CONSERVATION ACTIONS:
Jacobs (2008d) [in IUCN (2009)] and Monadjem and Jacobs (2017a) reports that it has been recorded from Kruger National Park, South Africa (Skinner and Chimimba, 2005), Dzanga-Sangha Special Dense Forest Reserve in the Central African Republic (Lunde *et al.*, 2001), and from the Manga Forest Reserve in Tanzania (Doggart *et al.*, 1999b), and in view of the species wide range it is presumed to be present in many more protected areas. There are no direct conservation measures currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Myotis bocagii is widespread throughout much of sub-Saharan Africa. It occurs from Sierra Leone and Senegal in West Africa, eastwards through Cameroon and Central Africa, to Ethiopia and East Africa, being recorded as far south as northeastern South Africa. Outside of Africa it has been recorded from southern Yemen.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 594,469 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 564); Benin; Burkina Faso (Kangoyé *et al.*, 2015a: 618); Burundi; Cameroon; Central African Republic; Congo (The Democratic Republic of the) (Allen, 1917; Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 564); Côte d'Ivoire; Equatorial Guinea; Eswatini (Monadjem *et al.*, 2010d: 564; Shapiro and Monadjem, 2015: 353, Monadjem *et al.*, 2021: 5); Ethiopia; Gabon; Ghana; Guinea (Fahr *et al.*, 2006a: 73); Kenya; Liberia (Monadjem and Fahr, 2007: 50); Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 564); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 564; Monadjem *et al.*, 2010c: 383); Nigeria; Rwanda; Senegal; Sierra Leone (Weber *et al.*, 2019: 25); South Africa (Monadjem *et al.*, 2010d: 564); Sudan; Tanzania (Stanley and Goodman, 2011: 43); Togo; Uganda; Yemen; Zambia (Monadjem *et al.*, 2010d: 564); Zimbabwe (Monadjem *et al.*, 2010d: 564).

Bates *et al.* (2013: 339) reject the occurrence of *M. bocagii* in the Republic of Congo as Happold (2013dn: 693) only provided a map without any supporting data.

DETAILED MORPHOLOGY:
Brain
Szubert-Kruszyńska *et al.* (2018: Suppl.) mention a brain mass of 0.21 g for an average body mass of 7.6 g.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.4 Pa, aspect ratio 8.5 for a wingspan of 32 cm and a wing area of 123 cm^2 and a body mass of 8 g.

ECHOLOCATION:
Schoeman and Waddington (2011: 291) mention a F_{peak}: 43.2 ± 0.2 kHz and a duration: 2.0 ± 0.1 ms for specimens from Durban, South Africa. Monadjem *et al.* (2017c: 179) reported for one specimen the following parameters from Swaziland: F_{min}: 30.1 kHz, F_{knee}: 41.2 kHz, F_c: 36.6 kHz, and duration: 2.8 ms. They were also to capture the call up to a distance of 5 m.

Moir (2020: 30) and Moir *et al.* (2021a: 371) reported 69 calls of two bats from southern KwaZulu-Natal and Eastern Cape with F_{max}: 64.98 ± 2.71 (58.57 - 69.35) kHz, F_{min}: 35.69 ± 0.16 (35.31 - 35.69) kHz, F_{char}: 39.68 ± 1.08 (38.31 - 46.99) kHz, F_{knee}: 59.01 ± 6.41 (50.35 - 65.79) kHz, and duration: 2.27 ± 0.13 (2.18 - 2.36) ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 8 bats: F_{max}: 56.97 ± 7.52 kHz, F_{min}: 27.67 ± 3.64 kHz, F_{knee}: 43.99 ± 7.41 kHz, F_{char}: 40.53 ± 6.86 kHz, slope: 124.2 ± 3364.36 OPS, duration: 2.76 ± 0.51 ms.

In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 3 calls: Interpulse interval: 91.6 ± 25.1 (62.6 - 107.0) ms; F_{max}: 47.6 ± 3.4 (44.9 - 51.4) kHz; Start slope: -14.2 ± 2.9 (-10.8 - -16.0) kHz/ms; End slope: -20.2 ± 6.6 (-13.3 - -26.4) kHz/ms; Ledge duration: 0.3 ± 0.0 (0.3 - 0.3) ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 133 calls of 2 bats: F_{peak}: 40.1 ± 1.0 (39.0 - 42.0) kHz, F_{min}: 31.4 ± 4.2 (28.8 - 42.0) kHz, F_{max}: 67.9 ± 5.6 (61.9 - 76.5) kHz, duration: 3.2 ± 0.7 (2.2 - 4.3) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd (Frequency modulation downward) sonotype.

Sound files are available at the Chirovox website (https://www.chirovox.org/), e.g.: https://chirovox.elte.hu/sounds/A003663_WQKZZOVOSU.WAV, https://chirovox.elte.hu/sounds/A003664_SRAHXRVJTL.WAV, https://chirovox.elte.hu/sounds/A003665_BEMWQOEXAP.WAV, https://chirovox.elte.hu/sounds/A003666_KBLUCEWOVT.WAV

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 44, FN = 50, BA = 8, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa. These results are the same as those obtained for *M. tricolor* specimens from South Africa and Zimbabwe (Rautenbach *et al.*, 1993).

Genetics
See Hoofer and Van Den Bussche (2003).

Morales *et al.* (2024: Suppl.) reported the total length of the genome to consist of 2001.76M base pairs.

HABITAT:
In southern Africa, this species primarily (82 %) occurs in Savanna habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

In the Mount Nimba area, Monadjem *et al.* (2016y: 369) collected one specimen in old growth forest at 420 m.

HABITS:
Brosset (1976) found that harem groups of female *M. bocagii*'s remained very stable over a period of several years. The males in these groups were replaced more often.

ROOST:
Mamba *et al.* (2020: 134) reported on a female, which was captured inside the leaves of a banana plants. Happold and Happold (2023: 143) indicate that they are also found roosting among leaves of other trees (e.g., *Hyphaene* palms). In Gabon, these bats live in harems (one adult male and two to seven adult females and their young)..

DIET:
From the Umbilo River in KwaZulu Natal (RSA), Naidoo *et al.* (2011: 26) reported the following prey volume percentages: during summer: Lepidoptera (1.3 ± 1.9), Coleoptera (0.8 ± 1.0), Hemiptera (8.5 ± 13.1), Diptera (37.8 ± 25.8), and Trichoptera (51.8 ± 29.9); during winter: Lepidoptera (7.5 ± 10.6), Coleoptera (32.5 ±

46.1), Hemiptera (20.0 ± 28.3), Diptera (33.4 ± 33.0), and Trichoptera (6.7 ± 4.7).

Weier *et al.* (2019c: 6) investigated droppings from this species in the Levubu region (Limpopo, RSA) and found DNA sequences of *Bathycoelia distincta* Distant, 1878 (Hemiptera).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 78 minutes, and the digestibility rate about 79.8 %.

Morales *et al.* (2024: Suppl.) assigned this species to the Trawler ecomorph type.

POPULATION:
Structure and Density
Although this species is difficult to catch it is possibly not very rare (Jacobs, 2008d; IUCN, 2009; Monadjem and Jacobs, 2017a).

Trend
2016: Unknown (Monadjem and Jacobs, 2017a).
2008: Unknown (Jacobs, 2008d; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Happold and Happold (1990b: 567) reported that young were born in the middle of the wet season in Malawi.

Stanley and Goodman (2011: 43) report on a male with scrotal testes collected in the East Usambara Mountains (Tanzania) on 30 July 1992.

One female captured on 4 June in Sierra Leone by Weber *et al.* (2019: 25) was pregnant.

PARASITES:
TREMATODA
Urotrematidae
Castiblanco and Vélez (1982: 134) reported the presence of *Urotrema scabridum* in a "*Myotis bocagei*" from Congo.

ARACHNIDA
Psorergatidae
Cierocka *et al.* (2022: 10) mentioned *Psorergatoides kerivoluae* Fain, 1959 being found on the wing membrane of *Myotis bocagii* specimens from Côte d'Ivoire.

Spinturnicidae
Orlova *et al.* (2024: 151) reported the first assocation of this species with *Spinturnix scotophili* Zumpt and Till, 1954

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibodies to SARS-CoV in serum of one individual from Limpopo Province, South Africa, which tested negative (0/1).

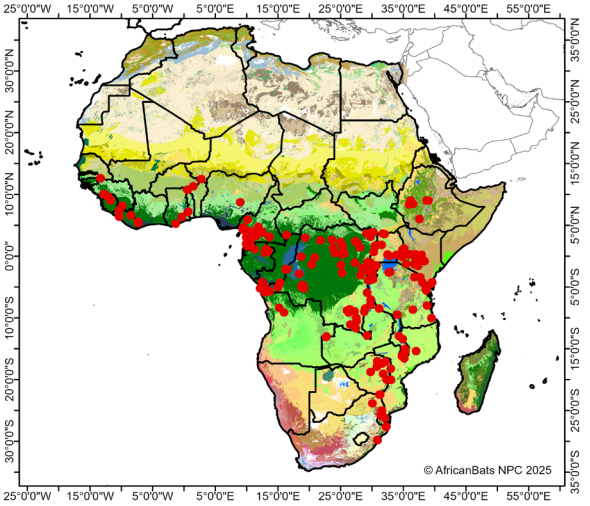

Figure 262. Distribution of *Myotis (Chrysopteron) bocagii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Central African Republic, Congo, Congo (Democratic Republic of the), Ethiopia, Liberia, Mozambique, Sierra Leone.

Myotis (Chrysopteron) bocagii bocagii (Peters, 1870)

*1870.	*Vespertilio Bocagii* Peters, J. Sci. mat. phys. nat., ser 1, 3 (10): 125. Publication date: December 1870. Type locality: Angola: Duque de Bragança [08 55 S 16 10 E]. [Goto Description].
1904.	*Myotis Hildegardeæ* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (75): 209. Publication date: 1 March 1904. Type locality: Kenya: Fort Hall [=Muranga] [00 43 S 37 09 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1903.3.2.2: ♂. Collected by: Mrs. Hildegarde Beatrice Hinde; collection date: 17 October 1902; original number: 115.
?	*Myotis (Chrysopteron) bocagii bocagii:* (Current Combination).
?	*Myotis bocagei bocagei:* (Alternate Spelling).
?	*Myotis bocagei hildegardeae:* (Name Combination, Alternate Spelling).
?	*Myotis bocagii bocagii:* (Name Combination).

GENERAL DISTRIBUTION:
Uganda to Ethiopia, south to Angola, Zambia, Malawi, and Transvaal (South Africa).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Congo (Democratic Republic of the), Eswatini, Ethiopia, Kenya, Malawi, Mozambique, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe.

Myotis (Chrysopteron) bocagii cupreolus Thomas, 1904

*1904. *Myotis Bocagei cupreolus* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (78): 407. Publication date: 1 June 1904. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1903.2.4.6: ♂. Collected by: George Latimer Bates Esq. Collection date: 14 August 1901. - Comments: Evenhuis (2003: 36) states that pages 329 to 424 were included in part 77, which appeared on 1 May 1904. However, the title page of the publication indicates that the part is 78, which was published on 1 June 1904. (Current Combination).
? *Myotis (Chrysopteron) bocagii cupreolus:* (Current Combination).
? *Myotis bocagii cupreolus:* (Current Spelling).

GENERAL DISTRIBUTION:
West Africa, from Senegal to the DRC.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Liberia, Niger, Nigeria, Senegal, Sierra Leone, Togo.

Myotis (Chrysopteron) dieteri M. Happold, 2005

*2005. *Myotis dieteri* M. Happold, Acta Chiropt., 7 (1): 11, figs 1 - 2. Type locality: Congo: Loudima: Grotte du Viaduc [04 15 S 13 00 E]. Holotype: MNHN ZM-MO-1985-1925: ad ♀, skull and alcoholic. Collected by: Jean-Paul Adam; collection date: between 1961 and 1968. - Etymology: In honour of Dr. Dieter Kock of the Senkenberg Museum, Frankfurt, Germany, in recognition of the great contribution he made to the knowledge of African mammals, in recognition of the kindness and generosity with which he has helped so many others with their studies, and in gratitude for our long firendship (see Happold, 2005: 11).
? *Myotis (Chrysopteron) dieteri:* (Current Combination).

TAXONOMY:
Known only from the type specimen (Happold, 2005: 11).

Csorba *et al.* (2014: 668) indicate that *dieteri* is probably the only sub-Saharan *Myotis* that doesn't belong to the subgenus *Chrysopteron*, but molecular data are missing to confirm this. However, Simmons and Cirranello (2023b: 79) assigned it to the subgenus *Chrysopteron* nevertheless.

COMMON NAMES:
Czech: netopýr Kockův. French: Murin de Kock. German: Kocks Mausohr.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since it has only recently been described, and there is still very little information on its extent of occurrence, status, threats and ecological requirements (Happold, 2008; IUCN, 2009; Happold, 2019).

Assessment History
Global
2018: DD ver 3.1 (2001) (Happold, 2019). 2008: DD ver 3.1 (2001) (Happold, 2008; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The threats to this species remain unknown (Happold, 2008; IUCN, 2009; Happold, 2019).

CONSERVATION ACTIONS:
Happold (2008) [in IUCN (2009)] and Happold (2019) reports that it is not known if the species is present within any protected areas. Additional studies are needed into the distribution, abundance, breeding biology and general ecology of this species. There is a need to determine if the species is still present at Grotte du Viaduc à Loudima, and to locate additional populations through directed surveys.

GENERAL DISTRIBUTION:
Myotis dieteri has only been recorded from type locality of 'Grotte du Viaduc à Loudima, Republic of Congo (04º15'S, 13º00'E) (Happold, 2005: 11). Despite extensive surveys of other seemingly

suitable localities, it has not been recorded from additional caves in the Loudima-Kimongo region, or from caves in the Mayombe and lower Kouilou regions of Congo, the Haut-Ivindo region of Gabon, or Kikwit in the Democratic Republic of Congo (Happold, 2005).

Native: Congo (Happold, 2005: 11; Bates *et al.*, 2013: 337).

POPULATION:
Structure and Density
It is known only from the holotype collected by Jean-Paul Adam sometime between 1961 and 1968, from a small number of this species present in the cave (Happold, 2005).

Trend
2018: Unknown (Happold, 2019). 2008: Unknown (Happold, 2008; IUCN, 2009).

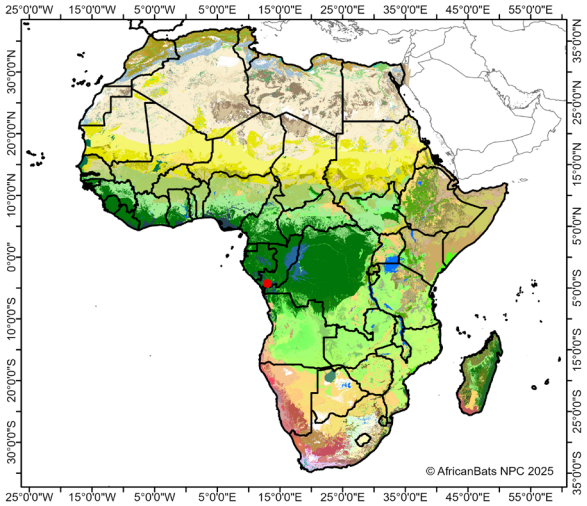

Figure 263. Distribution of *Myotis (Chrysopteron) dieteri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo.

Myotis (Chrysopteron) emarginatus (E. Geoffroy St.-Hilaire, 1806)

*1806.	*Vespertilio emarginatus* E. Geoffroy Saint-Hilaire, Ann. Mus. Hist. nat. Paris, 8: 198. Type locality: France: Ardennes: Givet: Charlemont. Holotype: MNHN 819-202: ad, mounted skin (skull not removed). Additional skull A6953: see Rode (1941: 244), who mentions Abbeville as locality, and M. Baillon as collector.
?	*Myotis (Chrysopteron) emarginatus:* (Current Combination).
?	*Myotis emarginata:* - Comments: corrected gender for specific name. (Alternate Spelling).
?	*Myotis emarginatus emarginatus:* (Name Combination).
?	*Myotis emarginatus:* (Name Combination).

TAXONOMY:
Assigned to the subgenus *Isotus* by Pavlinov *et al.* (1995: 97), but Csorba *et al.* (2014: 667) and Simmons and Cirranello (2024a: 79) include it in the subgenus *Chrysopteron*.

Dietz and Pir (2023: 258) indicate that *Myotis emarginatus* is probably more related to the Afrotropic species such as *Myotis tricolor* than to any other Palearctic species. Stadelmann *et al.* (2004b: 186) already suggested that this species that this species is derived from two African ancestors that secondarily colonized Eurasia.

Uvizl and Benda (2022: 285) indicate that - based on morphometrics and mitochondrial genes - *Myotis emarginatus* can be divided into two groups: one of small-sized and more variable bats from Europe, the Maghreb and the Levant; and a second covering the large-sized bats of the rest of the Asian range. Each of these was subdivided into two sublineages. For the western group, one of these sublineages occurred in the Holy Land and the other in the rest of the Mediterranean range. The nuclear genes displayed no subdivision, which suggests that this species is monophyletic. Nevertheless, Uvizl and Benda (2022: 285) recognize two subspecies: a small-sized *M. e. emarginatus* from the Mediterranean, western and central Europe and the Levant; and a large-sized *M. e. desertorum* in the eastern Middle East, from Oman to West Turkestan. However, Benda and Uvizl (2021: 25) restricted the latter to the south-eastern Middle East, including southern Iran, Oman, and Afghanistan.

Woodman (1993) notes that many mammalian generic names ending in *-otis* use the wrong gender for specific names therefore this name should be *M. emarginata*. However, see also Benda and Tsytsulina (2000: 335), and Simmons (2005).

COMMON NAMES:
Albanian: Lakuriq nate i Geoffroy-it. Arabian: Khaffash. Armenian: Եռագույն գիշերաչղջիկ. Azerbaijani: Üçrəng gecə şəbpərəsi. Basque: Geoffroy saguzar. Belarusian: Начніца трохкаляровая. Bosnian: Trobojni šišmiš. Breton: Gousperell Geoffroy. Bulgarian: Трицветен нощник. Castilian (Spain): Murciélago orejirroto, Murciélago de Geoffroy, Murciélago ratonero pardo. Catalan (Spain): Ratpenat d'orelles dentades, Ratapinyada d'orella escapçada. Croatian: Riđi šišmiš, Trobojni šišmiš. Czech: Netopýr brvitý, Netopýra brvitého, Nedopír wraubkowaný, Stejnoušan zejkatý,

Netopýrec brvitý. Danish: Geoffroys flagermus. Dutch: Ingekorven vleermuis. English: Geoffroy's Bat, Notch-eared Bat, Geoffroy's Myotis. Estonian: Ripslendlane. Finnish: Ruskosiippa. French: Murin à oreilles échancrées, Vespertilion à oreilles échancrées, Vespertilion échancré. Frisian: Ynsniene flearmûs. Galician (Spain): Morcego de orellas fendidas. Georgian: სამფერი მღამიობი. German: Wimperfledermaus, Kerbohrige Ohrenfledermaus, Fledermaus mit gerändelten Ohren. Greek: Πυρρομυωτίδα. Hebrew: Nishpon Pgoom Ozen. Hungarian: Csonkafülű denevér, Nycteris i blephardoti. Irish Gaelic: Ialtóg Geoffroy. Italian: Vespertilio smarginato, Vespertilio smarginato. Latvian: Skropstainais naktssikspārnis. Lithuanian: Trispalvis pelėausis. Luxembourgish: Wimperefliedermaus. Macedonian: Тробоен ноќник [= Troboen Nokjnik]. Maltese: Farfett il-Lejl ta' Widnejħ Imnaqqxa. Montenegrin: Riđi večernjak. Norwegian: Vinkeløreflaggermus, Geoffroyflaggermus. Polish: Nocek orzęsiony. Portuguese: Morcego-lanudo. Rhaeto-Romance: Vespertil cun tschegls, Vespertil cun tscheglias. Romanian: Liliacul cărămiziu, Liliac-cu-gene-lungi. Russian: Ночница трёхцветная, Трехцветная ничница [= Tryokhtsvetnaya nochnitsa]. Serbian: Риђи вечерњак [= Riđi večernjak]. Scottish Gaelic: Ialtag Geoffroy. Slovak: Netopier brvitý. Slovenian: Vejicati netopir. Swedish: Flikörad fladdermus. Turkish: Kirpikli Yarasa. Ukrainian: Нічниця триколірна [= Nichnytsya trykolirna]. Welsh: Ystlum Geoffroy.

Conservation status:

Global Justification

The species experienced a significant decline in at least parts of its range from the 1960s to the 1990s, but now it is expanding in central Europe and is stable or not significantly declining elsewhere. The range is still large, and the species is not specialized to restricted habitat, although it has a very specialized diet. Assessed as Least Concern (LC ver 3.1 (2001)) (Hutson *et al.*, 2008m; IUCN, 2009; Piraccini, 2016a).

Assessment History

Global

2016: LC ver 3.1 (2001) (Piraccini, 2016a). 2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008m; IUCN, 2009). 1996: VU A2c ver 2.3 (1994) (Baillie and Groombridge, 1996).

Regional

None known.

Major threats:

In Europe the species is mainly associated with agricultural landscapes, therefore all agricultural activities can affect populations of this species. Loss of and disturbance to roost sites in buildings (including remedial timber treatment in attics) and underground sites are also threats. In the African part of the range, cave habitats, where the species roosts, are being destroyed by fires and vandalism. The species is also collected for traditional medicine practices in North Africa (Hutson *et al.*, 2008m; IUCN, 2009; Piraccini, 2016a).

Conservation actions:

Piraccini (2016a) supports Hutson *et al.* (2008m) [in IUCN (2009)] who report that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in the range states where these apply. It is included in Annex IV of EU Habitats and Species Directive, and there is some habitat protection through Natura 2000.

Protection of roosts and promotion of awareness about the lack of medicinal value of the species is required.

General distribution:

Myotis emarginatus occurs in southern Europe from Portugal in the west to the Balkans in the east and southern part of western and central Europe and non-arid parts of southwestern Asia from Asia Minor, Caucasus region and Palestine to Oman, Uzbekistan and Tajikistan; also in north-west Africa (recorded from northern Maghreb (Algeria, Morocco and Tunisia)). In the eastern part of the Mediterranean it occurs in various parts of Turkey, Syria, Lebanon and Israel. It occurs from sea level to 1,800 m, highest records in the Alps are 812 m (maternity colony) and 1,505 m (hibernaculum) (Spitzenberger, 2002).

Native: Afghanistan; Albania; Algeria; Andorra; Armenia; Austria; Azerbaijan; Belgium; Bosnia and Herzegovina; Bulgaria; Croatia; Cyprus; Czech Republic; France [Corse]; Georgia; Germany; Gibraltar; Greece [Kriti] (Benda *et al.*, 2007: 71); Hungary; Iran, Islamic Republic of; Israel; Italy [Sardinia]; Jordan; Kazakhstan; Kyrgyzstan; Lebanon; Luxembourg; Macedonia, the former Yugoslav Republic of; Monaco; Montenegro; Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 360; Dbiba *et al.*, 2025: 8); Netherlands; Oman; Poland; Portugal; Romania; Russian Federation; San Marino; Saudi Arabia; Serbia; Slovakia; Slovenia; Spain [Baleares]; Switzerland; Syrian Arab Republic; Tajikistan; Tunisia (Dalhoumi *et al.*, 2014: 53); Turkey; Turkmenistan; Ukraine; Uzbekistan.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.1 Pa, aspect ratio 5.9 and tip shape index of 2.05 for a wingspan of 24 cm and a wing area of 93 cm^2 and a body mass of 7 g.

ECHOLOCATION:
Highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (close to foliage): steep linear FM. Start-frequency: 110 kHz; end-frequency: 39 kHz; frequency with maximum energy: 65 kHz; call-duration: 2.6 ms; inter-call interval: 26-32 ms (Barataud, 2005).

The data for 42 animals from Greece were the following: F_{start}: 110.5 ± 10.90 kHz, F_{end}: 42.6 ± 5.57 kHz, F_{peak}: 72.8 ± 7.28 kHz, bandwidth: 43.4 ± 8.29 kHz, duration 3.3 ± 0.73 ms and interpulse interval: 79.4 ± 23.83 ms (Papadatou *et al.*, 2008b: 132).

Walters *et al.* (2012: suppl.) report the following figures for 26 calls (24 sequences) from France and Germany: duration: 2.29 ± 0.70 ms, F_{max}: 93.23 ± 20.18 kHz, F_{min}: 42.00 ± 3.47 kHz, bandwidth: 51.23 ± 17.78 kHz, F_{peak}: 60.23 ± 15.14 kHz.

MOLECULAR BIOLOGY:
Karyotype
Bovey (1949) and Pérez-Suárez *et al.*, 1991) reported 2*n* = 44, aFN = 50, X = submetacentric, Y = acrocentric, while Radjhabli *et al.* (1970) reported aFN = 56 and Zima (1978) aFN = 52 with X = metacentric. The autosomal component consists of three large metacentric, one small metacentric, 15 acrocentric and two dot-like pairs (with one being bi-armed) (Arslan and Zima, 2014: 10). The latter authors also refer to the X chromosome as being a medium-sized metacentric.

Genetics
See García-Mudarra *et al.* (2009).

HABITAT:
In Spain, Goiti *et al.* (2011: 19) found that *M. emarginatus* flew on average 5 km to its foraging areas, with a maximum distance of almost 10 km. The foraging area covered between 120 and 371 ha, and consisted mainly of scrubland (35 % of mean individual foraging time) and pine plantations (34 % of mean individual foraging locations), followed by isolated trees (oak, pine, or eucalyptus - on average 11 %), riparian woods (7 %), oak dehesas (6 %), and eucalyptus plantations (5 %).

DIET:
Goiti *et al.* (2011: 20) found that, in Spain, spiders made up the major part of the diet by both volume (mean 79 %) and frequency (in faeces of all examined bats, and in 95 % of the faeces). The next most important group was formed by moths, with a mean consumption of 7 % of the diet by volume; dipterans (flies and midges - 6.3 %), and lacewings (especially the family Hemerobiidae - 4.4 %). Earwings, harvestmen, wasps, and beetles all made up less than 2 % of the diet.
Benda *et al.* (2012a: 325) summarizes the European food groups as: Araneae, Lepidoptera, brachyceran Diptera, and Lepidoptera larvae. In the Middle East Diptera, Lepidoptera, Coleoptera, and Homoptera are prevailing in Azerbaijan, Araneae and Brachycera in Syria, and Hemiptera, Araneae, and Brachycera in Turkey. In Iran, there was a high proportion of Tipulidae, and in Jordan of scarabaeid beetles. This lead Benda *et al.* (2012a: 325) to conclude that a certain level of flexibility of the trophic niche in *M. emarginatus*.

POPULATION:
Structure and Density
Locally it can be rare or common. The species experienced a significant decline from the 1960s to the 1990s, but in recent time the numbers in several regions have increased and the species has spread into new areas. It lives in large colonies (up to 1,200 individuals in Austria in one maternity colony) (Hutson *et al.*, 2008m; IUCN, 2009; Piraccini, 2016a).

Trend
2016: Stable (Piraccini, 2016a). 2008: Stable (Hutson *et al.*, 2008m; IUCN, 2009).
M. emarginatus populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

PARASITES:
Frank *et al.* (2015: 8) mention the following parasites for European *M. emarginatus*:
Arachnida: *Eyndhovenia euryalis* (G. Canestrini, 1885), *Macronyssus rhinolophi* (Oudemans, 1902), *Steatonyssus periblepharus* Kolenati, 1858, *Spinturnix emarginata* (Kolenati, 1856).

Insecta: *Basilia nana* Theodor & Moscona, 1954, *Basilia italica* Theodor, 1954, *Cimex pipistrelli* Jenyns, 1839, *Ischnopsyllus emarginatus*, *Ischnopsyllus simplex* Rothschild, 1906, *Penicillidia dufourii* (Westwood, 1835), *Phthiridium biarcticulatum*, *Rhinolophopsylla unipectinata* (Taschenberg, 1880).

Trematoda - Digenea: *Lecithodendrium linstowi* Dollfus, 1931, *Prosthodendrium aelleni* Dubois, 1956, *Prosthodendrium chilostomum* (Mehlis, 1831).

Cestoda: *Myotolepis grisea* (Beneden, 1873).

Bendjeddou *et al.* (2017: 15) and Khelfaoui *et al.* (2018: 67) mention the following parasites from bats from Algeria: Nycteribiidae: *Nycteribia (Nycteribia) latreillii* (Leach, 1817) and *Penicillidia (Penicillidia) dufourii* Westwood, 1835; Arachnida: *Spinturnix myoti* (Kolenati, 1856) and *Ixodes vespertilionis* Koch, 1844.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ixodidae: *Ixodes vespertilionis* Koch, 1844; Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Penicillidia dufourii* (Westwood, 1834); Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856).

VIRUSES:
Orthomyxoviridae
Despite sampling and testing of 3 individuals of this species, no evidence of influenza A-like viruses (Orthomyxoviridae) were obtained (Fereidouni *et al.*, 2015).

UTILISATION:
The species is also collected for traditional medicine practices in North Africa (Hutson *et al.*, 2008m; IUCN, 2009).

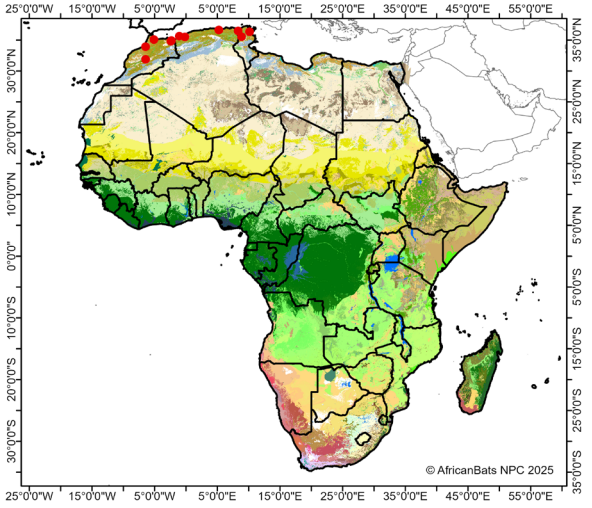

Figure 264. Distribution of *Myotis (Chrysopteron) emarginatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, France, Morocco, Tunisia.

Myotis (Chrysopteron) goudotii (A. Smith, 1834)

*1834. *Vespertilio Goudotii* A. Smith, S. Afr. Quart. J., ser 2, 2: 244. Publication date: June 1834. Type locality: Madagascar: "Madagascar". [Goto Description].
1858. *Vespertilio Madagascariensis* Tomes, Proc. zool. Soc. Lond., 1858, XXVI (ccclii): 89. Publication date: 27 April 1858. Type locality: Madagascar: "Madagascar". Holotype: NHMUK 1907.1.1.503.
1870. *Vespertilio sylvicola* A. Grandidier, Rev. Mag. Zool., ser 2, 22: 49. Publication date: February 1870. Type locality: Madagascar: Ambaravantao forest. [Goto Description]. - Comments: The type locality was mentioned as "Forests of Ambaravaranvatou" by Allen (1939a: 91). Dobson (1878: 301, footnote) indicates that the type has been lost and that the description is insufficient. He, therefore, included it with a question mark.
1908. *Myotis goudoti:* G. M. Allen, Bull. Mus. comp. Zool., 52 (3): 43. Publication date: July 1908. (Name Combination).
1939. *Myotis goudotii:* G. M. Allen, Bull. Mus. comp. Zool., 83: 91. Publication date: February 1939. (Name Combination).
? *Myotis (Chrysopteron) goudoti:* (Current Combination).
? *Myotis goudoti goudoti:* (Name Combination).

TAXONOMY:
Simmons (2005) states that it does not appear to include *anjouanensis*; see Peterson *et al.* (1995).

Generally mentioned as *goudoti*, but Andrew Smith (1834: 244) did describe it using a double "i": *Vespertilio Goudotii* (Simmons and Cirranello, 2023a: 79).

Csorba *et al.* (2014: 667) include *goudotii* in the subgenus *Chrysopteron*, but Ruedi and Mayer (2001: 436), Ghazali *et al.* (2016: 476) and Patterson *et al.* (2019a: "2") reject the division in subgenera.

COMMON NAMES:
Czech: netopýr madagaskarský. English: Malagasy Mouse-eared Bat, Malagasy Myotis. French: Murin de Madagascar, Chauve-souris malgache à oreille de souris, Vespertilion de Madagascar. German: Madagaskar-Mausohr.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Samonds (2007: 60) found samples in deposit (SS2), which was collected from the surface near the main cave entrance, dating attempts revealed this sample was contaminated, therefore no date is known for this locality in Anjohibe cave, Madagascar.

Weyeneth (2010) indicated that, during the Pleistocene, populations of this species diverged into a southern and a northern component, with subsequent expansion and adaptation to all biomes.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) in view of its widespread distribution across Madagascar, and the absence of any major threats. Close monitoring of roosting colonies in areas where the forest is subject to disturbance is needed (Andriafidison *et al.*, 2008h; IUCN, 2009; Monadjem *et al.*, 2017bv).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bv). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008h; IUCN, 2009). 1996: LR/nt ver 2.3 (1994) (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There are no known threats to this species although additional research is needed to determine the impact of forest degradation on its persistence in cave roosts (IUCN, 2009; IUCN, 2009; Monadjem *et al.*, 2017bv).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008h) [in IUCN (2009)] and Monadjem *et al.* (2017bv) report that this is a widespread species that is found in many of Madagascar's protected areas, including those in the east and west of the island (Goodman, 1999; Russ *et al.*, 2003; Goodman *et al.*, 2005a).

GENERAL DISTRIBUTION:
Myotis goudotii is endemic to the island of Madagascar (Simmons, 2005) where it is widely distributed across a range of different vegetation types (Peterson *et al.*, 1995; Goodman, 1999; Eger and Mitchell, 2003; Russ *et al.*, 2003; Goodman *et al.*, 2005a), including Nosy Be and Nosy Komba (Rakotonandrasana and Goodman, 2007: 6). It occurs on altitudes between 0 and 800 m (with one record from 1,600 m) (Garbutt, 2022: 99)..

Native: Madagascar (Peterson *et al.*, 1995; Goodman, 1999; Eger and Mitchell, 2003; Russ *et al.*, 2003; Goodman *et al.*, 2005a; Rakotonandrasana and Goodman, 2007: 6).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 64) reported the structure as being triangular, and in some cases, with a pronounced proximal indentation; length: 0.87 ± 0.111 (0.68 - 1.02) mm, width: 0.53 ± 0.081 (0.43 - 0.67) mm.

ECHOLOCATION:
Russ *et al.* (2003) describe the echolocation as a single frequency-modulated sweep from 75 kHz to 55 kHz. Kofoky *et al.* (2009: 382) reported the calls of 11 individuals, which were characterized by broadband FM sweeps produced at low duty cycle. The most energy always found in the fundamental at about 64.4 kHz, and the pulses were very short about 3 ms.

Hending *et al.* (2023: 372) reported F_{peak}: 59.0 ± 3.9 kHz, duration: 5 ± 4 ms, and interpulse interval: 66 ± 30 ms.

MOLECULAR BIOLOGY:
Karyotype
Richards *et al.* (2010) examined one female and one male having a 2*n*=44 and a FNa= 50, a submetacentric X and small acrocentric Y chromosome. In addition, Volleth and Eick (2012: 167) mention a segment number of 22.

HABITAT:
Dammhahn and Goodman (2013: 108) mention the lower portion of forest structure and partially open areas as the foraging habitat for this species.

Goodman *et al.* (2023b: 239) [referring to Rafanomezanjanahary (2021)] indicated that 108 individuals captured at Antsahabe were found in *savoka* (regenerating secondary grassland - 53 %), relatively intact forest (23 %), secondary forest (18 %), and the remaining 6 % in a variety of agroforestry habitats and rice fields.

Crowley and Goodman (2025: 4) report this species to be widespread in various habitats between sea level and 1,600 m.

ROOST:
Wilkinson *et al.* (2012: 160) indicate that caves are the typical roosting sites for these bats on Madagascar. Ravelomanantsoa *et al.* (2019: 110) added crevices and possibly tree holes. The colony size is generally small, although in Namoroka a colony of 1,000 animals was recorded (Garbutt, 2022: 99).

DIET:
Razakarivony *et al.* (2005) found Araneae in 27 % of stomachs examined. Rakotoarivelo *et al.*

(2007) in Madagascar found *M. goudotii* to mainly consumed Hymenoptera, Neuroptera, Araneae and fragments of spiders were present in 55 % of the faecal samples.

Rakotondramanana *et al.* (2015: 78) report the following diet items (volume percent, frequency percent): Coleoptera (34.0, 100.00); Hymenoptera (4.0, 60.0); Lepidoptera (62.0, 100.0). Rasoanoro *et al.* (2015: 64) found the following volume percentages for two specimens: Aranea (40.7), Coleoptera (43.7), Hymenoptera (8.4), Isoptera (4.6), Lepidoptera (2.5).

For bats from Kianjavato, Rasoanoro *et al.* (2015: 64) reported Coleoptera (43.7 %), Araneae (40.7 %), and Hymenoptera (8.4 %).

Goodman *et al.* (2023b: 239) [referring to Falimiarintsoa (2022)] indicated that the fecal pellets of 28 bats collected at Sarahandrano contained Coleoptera (55.6 %), Diptera (20.4 %), Lepidoptera (17.7 %), and less than 3 % of Hemiptera and Hymenoptera, and at Antsahabe [referring to Rafanomezanjanahary (2021)]: Coleoptera (44 %), Lepidoptera (22 %), Diptera (14 %), Orthoptera (5 %), and Araneae, Blattoptera, Ephemeroptera, Hemiptera, and Hymenoptera (each less than 4 %).

Kemp *et al.* (2018: Suppl.) used DNA metacarcoding to detect insect pest species in the diet of these bats and found the following prey orders (in descending order): Coleoptera, Hymenoptera, Lepidoptera (*Homona* sp., *Thaumatotibia batrachopa* (Meyrick, 1908)), Diptera (*Simulium lineatum* (Meigen, 1804), *Culex* sp., *Culex annulioris* Theobald, 1901, *Coquillettidia* sp., *Anopheles* sp.), Sarcoptiformes, Ephemeroptera, Hemiptera, Araneae, Blattodea, Trichoptera, Symphypleona, Mesostigmata, Trombidiformes.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 65 minutes, and the digestibility rate about 81.8 %.

Predators:
Goodman *et al.* (2015c: 78) found the remains of one individual in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

Population:
Structure and Density
Although widespread, there is a paucity of information on the population status of *M. goudotii*. It is frequently trapped in mist nets during bat surveys and appears to be at least locally abundant in west (Kofoky *et al.*, 2007; Rakotoarivelo and Randrianandrianina, 2007), but is more difficult to net, or is less abundant in the east (Russ *et al.*, 2003; Randrianandriananina *et al.*, 2006). There are few data available on roosting colonies but aggregations of up to 1,000 individuals have been recorded (Monadjem *et al.*, 2017bv).

Trend
2016: Unknown (Monadjem *et al.*, 2017bv).
2008: Unknown (Andriafidison *et al.*, 2008h; IUCN, 2009).

Activity and behaviour:
Rakotoarivelo *et al.* (2007) suggest that *M. goudotii* is better adapted to forage in cluttered areas and may have a closer association with forest vegetation. They also suggest that *M. goudotii* may be a gleaner.

Reproduction and ontogeny:
55 adult females captured at Antsahabe in late September to late November 2019, only three showed signs of breeding activity (no fur around the mammae), and 34 of the 55 males had descended testes. 11 of 21 females collected in Sarahandrano between late March and late April were adults without embryos, whereas the remaining females were subadults. 14 of the 15 males captured in the same timeframe had descended testes (Goodman *et al.*, 2023b: 240).

Of the two males reported by Goodman *et al.* (2025: 215) and collected between mid November and early December, one had abdominal testes and the other only slightly enlarged testes. Two females were pregnant with embryos with crown-rump length of 17 and 20 mm.

Parasites:
BACTERIA
Lagadec *et al.* (2012: 1696), Dietrich *et al.* (2014: Suppl.) and Gomard *et al.* (2016: 5) report the presence of spirochaetes bacteria of the genus *Leptospira*, which are assigned to *L. borghpetersenii* by Dietrich *et al.* (2018a: 3). Lei and Olival (2014: Suppl.) mention "*Myotis goudoti*" as host for *Bartonella* bacteria.

HAEMOSPORIDA
Megali *et al.* (2010: 1042) and Duval *et al.* (2012: 1563) reported Genbank data for *Polychromophilus* sp. from *M. goudotii*. Ramasindrazana *et al.* (2018: Suppl.) identified this parasite as *Polychromophilus murinus* Dionisi, 1899 (see also Chumnandee *et al.*, 2020: Suppl.; Rasoanoro *et al.*, 2021).

Ramasindrazana *et al.* (2016: 6) reported the presence of an unnamed filariod in this bat species.

DIPTERA
Nycteribiidae
Ramasindrazana *et al.* (2017: Suppl.) found the bat flies *Nycteribia stylidiopsis* and *Penicillidia* sp. on specimens from this bat species.

ACARI
Trombiculidae
Stekolnikov (2018a: 116) reported *Trisetica aethiopica* (Hirst, 1926) from this bat species.

VIRUSES:
Astroviridae
Lebarbenchon *et al.* (2017 Suppl.) tested 14 animals and three of them was positive for Astroviruses.

Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 2 individuals from the Madagascar using RT-PCR specific for Respirovirus/Morbillivirus/Henipahvirus (RMH) and Paramyxovirinae (PMV) and found 0 positive results for viral nucleic acids. Wilkinson *et al.* (2014) tested 8 individuals from Anjohikinakia and Bekoaky in Madagascar with an RT-PCR specific for the *Respiro-*, *Morbilli-* and *Henipavirus* genera, two of the 8 individuals tested positive for paramyxovirus RNA.

48 Madagascan *M. goudotii* specimens were tested by Mélade *et al.* (2016b: 4) and five of them were positive for paramyxoviruses.

Rhabdoviridae
Of the 11 bats tested by Mélade *et al.* (2016a: 6), four showed a seroreaction.

UTILISATION:
See Goodman *et al.* (2008d).

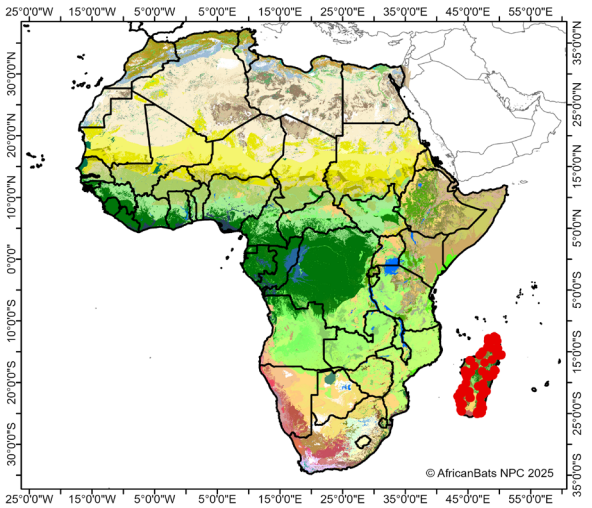

Figure 265. Distribution of *Myotis (Chrysopteron) goudotii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Myotis (Chrysopteron) morrisi Hill, 1971

*1971. *Myotis morrisi* Hill, in: Hill and Morris, Bull. Br. Mus. (nat. Hist.) Zool., 21 (2): 43, pl 1, 2 (a, b). Publication date: 28 April 1971. Type locality: Ethiopia: Walaga, Blue Nile Gorge: Didessa River mouth: "Forward Base Three" [10 05 N 35 38 E, ca. 1 000 m]. [Goto Description]. Holotype: NHMUK 1970.488: ad ♀, skin and skull. Collected by: The Great Abbai Expedition; collection date: 28 August 1968; original number: A107. (Largen, Yalden & King). Also see Hill and Morris (1971: 43). - Etymology: In honour of Dr. Pat Morris of Royal Holloway College, University of London, in recognition of his many services to the study of the Ethiopian fauna while with the Great Abbai Expedition (Hill in Hill and Morris, 1971: 44).

? *Myotis (Chrysopteron) morrisi:* (Current Combination).

TAXONOMY:
Known only from two specimens (see Stadelmann *et al.*, 2004b: 179).

Simmons and Cirranello (2023b: 79) assigned it to the subgenus *Chrysopteron*.

COMMON NAMES:
Czech: netopýr Morrisův. English: Morris's Mouse-eared Bat, Morris's Bat, Morris's Myotis. French: Murin d'Ethiopie, Vespertilion de Morris. German: Morris' Mausohr.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, threats and conservation status (Jacobs *et al.*, 2008o; IUCN, 2009; Jacobs *et al.*, 2019c).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019c). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008o; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Jacobs *et al.*, 2004b; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are unclear. It may be threatened by cave disturbance and subsistence harvesting for food (Jacobs *et al.*, 2008o; IUCN, 2009; Jacobs *et al.*, 2019c).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008o) [in IUCN (2009)] and Jacobs *et al.* (2019c) report that it is not known if the species is present in any protected areas. Further studies are needed into the distribution, abundance, natural history, and threats to this poorly known species.

GENERAL DISTRIBUTION:
Myotis morrisi has only been recorded from two very disjunct sites, the type locality of 'Didessa River mouth, Walaga' in Ethiopia (Hill and Morris, 1971) and from Numan, Adamawa Province, in northeastern Nigeria (Hill *et al.*, 1988).

Native: Ethiopia (Hill and Morris, 1971); Nigeria (Hill *et al.*, 1988).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 84 minutes, and the digestibility rate about 79.1 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008o; IUCN, 2009; Jacobs *et al.*, 2019c).

Trend
2018: Unknown (Jacobs *et al.*, 2019c). 2008: Unknown (Jacobs *et al.*, 2008o; IUCN, 2009).

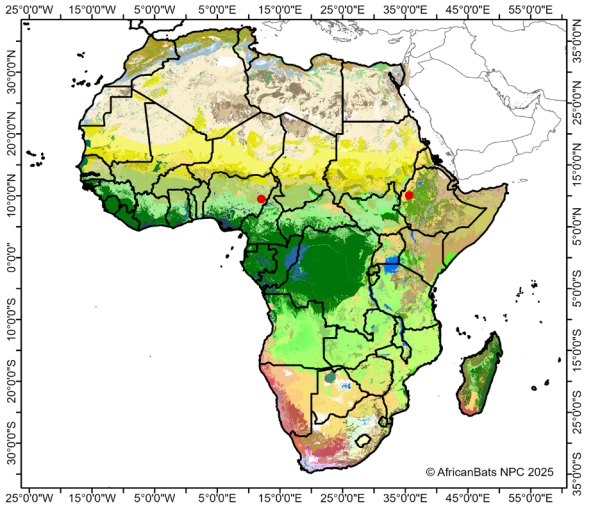

Figure 266. Distribution of *Myotis (Chrysopteron) morrisi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Nigeria.

Myotis (Chrysopteron) nimbaensis Simmons, Flanders, Bakwo Fils, Parker, Suter, Bamba, Douno, Keita, Morales and Frick, 2021

*2021. *Myotis nimbaensis* Simmons, Flanders, Bakwo Fils, Parker, Suter, Bamba, Douno, Keita, Morales and Frick, Am. Mus. Novit., 3963: 3, 8, figs 3 - 8. Publication date: 13 January 2021. Type locality: Guinea: N'Zérékoré region: Mount Nimba: Kaiser Adit 1 [07 39 54 N 08 22 20 W]. Holotype: AMNH 279589: ad ♂, skull and alcoholic and tissue. Collected by: Jon Flanders and Eric Moise Bakwo Fils; collection date: 2 February 2018; original number: BCIGU133. Paratype: AMNH 279590: ad ♀, skull and alcoholic and tissue. Collected by: Jon Flanders and Eric Moise Bakwo Fils; collection date: 2 February 2018; original number: BCIGU132. - Etymology: The name refers to Mount Nimba where the type specimen was collected.

? *Myotis (Chrysopteron) nimbaensis:* (Current Combination).

TAXONOMY:
Simmons *et al.* (2021: 8) and Simmons and Cirranello (2023b: 79) assigned this species to the subgenus *Chrysopteron*.

CONSERVATION STATUS:
Simmons *et al.* (2021: 28) suspected, that once assessed by the IUCN, the status would be "Critically Endangered" based on its currently known occurrence area of less than 100 km^2.

GENERAL DISTRIBUTION:
This species is only known from the type locality.

ECHOLOCATION:
Simmons *et al.* (2021: 20) mention a steep frequency-modulated pulse with a bandwidth of 84.1 ± 13.1 kHz; F_{max}: 104 kHz, F_{min}: 20 kHz, F_{peak}: 42.5 ± 4.2 kHz, duration: 3.5 ± 0.3 ms, and an interpulse interval of 113 ± 5.3 ms.

ROOST:
The two specimens collected by Simmons *et al.* (2021: 21) were captured while emerging from a disused mine adit.

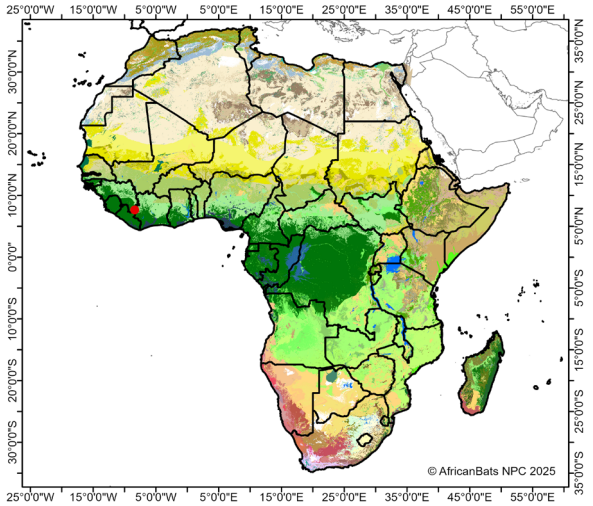

Figure 267. Distribution of *Myotis (Chrysopteron) nimbaensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea.

Myotis (Chrysopteron) scotti Thomas, 1927

*1927. *Myotis scotti* Thomas, Ann. Mag. nat. Hist., ser 9, 19 (113): 554. Publication date: 1 May 1927. Type locality: Ethiopia: Shoa province: ca. 40 mi (64 km) W Addis Ababa: Djem-djem Forest [09 00 N 38 12 E, 8 000 ft]. Holotype: NHMUK 1927.3.4.1. Paratype: NHMUK 1927.3.4.2. Paratype: NHMUK 1927.3.4.3. Paratype: NHMUK 1927.3.4.4. Paratype: NHMUK 1927.3.4.5.

? *Myotis (Chrysopteron) scotti:* (Current Combination).

TAXONOMY:
See Simmons (2005).

Csorba *et al.* (2014: 667) and Simmons and Cirranello (2023b: 79) include *scotti* in the subgenus *Chrysopteron*.

COMMON NAMES:
Czech: netopýr habešský. English: Scott's Mouse-eared Bat, Scott's Mouse-eared Myotis. French: Murin de Scott, Vespertilion de Scott. German: Scotts Mausohr.

CONSERVATION STATUS:
Global Justification
Listed as Vulnerable (VU B2ab(iii) ver 3.1 (2001)) because its area of occupancy (AOO) is possibly less than 2,000 km^2, its distribution is likely to be severely fragmented, and there is continuing decline in the extent and quality of its forest habitat in Ethiopia (Benda and Lavrenchenko, 2008; IUCN, 2009; Benda and Lavrenchenko, 2017).

Assessment History
Global
2016: VU B2ab(iii) ver 3.1 (2001) (Benda and Lavrenchenko, 2017). 2008: VU B2ab(iii) ver 3.1 (2001) (Benda and Lavrenchenko, 2008; IUCN, 2009). 2004: VU B2ab(iii) ver 3.1 (2001) (Benda and Lavrenchenko, 2004; IUCN, 2004). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The forest habitat of this species is being impacted through conversion of land to agricultural use and logging (Benda and Lavrenchenko, 2008; IUCN, 2009; Benda and Lavrenchenko, 2017).

CONSERVATION ACTIONS:
Benda and Lavrenchenko (2008) [in IUCN (2009)] and Benda and Lavrenchenko (2017) report that there appear to be no conservation measures in place, and it is not known if the species is present in any protected areas. There is a need to conserve areas of suitable montane forest habitat for this species. Further studies are needed into the abundance, biology and ecology.

GENERAL DISTRIBUTION:
Myotis scotti is endemic to the highlands of Ethiopia, where it has been recorded from ten localities between 1,300 and 2,500 m asl.

Native: Ethiopia.

MOLECULAR BIOLOGY:
Genetics

Morales *et al.* (2024: Suppl.) reported the total length of the genome to consist of 2002.52M base pairs.

HABITAT:
Chakravarty *et al.* (2024: 7) considers this species to be a "highland dwelling species".

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 73 minutes, and the digestibility rate about 80.6 %.

Morales *et al.* (2024: Suppl.) assigned this species to the Aerial Hawker ecomorph type.

POPULATION:
Structure and Density
It appears to be a rare species that is known from only about 20 specimens (Benda and Lavrenchenko, 2008; IUCN, 2009; Benda and Lavrenchenko, 2017).

Trend
2016: Unknown (Benda and Lavrenchenko, 2017). 2008: Decreasing (Benda and Lavrenchenko, 2008; IUCN, 2009).

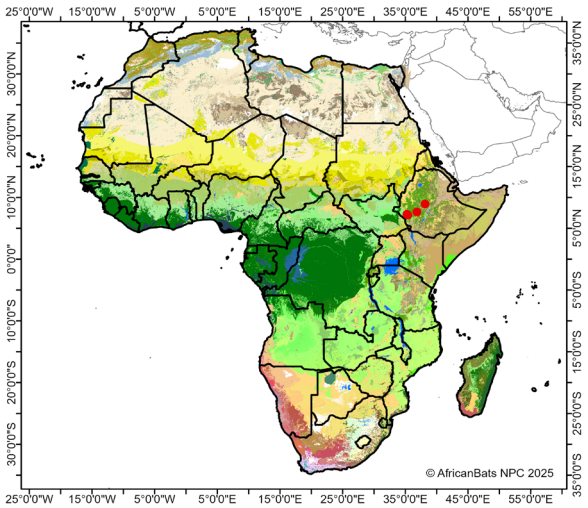

Figure 268. Distribution of *Myotis (Chrysopteron) scotti*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

Myotis (Chrysopteron) tricolor (Temminck, 1832)

*1832. *V[espertilio] tricolor* Temminck, in: Smuts, Enumer. Mamm. Capensium, 106. Publication date: 1832. Type locality: South Africa: Cape province: Cape Town [33 56 S 18 28 E]. [Goto Description]. Lectotype: RMNH MAM.35899: ad ♀, skull only. Collected by: Dr. Hubertus Benedictus Van Horstok; collection date: 1828 - 1832. Paralectotype: RMNH MAM.35898: ad ♀, mounted skin and skull. Collected by: Dr. Hubertus Benedictus Van Horstok; collection date: 1828 - 1832. - Comments: Type specimen: RMNH ???.
1901. *Myotis tricolor:* Sclater, The mammals of South Africa, 131. (Name Combination).
*1924. *Epetiscus loveni* Granvik, Acta Univ. Lund, ser 2, 21 (3): 12. Publication date: 1924. Type locality: Kenya: E slopes of Mount Elgon [01 07 N 34 35 E, 8 000 ft]. [Goto Description]. Holotype: NRM 100903:; collection date: 1920.
1939. *Eptesicus loveni:* G. M. Allen, Bull. Mus. comp. Zool., 83: 86. Publication date: February 1939. (Name Combination).
2013. *Myotis tricolor 1:* Ruedi, Stadelmann, Gager, Douzery, Francis, Lin, Guillén-Servent and Cibois, Mol. Phylog. Evol., 69 (3): Suppl. Publication date: 27 August 2013.
2013. *Myotis tricolor 2:* Ruedi, Stadelmann, Gager, Douzery, Francis, Lin, Guillén-Servent and Cibois, Mol. Phylog. Evol., 69 (3): Suppl. Publication date: 27 August 2013.
? *Myotis (Chrysopteron) tricolor:* (Current Combination).
? *Myotis (Selysius) tricolor:* (Name Combination).
? *Myotis tricolor A:*

TAXONOMY:
Includes *Eptesicus loveni*, see Aggundey and Schlitter (1986).

Csorba *et al.* (2014: 667) and Simmons and Cirranello (2023b: 79) include *tricolor* in the subgenus *Chrysopteron*, but see Ruedi and Mayer (2001: 436), Ghazali *et al.* (2016: 476) and Patterson *et al.* (2019a: "2"), who reject the division into subgenera.

The phylogenetic analyses on mitochondrial DNA performed by Patterson *et al.* (2019a: "5", "9"') identified three separate groups, two corresponding to South African samples and a third from Kenya (close to the type locality of *loveni*, which might possibly represent a separate (sub)species. The cyt-*b* sequences of these groups differed by 3.7 - 3.8 %.

COMMON NAMES:
Afrikaans: Temminck se langhaarvlermuis, Temminck-langhaarvlermuis, Kaapse Langhaarvlermuis. Chinese: 南非鼠耳蝠. Czech: netopýr trojbarvý. English: Temminck's Mouse-eared Bat, Cape Myotis, Cape Hairy Bat, Tricoloured Mouse-eared Bat, Cape Hairy Myotis, Temminck's Hairy Bat, Three-coloured bat. French: Murin tricolore, Petit murin brun, Murin

velu du Cap, Vespertilion d'Angola, Murin d'Angola. German: Dreifarb-Mausohr.



Figure 269. *Myotis tricolor* (TM 48188) caught at the Farm Schaapplaats, Free State, South Africa.

ETYMOLOGY OF COMMON NAME:
The colloquial name is after C.J. Temminck, who was the author of *Monographies de Mammalogie* (1827) (Taylor, 2005).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
This species was represented in the very late Holocene at Border Cave, South Africa (Avery, 1991: 6).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs, 2008e; IUCN, 2009; Monadjem and Jacobs, 2017b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Jacobs, 2017b). 2008: LC ver 3.1 (2001) (Jacobs, 2008e; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs, 2004e; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016k). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Jacobs, 2008e; IUCN, 2009; Monadjem and Jacobs, 2017b).

CONSERVATION ACTIONS:
Jacobs (2008e) [in IUCN (2009)] and Monadjem and Jacobs (2017b) report that it has been recorded from the Virunga National Park in the Democratic Republic of the Congo (Baeten *et al.*, 1984) and in view of its East African range, it seems likely that it is present in additional protected areas. Further studies are needed into the range of this species in West and Central Africa.

GENERAL DISTRIBUTION:
Myotis tricolor has been patchily recorded in sub-Saharan Africa. In West Africa the species has currently only been reported from the northwestern uplands of Liberia (Koopman *et al.*, 1995), while in Central Africa it is known only from a few records in the Democratic Republic of the Congo and Rwanda (Hayman *et al.*, 1966; Baeten *et al.*, 1984). *Myotis tricolor* is much more widely recorded in East Africa, ranging from Ethiopia in the north, through Uganda, Kenya, Tanzania, Malawi, Zambia, Mozambique and Zimbabwe through to southern South Africa.

In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

Native: Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 564); Eswatini (Monadjem *et al.*, 2010d: 565 Monadjem *et al.*, 2021: 5); Ethiopia; Kenya; Lesotho (Lynch, 1994: 193; Monadjem *et al.*, 2010d: 564); Liberia (Fahr, 2007a: 104); Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 564); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 564; Monadjem *et al.*, 2010c: 384); Nigeria (Tanshi *et al.*, 2022a: 314); Rwanda; Saõ Tomé (Rainho *et al.*, 2010a: 31); South Africa (Monadjem *et al.*, 2010d: 564); Tanzania; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 565); Zimbabwe (Monadjem *et al.*, 2010d: 565).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Schoeman and Jacobs (2002: 157) mention the following parameters for 1 specimen from the Algeria Forestry Station (RSA): Fa: 46.9 mm, Wing area: 156.6 cm^2, Wing span: 30.6 cm, Wing loading: 6.9 N/m^2, and aspect ratio: 6.0.

Shockney and Rummel (2025: 6) mention the pelage density for this species to be significant on both the dorsal and ventral sides of the proximal arm and the dorsal side of the proximal arm, and moderate on the dorsal side of the plagiopatagium.

DETAILED MORPHOLOGY:
Baculum
Kearney *et al.* (2002).

FUNCTIONAL MORPHOLOGY:
Jordaan and Jacobs (2009: 35) indicate that the wing morphology of *M. tricolor* is intermediate

between that of a typical aerial forager, gleaner (takes insects off a substrate) and trawler (takes prey from the water surface).

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 8.2 Pa, aspect ratio 6.2 for a wingspan of 34 cm and a wing area of 191 cm^2 and a body mass of 16 g.

ECHOLOCATION:
See Taylor (1999b).

Rainho *et al.* (2010a: 21) and Rainho *et al.* (2022: 605) reported the calls of 5 "cf. *tricolor* individuals from São Tomé: F_{min}: 39.3 ± 2.0 (36.6 - 41.6) kHz, F_{max}: 117.3 ± 3.3 (112.0 - 120.8) kHz, F_{maxE}: 78.4 ± 2.1 (76.4 - 81.8) kHz, duration: 1.84 ± 0.1 (1.74 - 1.92) ms and interpulse interval: 82.7 ± 16.2 (58.4 - 102.6) ms.

From Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the type of calls to be low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 50.0 kHz.

Jordaan and Jacobs (2009: 35) found that its echolocation call structure is intermediate between that of typical aerial foragers, gleaners and trawlers.

Schoeman and Waddington (2011: 291) mention a F_{peak}: 40.8 kHz and a duration: 4.4 ms for a specimen from Durban, South Africa.

In Waterberg, South Africa and Swaziland, Taylor *et al.* (2013b: 17) recorded 6 calls with the following parameters: F_{max}: 86.1 ± 5.92 (76.6 - 91.9) kHz, F_{min}: 42.7 ± 4.43 (37.1 - 50.0) kHz, F_{knee}: 57.6 ± 7.25 (48.5 - 67.5) kHz, F_{char}: 52.4 ± 6.13 (45.3 - 62.2) kHz, duration: 2.0 ± 0.40 (1.6 - 2.6) ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee}: 58 (48 - 68) kHz.

Four calls recorded at Mapungubwe National Park (RSA) by Parker and Bernard (2018: 57) had the following values: F_{char}: 42.68 ± 0.70 kHz, F_{max}: 70.40 ± 3.85 kHz, F_{min}: 40.88 ± 1.98 kHz, F_{knee}: 52.68 ± 3.43 kHz, duration: 3.03 ± 0.70 ms and 11.20 ± 7.85 calls/sec.

Release calls recorded at Telperion Nature Reserve by Kearney *et al.* (2019: 37) had a F_{char}: 37.04 kHz, slope at the start of the call: 372.62, time from start of call to F_{char}: 2.62 ms and duration: 3.13 ms. From the same location, De Jong *et al.* (2025: 322) reported the following parameters for 22 calls from 5 bats: F_{char}: 54.88 ± 10.55 kHz, F_{knee}: 60.73 ± 6.23 kHz, F_{min}: 36.49 ± 1.41 kHz, F_{max}: 80.12 ± 10.13 kHz, Bandwidth: 43.64 ± 10.05 kHz, Duration: 2.49 ± 0.42 ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 42.68 ± 0.70 kHz, F_{max}: 70.40 ± 3.85 kHz, F_{min}: 40.88 ± 1.98 kHz.

The 510 calls of 28 bats from southern KwaZulu-Natal and Eastern Cape (RSA), reported by Moir (2020: 30) and Moir *et al.* (2021a: 371), had the following characteristics: F_{max}: 77.20 ± 5.14 (70.53 - 86.49) kHz, F_{min}: 35.59 ± 3.51 (27.35 - 38.95) kHz, F_{char}: 56.38 ± 6.64 (48.32 - 69.75) kHz, F_{knee}: 75.09 ± 5.76 (68.16 - 85.59) kHz, and duration: 2.50 ± 0.47 (2.08 - 3.45) ms.

From Swaziland, Monadjem *et al.* (2017c: 179) reported F_{min}: 38.0 ± 3.78 (34.2 - 41.7) kHz, F_{knee}: 55.4 ± 10.8 (44.6 - 66.2) kHz, F_c: 49.4 ± 11.4 (38.0 - 60.8) kHz, duration: 2.4 ± 0.33 (2.07 - 2.72) ms. The maximum distance over which they were able to detect the calls was 10 m (mean: 4.6 ± 0.73 m).

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 45 calls of 12 bats: F_{max}: 62.29 ± 7.35 kHz, F_{min}: 29.13 ± 3.03 kHz, F_{knee}: 56.04 ± 7.82 kHz, F_{char}: 51.92 ± 7.66 kHz, slope: 468.23 ± 440.5 OPS, duration: 2.75 ± 0.7 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 3 *Myotis tricolor* calls from the Kruger Park (RSA): F_{min}: 40.3 ± 7.5 (31.7 45) kHz, duration: 2.5 ± 0.4 (2.2 3.8) ms, F_{max}: 60.8 ± 24.1 (38.7 86.5) kHz, F_{knee}: 44.9 ± 7.0 (36.8 49.4) kHz, F_{char}: 42.7 ± 4.9 (37.1 46.3) kHz.

Adams and Kwiecinski (2018: 4) reported F_{char}: 41.8 ± 4.3 kHz, F_{max}: 81.5 ± 6.2 kHz, F_{min}: 38.8 ± 2.2 kHz and duration: 2.9 ± 0.9 ms for six calls from the Kalahari Desert.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 47.8 kHz and duration: 3.3 ms.

22 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 31 - 50 kHz, F_{max}: 76 - 91 kHz, F_{char}: 45 - 62 kHz, F_{knee}: 48 - 67 kHz and duration 2 - 3 ms.

Parker (2022: 20) reported 47 passes of these bats in the Mountain Zebra National Park (RSA) with F_{min}: 36.09 ± 9.29 kHz, F_{char}: 39.55 ± 6.93 kHz and F_{max}: 47.24 ± 26.00 kHz.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 42.68 ± 0.70 kHz, F_{max}: 70.40 ± 3.85 kHz and F_{min}: 40.88 ± 1.98 kHz.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 44, FN = 50, BA = 8, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa and Zimbabwe. These results are the same as those obtained for *M. bocagii* specimens from South Africa (Rautenbach *et al.*, 1993).

HABITAT:
Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *M. tricolor* activity was not significantly, nor positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *M. tricolor* was observed near trees and in orchards but also in open habitats surrounding wetlands (Sirami *et al.*, 2013: 35).

On São Tomé, Castro-Fernandes *et al.* (2024: 2) reported *Myotis* cf. *tricolor* to be an edge forager.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 820,776 km^2.

HABITS:
In the Long One cave (RSA), Norton and van der Merwe (1978: 219) found that *M. tricolor* was less sensitive to light and relatively higher temperatures than *Miniopterus natalensis*, which resulted in these bats remaining longer in torpid and preferring dimly illuminated places.

ROOST:
In the Durban area, Taylor *et al.* (1999: 69) reported it roosting in the Shongweni Dam tunnel, with a colony size between 100 and 400. A colony consisting of females only, occupied this tunnel from September to the end of January.

In South Africa; these bats can migrate over hundreds of kilometers between the maternity colonies and the hibernation caves (Happold and Happold, 2023: 145).

DIET:
From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 11 faecal pellets from 1 bat (in volume percent): Coleoptera (50), Hemiptera (25), Hymenoptera (25).

Moyo and Jacobs (2020: 1) found that the diet of *M. tricolor* contained high proportions of fatty acids that were only obtainable from aquatic insects such as pond skaters (Gerridae) and whirligig beetles (Gyrinidae), This suggests that this bat probably uses both aerial hawking and trawling (or at least gleaning) to take insects from water surfaces.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 105 minutes, and the digestibility rate about 76.7 %.

PREDATORS:
Avery *et al.* (2005: 1054) found this bat species in pellets from *Tyto alba* (Scopoli, 1769) in South Africa.

Malan *et al.* (2022: 167) reported two individual found in pellets from a bat hawk (*Macheiramphus alcinus* Bonaparte, 1850.

POPULATION:
Structure and Density
This is a common species with colonies often consisting of thousands of animals (Jacobs, 2008e; IUCN, 2009; Monadjem and Jacobs, 2017b).

Trend
2016: Unknown (Monadjem and Jacobs, 2017b).
2008: Unknown (Jacobs, 2008e; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Bernard (1982b) [in Badwaik and Rasweiler (2000: 276) and Racey and Entwistle (2000: 374)] indicate that females exhibit partial regression of the corpus luteum during pregnancy, and that it has a restricted seasonal monoestry reproduction pattern. Bernard (1982b: 83) also indicated that in Natal copulation occurred in April, and that ovulation and fertilization probably occurred in mid-September, suggesting that sperm storage probably occurred during winter and ovulation was delayed until spring.

Jordaan and Jacobs (2009: 35) found that late pregnancy females forage for longer (307.0 ± 173.5 min) than early pregnant females (147.7 ± 154.5 min) to meet the high energy demands associated with the developing foetus.

Females lactate for about six weeks (Happold and Happold, 2023: 146).

PARASITES:
HAEMOSPORIDA
Lutz *et al.* (2016: 9) examined 3 *M. tricolor* specimens from East Africa and found one of

them infected with a haemosporidan parasite of the genus *Polychromophilus*.

DIPTERA
Streblidae
Raymondia hardyi Fiedler, 1954 from South Africa (Shapiro *et al.*, 2016: 254).

Nycteribiidae
Nycteribia capensis Karaman, 1939 which may be the natural parasite for this species (Haeselbarth *et al.*, 1966: 108). *Nycteribia latiterga* Theodor, 1957 from Mt. Menengai, Kenya (Haeselbarth *et al.*, 1966: 108). *Penicillidia fulvida* (Bigot, 1885) (Haeselbarth *et al.*, 1966:114; Verrett *et al.*, 2022: 8; Dick *et al.*, 2023).

SIPHONAPTERA
Ischnopsyllidae
Oxyparius isomalus (Waterston, 1915) locality not stated (Haeselbarth *et al.*, 1966: 188). *Rhinolophopsylla capensis* Jordan and Rothschild.

ACARI
Trombiculidae
Stekolnikov (2018a: 189) reported *Willmannium natalense* (Lawrence, 1949) from bats in South Africa.

VIRUSES:
In their country-wide survey of Kenyan bats, Waruhiu *et al.* (2017) found the following viruses in *Myotis tricolor*: Astroviruses and Polyomaviruses. Kamau *et al.* (2022: 5) reported Astroviridae and Retroviridae

Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)
Oelofsen and Van der Ryst (1999) tested two individuals from two localities in the Free State Province, South Africa and Lesotho for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 10 individual brains, from four localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

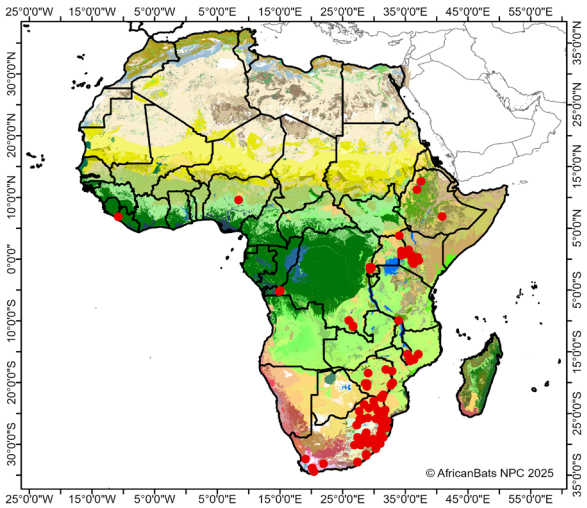

Figure 270. Distribution of *Myotis (Chrysopteron) tricolor*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Eswatini, Ethiopia, Kenya, Lesotho, Liberia, Malawi, Mozambique, Nigeria, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe.

Myotis (Chrysopteron) welwitschii (J. E. Gray, 1866)

*1866. *Scotophilus welwitschii* J. E. Gray, Proc. zool. Soc. Lond., 1866, II: 211, pl 24. Publication date: September 1866. Type locality: Angola: NE Angola: (probably near Pungo Andongo: see Crawford-Cabral (1989: 17) in Thorn *et al.* (2009: 50)). [Goto Description]. Holotype: NHMUK 1866.4.12.2: ♂. Collected by: Dr. F.M. Welwitsch. - Etymology: Named after Welwitsch, an Austrian botanist who made extensive collections in Angola (Taylor, 2005).
1878. *Vespertilio welwitschii:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 306. Publication date: 15 June 1878. (Name Combination).
1899. *Vespertilio venustus* Matschie, Sber. Ges. naturf. Freunde Berlin, 74. Publication date: 1899. Type locality: Tanzania: Morogoro district: Ukami Mts., [north slope of Uluguru Mountains]: Kinole [06 50 S 37 42]. Holotype: ZMB 54653: ♂, skin and skull. Vendor: Schlüter; see Turni and Kock (2008: 63).
1922. *Myotis welwitschii:* Kershaw, Ann. Mag. nat. Hist., ser 9, 10 (56): 181. Publication date: 1 August 1922. (Name Combination, Current Combination).
1951. *Scotophilus welwetschii:* Roberts, Mammals of South Africa, 80. (Lapsus).
1967. *Myotis venustus:* Kock, Senckenb. biol., 48 (5/6): 319. (Name Combination).
2013. *Myotis welwitschii 1:* Ruedi, Stadelmann, Gager, Douzery, Francis, Lin, Guillèn-Servent and Cibois, Mol. Phylog. Evol., 69 (3): Suppl. Publication date: 27 August 2013.
2013. *Myotis welwitschii 2:* Ruedi, Stadelmann, Gager, Douzery, Francis, Lin, Guillén-Servent and Cibois, Mol. Phylog. Evol., 69 (3): Supp. Publication date: 27 August 2013.
2013. *Myotis welwitschii 3:* Ruedi, Stadelmann, Gager, Douzery, Francis, Lin, Guillèn-Servent and Cibois, Mol. Phylog. Evol., 69 (3): Suppl. Publication date: 27 August 2013.
2014. *Myotis wilwitschii:* Ndara R., IJISR, 12 (1): 254. Publication date: November 2014. (Lapsus).

2016. *Myotis weltwitschii:* Simmons, Seiffert and Gunnell, Am. Mus. Novit., 3857: 43. Publication date: 9 May 2016. (Lapsus).
2022. *Myotis welwitschia:* Mushabati, Eiseb, Benda and Laverty, Afr. J. Ecol., 7. Publication date: 27 February 2022. (Lapsus).
? *Myotis (Chrysopteron) welwitschii:* (Name Combination).

TAXONOMY:



Figure 271. *Myotis welwitschii* (TM 47968) caught at Lapalala Wilderness area, Limpopo Province, South Africa.

Csorba *et al.* (2014: 667) and Simmons and Cirranello (2023b: 79) include *welwitschii* in the subgenus *Chrysopteron*, although Ruedi and Mayer (2001: 436), Ghazali *et al.* (2016: 476) and Patterson *et al.* (2019a: "2") reject the division in subgenera.

Myotis welwitschii is monotypic (Kershaw, 1922b: 181; Hayman and Hill, 1971; Findley, 1972; Kock, 1967; Meester *et al.*, 1986; Simmons, 2005). However, the phylogenetic analyses by Patterson *et al.* (2019a: "5", "9") indicate the existence of two groups within this species: one corresponding to an equatorial group occurring from Guinea to western Kenya and a second group existing in eastern and southern Africa, from Tanzania to South Africa (possibly representing *venustus*). These groups differ by 5 % in their cyt-*b* sequence.

COMMON NAMES:

Afrikaans: Welwitsch se langhaarvlermuis, Welwitsch-langhaarvlermuis. Chinese: 魏氏鼠耳蝠. Czech: netopýr Welwitschův, netopýr Welwitschiův. English: Welwitsch's Mouse-eared Bat, Welwitsch's Hairy Bat, Welwitch's Bat, Welwitsch's Myotis. French: Murin de Welwitsch, Myotis de Welwitsch, Vespertilion de Welwitsch. German: Welwitschs Mausohr. Kiluba (DRC): Mulima. Malawian: Liputiputi, Ndemiya, Namsimsi, Namzeze. Portuguese: Morcego lanudo de weltsch. Tshokwe (Angola): Kafukufuku.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

No fossils are known (Ratcliffe, 2002).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008p; IUCN, 2009; Monadjem *et al.*, 2017ck).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017ck). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008p; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004d; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016l). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:

There appear to be no major threats to this species as a whole (Jacobs *et al.*, 2008p; IUCN, 2009; Monadjem *et al.*, 2017ck).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008p) [in IUCN (2009)] and Monadjem *et al.* (2017ck) report that this species has been recorded from the Sengwa Wildlife Research Area and Kruger National Park in South Africa, and seem likely to be present in additional East or southern African protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:

Myotis welwitschii has been widely, but patchily, recorded over much of East Africa and southern Africa, parts of southern Central Africa, and with a single West African locality in southeastern Guinea. In East and southern Africa, it is distributed from Ethiopia and the Sudan in the north, through Kenya, Tanzania and Malawi, to Zambia, Mozambique, Zimbabwe and northeastern South Africa (where its distribution is linked with land use/land cover (Babiker Salata, 2012: 50)). In Central Africa, it is largely confined to southern Democratic Republic of the Congo, northern Angola, Rwanda and Burundi and western Uganda. It has not been recorded from Namibia or Botswana.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 920,261 km^2.

Native: Angola (Hayman, 1963; Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 565; Taylor *et al.*, 2018b: 63); Burundi (Fahr and Ebigbo, 2003: 128); Congo (The Democratic Republic of the) (Fahr and Ebigbo, 2003; Monadjem *et al.*, 2010d: 565); Eswatini (Monadjem *et al.*, 2021: 5); Ethiopia; Guinea (Fahr and Ebigbo, 2003: 128); Kenya; Malawi (Happold *et al.*, 1988; Happold and Happold, 1997b: 819; Fahr and Ebigbo, 2003; Monadjem *et al.*, 2010d: 565); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 565); Rwanda; South Africa (Fahr and Ebigbo, 2003; Monadjem *et al.*, 2010d: 565); Sudan; Tanzania; Uganda (Kityo and Kerbis, 1996: 61); Zambia (Fahr and Ebigbo, 2003; Monadjem *et al.*, 2010d: 565); Zimbabwe (Fahr and Ebigbo, 2003; Monadjem *et al.*, 2010d: 565).

GEOGRAPHIC VARIATION:

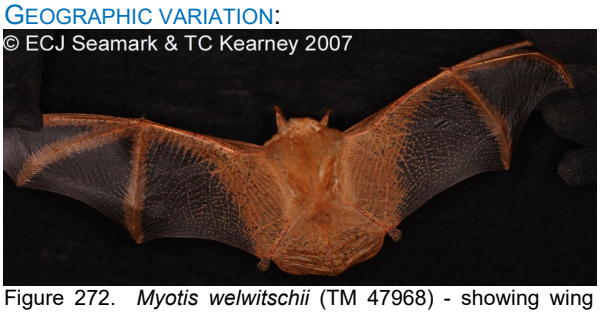

Figure 272. *Myotis welwitschii* (TM 47968) - showing wing reticulations.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Ratcliffe (2002).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Ratcliffe (2002).

DETAILED MORPHOLOGY:
Others
For a description of the skull, teeth, ears and tragus, and wingshape and aspect ratio see Ratcliffe (2002).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 7.5 Pa, aspect ratio 5.7 for a wingspan of 37 cm and a wing area of 235 cm^2 and a body mass of 18 g.

ECHOLOCATION:
In Soutpansberg, South Africa, Taylor *et al.* (2013b: 17) recorded 1 call with the following parameters: F_{max}: 73.8 kHz, F_{min}: 33.8 kHz, F_{knee}: 52.9 kHz, F_{char}: 50.3 kHz, duration: 2.1 ms.

Linden *et al.* (2014: 40) reported the following parameters from the Southpansberg range (RSA): F_{min}: 34 kHz, F_{char}:50 kHz, F_{knee}: 53, slope: 563 OPS, duration: 2.1 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 36 calls of 11 bats: F_{max}: 58.88 ± 4.53 kHz, F_{min}: 30.3 ± 3.49 kHz, F_{knee}: 51.03 ± 4.84 kHz, F_{char}: 47.27 ± 4.98 kHz, slope: 493.64 ± 133.78 OPS, duration: 2.58 ± 0.42 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 4 *Myotis welwitschii* calls from the Kruger Park (RSA): F_{min}: 30.3 ± 3.7 (25.3 - 34.2) kHz, duration: 2.8 ± 0.7 (2.2 - 3.8) ms, F_{max}: 69.1 ± 3.8 (66.2 - 74.7) kHz, F_{knee}: 60.7 ± 11.5 (44.4 - 71.5) kHz, F_{char}: 49.2 ± 7.0 (39.6 - 56.0) kHz.

Thiagavel *et al.* (2017: Suppl.) mention a F_{peak} of 32.66 kHz.

9 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 33 kHz, F_{max}: 73 kHz, F_{char}: 50 kHz, F_{knee}: 52 kHz and duration 2 ms.

From Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 9 calls: Interpulse interval: 71.4 ± 32.3 (32.3 - 120.0) ms; F_{max}: 39.7 ± 5.0 (34.7 - 49.9) kHz; Start slope: -19.2 ± 3.7 (-14.1 - -24.8) kHz/ms; End slope: -18.8 ± 4.5 (-13.6 - -25.9) kHz/ms; Ledge duration: 0.4 ± 0.1 (0.3 - 0.6) ms.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 44, FN = 50, BA = 8, and submetacentric X and Y chromosomes, for specimens from South Africa.

Genetics
See Hoofer and Van Den Bussche (2003).

Morales *et al.* (2024: Suppl.) reported the total length of the genome to consist of 2001.87M base pairs.

HABITAT:
See Ratcliffe (2002).

In southern Africa, it occurs in Savanna (70 %) and Afromontane (20 %) habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

HABITS:
See Ratcliffe (2002).

ROOST:
See Ratcliffe (2002).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 111 minutes, and the digestibility rate about 76.1 %.

Morales *et al.* (2024: Suppl.) assigned this species to the Gleaner ecomorph type.

POPULATION:
Structure
Considered solitary in its roosting habits (Smithers and Wilson, 1979; Ratcliffe, 2002). However; in a single instance two animals were found roosting in the same bush (Smithers and Wilson, 1979).

Density
Unknown, although this species is widespread, it does not appear to be particularly common (Jacobs *et al.*, 2008p; IUCN, 2009; Monadjem *et al.*, 2017ck).

Trend
2016: Unknown (Monadjem *et al.*, 2017ck). 2008: Unknown (Jacobs *et al.*, 2008p; IUCN, 2009).

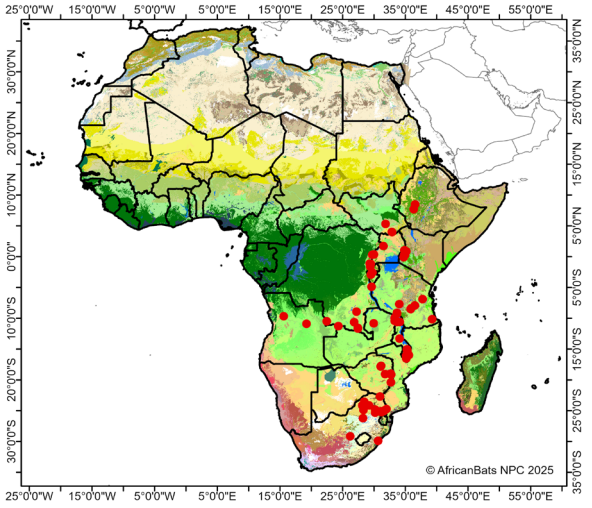

Figure 273. Distribution of *Myotis (Chrysopteron) welwitschii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Rwanda, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

†***Myotis darelbeidensis*** Gunnell, Eiting and Geraads, 2011

*2011. *Myotis darelbeidensis* Gunnell, Eiting and Geraads, N. Jb. Geol. Paläont. Abh., 260 (1): 59, figs 3C, 5A-C, 8A-C. Publication date: January 2011. Type locality: Morocco: Ahl al Oughlam [ca. 33 35 N 07 30 W]. Holotype: INSAP AaO 4571. Right dentary fragment with p2-m3. Paratype: INSAP AaO 4589. Left maxilla P4-M1. - Etymology: Name taken from Dar el Beida ("white house"), the Arabic name for Casablanca (see Gunnell *et al.*, 2011: 60). (Current Combination).

TAXONOMY:
Gunnell *et al.* (2011: 60) describe it as a large species of *Myotis*, similar in size to *M. blythii* and *M. myotis*, much larger than most other extant Mediterranean *Myotis* species (including *M. capaccinii, M. bechsteinii, M. emarginatus*).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pliocene (Brown *et al.*, 2019: Suppl.).

Subgenus *Myotis (Myotis)* Kaup, 1829

*1829. *Myotis* Kaup, Skizzierte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 106. Publication date: 1829. - Comments: Type species: *Vespertilio myotis* Borkhausen, 1797, by subsequent designation by Miller (1912: 167). Kaup (1829: 106) mentioned *Vespertilio murinus*, but for a discussion on the type species, see Jackson and Groves (2015: 280). - Etymology: From the Greek "*μύς*" or "*μυός*", meaning mouse and "*οὐς*" or "*ὠτός*" meaning ear (see Palmer, 1904: 442). Gardner (2005:184) considers the name to be masculine (My = mouse + ot = ear(ed) + is (Latin third declension ending)). - Phonetics: mie-oh'-tis.

Myotis (Myotis) capaccinii (Bonaparte, 1837)

*1837. *Vespertilio Capaccinii* Bonaparte, Iconografia Fauna italiana, 1, fasc 20 and pl, fig. Publication date: 1837. Type locality: Italy: Sicily. [Goto Description]. Holotype: NHMUK 1907.1.1.734. - Etymology: In honour of Francesco Capaccini, undersecretary of state of Rome about 1833-34, and a patron of Bonaparte's "Iconografia della Fauna Italica," published in 1832-1841 (Palmer, 1904: 49). (see Palmer, 1904: 49; Kozhurina, 2002: 15).

2022. *Myotis cappaccinii:* Mechouk, Mihalca, Deak and Bouslama, Parasites & Vectors, 15 (302): 8. Publication date: 27 August 2022. (Lapsus).
? *Myotis (Myotis) capaccinii:* (Current Combination).
? *Myotis capaccinii capaccinii:* (Name Combination).
? *Myotis capaccinii:* (Name Combination).

TAXONOMY:
Most recent authors consider *M. capaccinii* as a monotypic species (Spitzenberger and von Helversen, 2001; Simmons, 2005). However, Aihartza and Aizpurua (2023: 162) indicate that based on morphological characters, *Myotis capaccinii capaccinii* is recognized from North-western Africa to the Western Balkans, and *Myotis capaccinii bureschi* from Bulgaria to Iran. In 2019, another subspecies was described from southern Turkey: *Myotis capaccinii abidinbudaki*.

Simmons and Cirranello (2023b: 79) did not assigned it to a subgenus ("unassigned").

COMMON NAMES:
Albanian: Lakuriq nate gishtgjatë. Arabian: Khaffash. Armenian: Միջերկրածովային գիշերաչղջիկ. Azerbaijani: Uzunbarmaq gecə şəbpərəsi. Basque: Saguzar hatz-luze, Saguzar hankahandia. Belarusian: Начніца даўгапалая. Bosnian: Dugoprsti šišmiš. Breton: Gousperell Capaccini. Bulgarian: Дългопръст нощник. Castilian (Spain): Murciélago patudo, Murciélago ratonero patudo. Catalan (Spain): Ratpenat de peus grans, Rat penat de peus grans. Croatian: Dugonogi šišmiš, Dugoprsti šišmiš. Czech: Netopýr dlouhonohý. Danish: Capaccinis flagermus. Dutch: Capaccini's vleermuis. English: Capaccinii's Mouse-eared Bat, Long-fingered Bat, Long-fingered Myotis. Estonian: Pikkjalg-lendlane. Finnish: Pitkäsormisiippa. French: Murin de Capaccini, Vespertilion de Capaccini, Vespertilion des montagnes. Frisian: Grutfuottige flearmûs. Galician (Spain): Morcego de pés grandes. Georgian: კაპაჩინის მღამიობი. German: Langfußfledermaus, Freischeinige Stelzfussfledermaus. Greek: Ποδαρομυωτίδα. Hebrew: נשפון גדות, Nishpon Gadot. Hungarian: Hosszúlábú denevér, Nycteris i macropus. Irish Gaelic: Ialtóg fhadmhéarach. Italian: Vespertilio di Capaccini. Latvian: Garpirkstu naktssikspārnis. Lithuanian: Ilgapirštis pelėausis. Luxembourgish: Laangfoussfliedermaus. Macedonian: Долгопрст ноќник [= Dolgoprst Nokjnik]. Maltese: Farfett il-Lejl tas-Swaba Twal. Montenegrin: Dugoprsti večernjak. Norwegian: Langfotflaggermus. Polish: Nocek długopalcy. Portuguese: Morcego de Capaccini. Rhaeto-Romance: Vespertil da Capaccini. Romanian: Liliacul cu picioare lungi, Liliac-cu-picioare-lungi. Russian: Ночница средиземная (итальянская). Serbian: Дугопрсти вечерњак [= Dugoprsti večernjak]. Scottish Gaelic: Ialtag fhad-mheurach. Slovak: Netopier dlhonohý. Slovenian: Dolgonogi netopir. Swedish: Storfotsfladdermus. Turkish: Uzunayaklı Yarasa. Ukrainian: Нічниця довгопала. Welsh: Ystlum hirfys.

CONSERVATION STATUS:
Global Justification
The species occupies specialised habitat (caves and associated water systems). In the eastern part of the range it congregates in winter in a few sites which are threatened by human disturbance. It has declined between 30 and 50 % in Spain in the last 10 years, and there are indications of declines in other parts of the range. It only hunts in watercourses and is therefore threatened by water pollution and the development of tourist infrastructure, which is expected to continue in the future. It is suspected that population declines are underway that will exceed 30 % over 18 years (3 generations), and for that reason the species is considered Vulnerable (VU A4bce ver 3.1 (2001)) (Hutson *et al.*, 2008k; IUCN, 2009; Paunović, 2016).

Assessment History
Global
2016: VU A4bce ver 3.1 (2001) (Paunović, 2016). 2008: VU A4bce ver 3.1 (2001) (Hutson *et al.*, 2008k; IUCN, 2009). 1996: VU (Baillie and Groombridge, 1996). 1994: VU (IUCN, 1994). 1990: VU (IUCN, 1990). 1988: VU (IUCN, 1988).

Regional
None known.

MAJOR THREATS:
Threats include changes in water quality through pollution and dam building, and loss of water bodies and watercourses. Damage or disturbance to caves (tourism, fires and vandalism) used as roosts may also be a problem, as the species is very dependent on caves. The species is collected for medicinal purposes in North Africa (Hutson *et al.*, 2008k; IUCN, 2009; Paunović, 2016).

The species' small distribution range, cave or tree roosting, and aerial hawking feeding style are considered to be the most important risk factors related to climatic change (Sherwin *et al.*, 2012: 174). Bilgin *et al.* (2012: 434) predict that the range retraction for *M. capaccinii* as a result of climatic change may pose severe threats to its

survival as this species has the bulk of its range in the Mediterranean region.

CONSERVATION ACTIONS:
Paunović (2016) supports Hutson *et al.* (2008k) [in IUCN (2009)] who report that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in the range states where these apply. It is included in Annex II (and IV) of EU Habitats and Species Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. Some habitat protection through Natura 2000. In Spain, fences are in place to protect several known colonies. Measures needed include protection of colonies (these measures should avoid the blocking of any cave entrances with gates and control of tourist access) and improvement of water quality.

GENERAL DISTRIBUTION:
Myotis capaccinii is sparsely distributed from eastern Iberia, Spain through the northern Mediterranean to coastal Asia Minor and Israel, Lebanon and Jordan, and also in Mesopotamia from Turkey to Iran and in north-west Africa (limited to the Mediterranean fringe of western Maghreb: north Morocco and northwest Algeria). It occurs from sea level to 900 m.

Bilgin *et al.* (2012) examined climate change scenarios within the Asia Minor and Levant region, they predict that *M. capaccinii* will have a range contraction, which may pose severe threats to their survival of this species.

Native: Albania; Algeria (Kowalski and Rzebik-Kowalska, 1991: 91); Andorra; Austria (?); Bosnia and Herzegovina; Bulgaria; Croatia; Cyprus (Benda *et al.*, 2007: 71); France [Corsica]; Greece [Kriti]; Holy See [Vatican City State]; Iran, Islamic Republic of; Iraq; Israel; Italy [Sardinia, Sicily]; Jordan; Lebanon; Macedonia, the former Yugoslav Republic of; Montenegro; Morocco (Aulagnier and Thevenot, 1986: 44; Dbiba *et al.*, 2025: 8); Romania; Russian Federation (?); Serbia; Slovenia; Spain [Baleares]; Syrian Arab Republic; Tunisia (Dalhoumi *et al.*, 2019b: 26); Turkey; Uzbekistan.
Regionally extinct: Switzerland.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Almenar *et al.* (2006: 158) indicate that the large hind feet and pointed wings of this species are well suited for capturing prey while trawling through the water surface.

FUNCTIONAL MORPHOLOGY:
Gardiner and Nudds (2011: 2187), in their study of flight-initiating jumps, found that *M. capaccinii* did not show a reduced jumping performance, which could have been expected due to the large feet, which leads to extra weight at the extremities.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 10.5 Pa for a wingspan of 25 cm and a wing area of 56 cm^2 and a body mass of 6 g.

In their study on take-off performance, Gardiner *et al.* (2014: 1059) determined a wing beat frequency of 12.96 ± 0.18 Hz.

ECHOLOCATION:
Highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (while hunting above water surface): hyperbolic FM. F_{max}: 43 kHz; F_{min}: 22 kHz; F_{peak}: 28 - 35 kHz; call-duration: 6 - 9 ms, inter-call interval: 145 - 165 ms (Barataud, 2002, 2005).

The data for 56 animals from Greece were the following: F_{start}: 89.7 ± 7.35 kHz, F_{end}: 35.1 ± 2.18 kHz, F_{peak}: 48.9 ± 4.76 kHz, bandwidth: 14.2 ± 9.93 kHz, duration 4.6 ± 0.77 ms and interpulse interval: 75.4 ± 22.97 ms (Papadatou *et al.*, 2008b: 132).

Walters *et al.* (2012: suppl.) report the next figures for 30 calls of bats from France and Italy: duration: 3.62 ± 1.40 ms, F_{max}: 73.51 ± 9.28 kHz, F_{min}: 36.6 ± 3.18 kHz, bandwidth: 36.91 ± 10.73 kHz, F_{peak}: 52.2 ± 6.93 kHz.

The following data for 20 calls from Iran were reported by Benda *et al.* (2012a: 182): F_{start}: 66.0 ± 12.3 (53.1 - 87.1) kHz, F_{end}: 48.9 ± 2.0 (46.6 - 52.6) kHz, F_{peak}: 52.9 ± 1.9 (49.9 - 55.3) kHz, duration: 5.3 ± 0.7 (3.9 - 6.3) ms, and interpulse interval: 49.1 ± 20.4 (19.4 - 84.4) ms. Mehdizadeh *et al.* (2018: 1) reported that isolation calls of 1 to 4 day old Iranian *M. capaccinii* were FM shallow calls with longer duration (7.54 ± 1.83 ms) and lower F_{peak} (20.07 ± 0.89 kHz) as compared to adult female calls (2.35 ± 0.75 ms and 54.02 ± 4.34 kHz). Between days 12 and 16, the calls began to sound more like these of the adults.

Luo *et al.* (2019a: Supp.) reported the following data (from two calls): F_{peak}: 50.4, 48.9 kHz, F_{start}: 83.6, 89.7 kHz, F_{end}: 39.7, 35.1 kHz, Band width: 43.9, 54.6 kHz, and duration: 3.8, 4.6 ms.

Ait-Abdesselam *et al.* (2025: 40) mentioned an F_{end} value of 41.2 ± 5.17 kHz for Algerian bats.

Aizpurua *et al.* (2013: 4) indicate that *M. capaccinii* is able to regulate the temporal component of the echolocation call so that they can modify their capturing technique depending on whether they are hunting for aquatic arthropods or fish.

MOLECULAR BIOLOGY:
Karyotype
Capanna *et al.* (1968) and Rushton (1970: 463) reported 2*n* = 44, aFN = 50, X = metacentric, Y = acrocentric for specimens from Italy, while Pérez-Suárez *et al.* (1991) reported 2*n* = 44, aFN = 52, X = submetacentric, Y = acrocentric for specimens from Spain.

From Italy, Capanna and Manfredi Romanini (1971: 474) mention 2*n* = 44, aFN =60, 3 metacentric pairs of chromosomes, 1 submetacentric and 17 acrocentric; with the X chromosome being metacentric and the Y chromosome acrocentric.

Genetics
See Hoofer and Van Den Bussche (2003).

Karaman *et al.* (2017: 119) indicate that the ddRAD and mtDNA structure suggests that three lineages in the Mediterranean area could be considered different species, but this needs to be investigated further.

HABITAT:
In the eastern Iberian Peninsula, Almenar *et al.* (2006: 157) report that *M. capaccinii* only used aquatic habitats as foraging sites, and that most of their foraging activity was on rivers.

In northern Africa, this species occupies a narrow coastal band from Morocco to Tunisia.

M. capaccinii preferentially used river stretches characterised by an open course and smooth water surfaces (Almenar *et al.*, 2012). They shifted foraging stretches seasonally, likely following the spatiotemporal dynamics of prey production over the watershed (Almenar *et al.*, 2012).

HABITS:
Aihartza *et al.* (2008: 287) describe the fishing behaviour of *M. capaccinii* as observed in a flight tent containing an artificial pool. They distinguished two patterns: "A) long series of circular flights, skimming along the water and dipping in softly twice or three times in each roundabout; B) long figure-eight loops with bats flying faster and higher, swooping down on the centre of the pond, where they snapped their hind feet hard into the water." They also suggest (p. 297) that the bats detect the presence of fish by touching them when they dip their feet into the water.

ROOST:
Within the Iberian Peninsula, within the lower basin of the Xúquer River, Almenar *et al.* (2012) reported a main roost within a limestone cave with a variable colony size through the season: 81 *M. capaccinii* during pre-breeding, 219 during lactation and 113 during weaning of 2004. More than 100 individuals inhabit the second roost during lactation, located 8.4 km from the first. Both roosts are shared with other bat species (*Rhinolophus euryale*, *Rhinolophus mehelyi*, *Myotis blythii*, *Myotis myotis*, *Myotis emarginatus*, *Myotis nattereri* and *Miniopterus schreibersii*) (Almenar *et al.*, 2012).

DIET:
Aihartza *et al.* (2008: 288) indicate that in the Mediterranean area aquatic arthropods (e.g., Diptera: Culicidae and Chironomidae) form the main prey of this species, supplemented by Trichoptera, Neuroptera, Lepidoptera, Heteroptera and arachnids. But its diet also contains fish.

Although some *M. capaccinii* populations are known to eat fish in the wild Aihartza *et al.*, 2003; Levin *et al.*, 2006; Biscardi *et al.*, 2007), the diet of the surveyed individuals appeared to be exclusively arthropods (Almenar, 2008).

On the Iberian Peninsula, Aizpurua *et al.* (2011: 48) examined 2600 guano samples and retrieved 97 otoliths, all from the mosquitofish (*Gambusia holbrooki*) which would have been between 1.5 and 3.6 cm in length (maximum size of fishes: 5 cm in males and 8 cm in females, see Aihartza *et al.*, 2003: 196). They also found that one of the bats was able to eat between 8 and 15 fishes in one or two nights.

Piscivory is only reported for three geographically distinct colonies: Dénia (Iberian Peninsula), Hazorea (Levant) and Amaseno Valley (Italy) (Aihartza and Aizpurua, 2023: 176).

Aizpurua *et al.* (2021: 5) compared the gut microbiotas of bats with a piscivorous diet with that of conspecifics which were alleged to be non-piscivorous and found the microbiota composition to be very similar, which led them to believe that consumption of fish in this species is much more widespread than previously thought. Examination of faecal pellets, however, did not reveal the

presence of fish remains in the diet of non-piscivorous bats. Aizpurua *et al.* (2021: 5) hypothesize that the similar gut microbiota might be the result of an ancestral diet with more widespread fishing behavior.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 76 minutes, and the digestibility rate about 80.2 %.

POPULATION:
Structure and Density
See Hutson *et al.*, 2008k) [in IUCN (2009)] and Paunović (2016).

Trend
2016: Decreasing (Paunović, 2016). 2008: Decreasing (Hutson *et al.*, 2008k; IUCN, 2009). *Myotis capaccinii* populations within the Asia Minor and Levant region are predicted to have a declining population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

REPRODUCTION AND ONTOGENY:
In Greece, most females were pregnant by the second half of April and had given birth before the end of May. The first flying young were found by the end of June or the beginning of July (Papadatou *et al.*, 2008a 509).

In Iran, Mehdizadeh *et al.* (2018: 1) found the forearm length of neonates to be 19.59 ± 1.23 mm, with a linear growth of 0.74 mm/day until day 28. The weight at day one was 3.59 ± 0.23 g, and this increased linearly with 0.15 g/day until day 28.

POSTNATAL DEVELOPMENT:
Sharifi and Javanbakht (2018: 30) studied the post-natal growth of three captive bats. At birth the pups weighted 2.6 ± 0.1 g and a forearm length of 18 ± 1.5 mm. On day 54, the weight was increased to 6.7 ± 0.2 g (82.71 % of the adults) and the forearm to 34.56 ± 0.4 mm (80.37 % of the adult). Both increased lineary during the first three weeks (respectively 0.09 g/d and 0.6 mm/d).

PARASITES:
In Italy, Voyron *et al.* (2011: 193) reported the following fungal entities from carcasses: *Alternaria* sp., *Candida palmioleophila*, *Chrysosporium/Gymnoascus*, *Cladosporium cladosporioides*, Gimnoascacea, *Verticillium lecanii*, *Trichosporon chiropterorum*, *Mucor hiemalis f. hiemalis*, *Mucor racemosus*.

Ševčík *et al.* (2012: 35) report on the presence of the bat flies *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, and *Penicillidia dufourii* Westwood, 1835 on bats from Crete and Cyprus. *Nycteribia kolenati* Theodor & Moscona, 1954 and *Phthiridium biarticulatum* Hermann, 1804 were reported for the first time by Haelewaters *et al.* (2017: 1) from bats from Hungary.

From a non-specified area, Haelewaters *et al.* (2018: 794) added *Penicillidia conspicua* Speiser, 1901.

In Algeria, Bendjeddou *et al.* (2013: 325) reported two ectoparasites: *Cimex lectularius* (Linnaeus, 1758) (Hemiptera: Cimicidae) and *Rhipicephalus sanguineus* (Latreille, 1806) (Arachnidae: Ixodida: Ixodidae). Bendjeddou *et al.* (2017: 15) and Khelfaoui *et al.* (2018: 67) added the following species: *Nycteribia (Nycteribia) latreillii* (Leach, 1817) and *Phthiridium biarticulatum* Hermann, 1804 (Nycteribiidae); *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851 (Streblidae) and *Spinturnix myoti* (Kolenati, 1856) and *Ixodes vespertilionis* Koch, 1844 (Arachnida).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ixodidae: *Ixodes vespertilionis* Koch, 1844; Macronyssidae: *Rhipicephalus sanguineus* s.l.; Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856); Streblidae: *Brachytarsina flavipennis* Masquart, 1851.

Júnior *et al.* (2020: Suppl.) reported the presence of additional Nycteribiid flies (not specifically for Africa): *Basilia italica* Theodor, 1954, *Basilia nana* Theodor, 1954, *Basilia nattereri* (Kolenati, 1857), *Nycteribia schmidlii* Schiner, 1853, *Nycteribia kolenati* Theodor and Moscona, 1954, *Nycteribia latreillii* (Leach, 1817), *Nycteribia vexata* Westwood, 1835, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* Hermann, 1804.

VIRUSES:
Paramyxoviridae
Morbillivirus
This virus was reported from Bulgaria, Germany and Romania by Kohl and Kurth (2014: 3113).

UTILISATION:
The species is collected for medicinal purposes in North Africa (Hutson *et al.*, 2008k; IUCN, 2009).

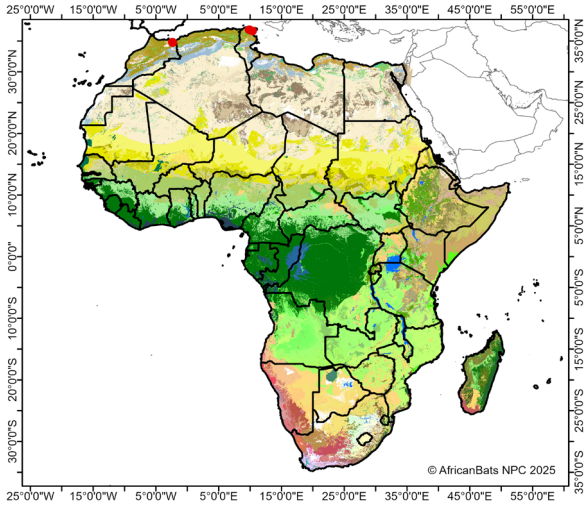

Figure 274. Distribution of *Myotis (Myotis) capaccinii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Morocco, Tunisia.

Myotis (Myotis) mystacinus (Kuhl, 1817)

*1817. *Vespertilio mystacinus* Kuhl, Die Deutsche Fledermäuse, 7, 58. Type locality: Germany. Syntype: ZMB 461: ♂, skin and skull. Unknown locality, presumably coll. Kuhl, purchased from Kuhl, 09.1818.: see Turni and Kock (2008: 60).
? *Myotis (Myotis) mystacinus:* (Current Combination).
? *Myotis mystacinus:* (Name Combination).

TAXONOMY:
Simmons and Cirranello (2023b: 79) did not assign this species to a subgenus ("unassigned").

Despite the fact that numerous species have been recently recognized within this complex, the whiskered bats from Morocco are still included in the nominal form (von Helversen *et al.*, 2001; Mayer *et al.*, 2007; García-Mudarra *et al.*, 2009).

At present, this species includes three forms differing in morphological traits: *M. mystacinus mystacinus* (most of European range), *M. mystacinus occidentalis* (Iberia and Morocco) and *M. mystacinus caucasicus* (Caucasus region).

COMMON NAMES:
Albanian: Lakuriq nate me mustaqe. Armenian: Բեղավոր գիշերաչղջիկ. Azerbaijani: Bığlı gecə şəbpərəsi. Basque: Saguzar biboteduna. Belarusian: Начніца вусатая. Bosnian: Mali brkati šišmiš. Breton: Gousperell varvek. Bulgarian: Мустакат нощник. Castilian (Spain): Murciélago bigotudo, Murciélago ratonero bigotudo. Catalan (Spain): Ratpenat de bigotis, Rat penat de bigotis. Croatian: Brkati šišmiš, Mali brkati šišmiš. Czech: Netopýr vousatý, nedopír walausatý, netopýrec vousatý. Danish: Skægflagermus. Dutch: Baardvleermuis, Gewone pisang blad vleermuis. English: Whiskered Mouse-eared Bat, Whiskered Bat, Whiskered Myotis, Mouse-eared bat. Estonian: Habelendlane. Finnish: Viiksisiippa. French: Murin à moustaches, Vespertilion à moustaches. Frisian: Burdflearmûs. Galician (Spain): Morcego bigotudo, Morcego de bigotes. Georgian: ულვაშა მღამიობი. German: Bartfledermaus, Kleine Bartfledermaus, Schnauzbärtige Fledermaus. Greek: Μουστακονυχτερίδα. Hungarian: Bajuszos denevér, Nycteris i mystakophoros. Indonesian: Kelelewar myotis pucuk. Irish Gaelic: Ialtóg ghiobach. Italian: Vespertilio mustacchino. Latvian: Bārdainais naktssikspārnis. Lithuanian: Ūsuotasis pelėausis. Luxembourgish: Kleng Baartfliedermaus. Macedonian: Мустаќест ноќник [= Mustakjest Nokjnik]. Maltese: Farfett il-Lejl Daqni. Montenegrin: Brkati večernjak. Norwegian: Skjeggflaggermus. Polish: Nocek wąsatek. Portuguese: Morcego-de-bigodes. Rhaeto-Romance: Vespertil dal barbis, Vespertil pitschen dal barbis. Romanian: Liliacul mustăcio, Liliac-cu-mustăți. Russian: Ночница усатая, Усатая ночница [= Usataya nochnitsa]. Serbian: Тамнолики бркати вечерњак [= Tamnoliki brkati večernjak]. Scottish Gaelic: Ialtag ghibeach. Slovak: Netopier fúzatý. Slovenian: Brkati netopir, Skupina brkatih netopirjev. Swedish: Mustaschfladdermus. Turkish: Bıyıklı Siyah Yarasa. Ukrainian: Нічниця вусата [= Nichnytsya vusata]. Welsh: Ystlum barfog.

CONSERVATION STATUS:
Global Justification
Myotis mystacinus has a large population size and a wide distribution. No declines in population size have been detected, and there are no known widespread major threats. Assessed as Least

Concern (LC ver 3.1 (2001)) (Hutson *et al.*, 2008r; IUCN, 2009; Coroiu, 2016).

Assessment History
Global
2016: LC ver 3.1 (2001) (Coroiu, 2016). 2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008r; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
There are no major threats to this species overall, but the species is affected by loss of woodland and other aspects of land management and development. It is also affected by loss of and damage to roost sites in trees, buildings and underground habitats. In the African part of the species' range, cave habitats where the species roosts are being destroyed by fires and vandalism. This species is also collected for medicine, but not at a level that constitutes a threat to the species (Hutson *et al.*, 2008r; IUCN, 2009; Coroiu, 2016).

CONSERVATION ACTIONS:
Coroiu (2016) supports Hutson *et al.* (2008r) [in IUCN (2009)] who report that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention. It is included in Annex IV of EU Habitats and Species Directive, and there is some habitat protection through Natura 2000. It occurs in protected areas throughout its range. Protection of cave roost sites is required.

GENERAL DISTRIBUTION:
Myotis mystacinus is a western Palaearctic species, occurring in western and central Europe, southern parts of Scandinavia, the British Isles, Morocco, northern parts of eastern Europe, western parts of the Caucasus and the Urals. The occurrence in southeast Europe is questionable but likely. It is marginal in Africa, restricted to Moroccan mountains from the Rif in the north to the southern slope of High Atlas in the south. It has been recorded from sea level up to 1,920 m asl (Gerell, 1999).

Native: Andorra; Armenia; Austria; Azerbaijan; Belgium; Bosnia and Herzegovina; Bulgaria; China; Croatia; Czech Republic; Denmark; Estonia; Finland; France [Corse]; Georgia; Germany; Greece [Kriti]; Hungary; Ireland; Italy; Latvia; Liechtenstein; Lithuania; Luxembourg; Macedonia, the former Yugoslav Republic of; Montenegro; Morocco (Benda *et al.*, 2004d; El Ibrahimi and Rguibi Idrissi, 2015: 360; Dbiba *et al.*, 2025: 8); Netherlands; Norway; Poland; Romania; Russian Federation; Serbia; Slovakia; Slovenia; Spain; Sweden; Switzerland; Turkey; Ukraine; United Kingdom.
Regionally extinct: Portugal.
Presence uncertain: Albania; Lebanon.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.1 Pa, aspect ratio 6.0 and tip shape index of 2.26 for a wingspan of 21 cm and a wing area of 75 cm^2 and a body mass of 5 g.

ECHOLOCATION:
Papadatou *et al.* (2008b: 132) report the following data for 1 Greek specimen belonging to *M. mustacinus bulgaricus*: F_{start}: 104.0 kHz, F_{end}: 33.6 kHz, F_{peak}: 47.7 kHz, bandwidth: 9.1 kHz, duration 3.8 ms and interpulse interval: 72.7 ms.
Data for 51 calls from France, Greece, Switzerland, and the UK, presented by Walters *et al.* (2012: suppl.) include: duration: 2.36 ± 0.59 ms, F_{max}: 84.76 ± 14.10 kHz, F_{min}: 37.04 ± 3.24 kHz, bandwidth: 47.72 ± 14.14 kHz, F_{peak}: 51.55 ± 7.70 kHz.

MOLECULAR BIOLOGY:
Karyotype
Bovey (1949) reported a $2n$ = 44, aFN = 50, X = metacentric, Y = acrocentric, while Zima (1978) found aFN = 52. Arslan and Zima (2014: 9) added an FN of 54 and that the autosomal component consists of three large metacentric, one small metacentric, 15 acrocentric and two dot-like pairs.

Genetics
See von Helversen *et al.* (2001), Mayer *et al.* (2007), García-Mudarra *et al.* (2009).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 61 minutes, and the digestibility rate about 82.4 %.

POPULATION:
Structure and Density
In Europe, it is one of the more common species within the regular distribution area. It is very rare in North Africa, with only 25 specimens in 4 locations (Hutson *et al.*, 2008r; IUCN, 2009; Coroiu, 2016).

Trend
2016: Unknown (Coroiu, 2016). 2008: Unknown (Hutson *et al.*, 2008r; IUCN, 2009).

PARASITES:
In Europe, Genov *et al.* (1992) reported the presence of the following Nematodes: *Molinostrongylus alatus* (Ortlepp, 1932), *M. skrjabini* Skarbilovitch, 1934, *M. spasskii* Andrejko, Pinchuk and Skvorzov, 1968, and *M. vespertilionis* Morosov and Spassky, 1961.

Frank *et al.* (2015: 8) provide the following overview for parasites in European *M. mystacinus*:
Arachnida: *Argas vespertilionis* (Latreille, 1796, *Ixodes* sp., *Ixodes vespertilionis* Koch, 1844, *Macronyssus ellipticus* (Kolenati, 1857), *Macronyssus flavus* (Kolenati, 1856), *Spinturnix kolenatii* Oudemans, 1910, *Spinturnix myoti* (Kolenati, 1856), *Spinturnix mystacinus* (Kolenati, 1857), *Steatonyssus periblepharus* Kolenati, 1858, *Steatonyssus spinosus* Wilmann, 1936.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following tick: Argasidae: *Secretargas transgariepinus* (White, 1846).

Insecta: *Basilia nana* Theodor & Moscona, 1954, *Basilia nattereri* Kolenati, 1857, *Basilia italica* Theodor, 1954, *Cimex pipistrelli* (Jenyns, 1839), *Ischnopsyllus hexactenus* (Kolenati, 1856), *Ischnopsyllus mysticus* Jordan, 1942, *Ischnopsyllus octactenus* (Kolenati, 1856), *Ischnopsyllus simplex* Rotschild, 1906, *Ischnopsyllus variabilis* (Wagner, 1898), *Myodopsylla trisellis* Jorda, 1929, *Nycteribia kolenatii* Theodor and Moscona, 1954, *Nycteribia pedicularia* Latreille, 1805, *Nycteridopsylla longiceps* Rotschild, 1908, *Nycteridopsylla pentactena* (Kolenati, 1856).

Trematoda - Digenea: *Lecithodendrium linstowi* Dollfus, 1931, *Plagiorchis vespertilionis* (Muller, 1784), *Prosthodendrium chilostomum* (Mehlis, 1831).

Nematoda: *Molinostrongylus alatus* (Ortlepp, 1932), *Molinostrongylus spasskii* Andrejko, Pintschuk and Skvorzov, 1968, *Molinostrongylus vespertilionis* Morosov and Spassky, 1961.

Cestoda: *Vampirolepis balsaci* (Joyeux and Baer, 1934).

VIRUSES:
Orthomyxoviridae
Despite sampling and testing of 44 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

UTILISATION:
In Northern Africa, this species is collected for traditional medicine, but not at a level that constitutes a threat to the species (Hutson *et al.*, 2008r; IUCN, 2009; Coroiu, 2016; Budinski and López-Baucells, 2023: 332).

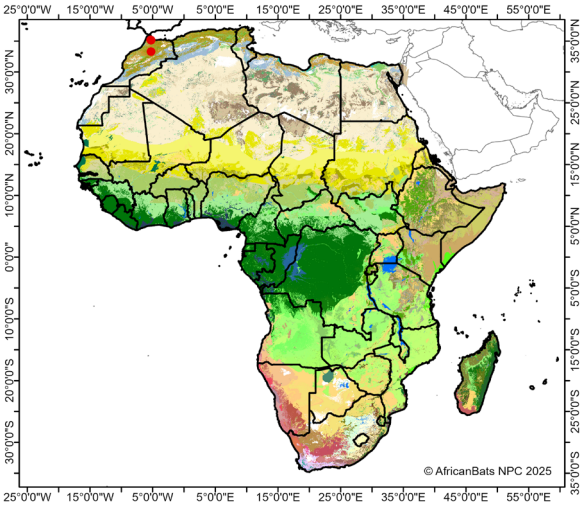

Figure 275. Distribution of *Myotis (Myotis) mystacinus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Morocco.

Myotis (Myotis) punicus Felten, 1977

1875. *Vespertilio [(Vespertilio)] africanus* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (94): 260. Publication date: 1 October 1875. Type locality: Gabon: "Gaboon". Holotype: NHMUK 1873.4.16.5. . - Comments: The type locality was originally mentioned as 'Gaboon', but the specimen is more probably from Kashmir, see Blanford (1888-91) and Hayman and Hill (1971: 35) (in Corbet and Hill, 1992: 120). However, see also Grubb (2004: 92); who indicates that Gabon might not be rejected.

*1977. *Myotis blythii punicus* Felten, in: Felten, Spitzenberger and Storch, Senckenb. biol., 58 (1/2): 39. Publication date: 22 August 1977. Type locality: Tunisia: Cap Bon: El Haouaria cave [37 03 N 11 01 E]. [Goto Description]. Holotype: SMF 44104: ad ♂, skull and alcoholic. Collected by: Nagel, Schubert and Indulis Evalds Vesmanis; collection date: 25 March 1971. See Felten *et al.* (1977: 39). Paratype: SMF 18946: ♂, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18947: ♂, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18948: ♂, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18949: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18950: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18951: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18952: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18955: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18956: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18957: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18958: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18959: ♀, skull and alcoholic.

Collection date: 15 May 1960. Paratype: SMF 18960: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18961: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18962: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18963: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 18964: ♀, skull and alcoholic. Collection date: 15 May 1960. Paratype: SMF 22214: ♂, skull and alcoholic. Collection date: 12 March 1963. Paratype: SMF 22217: ♀, skull and alcoholic. Collection date: 12 March 1963. Paratype: SMF 22218: ♀, skull and alcoholic. Collection date: 12 March 1963. Paratype: SMF 22219: ♀, skull and alcoholic. Collection date: 12 March 1963. Paratype: SMF 22220: ♀, skull and alcoholic. Collection date: 12 March 1963. Paratype: SMF 43386: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43387: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43388: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43389: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43390: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43392: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 43961: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43962: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43963: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43964: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43965: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43966: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43967: ♀, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 43968: ♂, skull and alcoholic. Collection date: 28 August 1972. Paratype: SMF 44097: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44098: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44099: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44100: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44101: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44102: ♀, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44103: ♂, skull and alcoholic. Collection date: 25 March 1971. Paratype: SMF 44618: ♀, skull and alcoholic. Collection date: 25 March 1971.

2000. *Myotis cf. punicus* Castella, Ruedi, Excoffier, Ibanez, Arlettaz and Hausser, Mol. Ecol., 9: 1761.

? *Myotis (Myotis) punicus:* (Current Combination).

? *Myotis blythii oxygnathus:*

? *Myotis blythii:*

? *Myotis myotis myotis:*

? *Myotis myotis:*

? *Myotis oxygnathus:*

? *Myotis punicus:* (Name Combination).

General Comments:

In the literature, a lot of information on this species has been published as pertaining to *Myotis blythii*.

Taxonomy:

Originally described as a subspecies of *M. blythii*, but recently shown to lie outside a clade including *blythii*, *myotis* and *oxygnathus* (Ruedi and Mayer, 2001). Considered a valid species by Castella *et al.* (2000), Dietz and von Helversen (2004: 71), Benda *et al.* (2004d) and Evin *et al.* (2008).

Biollaz *et al.* (2010) suggest that the Corsican and Sardinian populations are currently isolated from the continental gene pool and therefore should be considered as different evolutionary significant units. Baron (2012: 5) found that the population on Malta is a single panmitic unit with an tendency towards becoming isolated mating systems.

Simmons and Cirranello (2023b: 79) assigned it to the subgenus *Chrysopteron*.

Common Names:

Albanian: Lakuriq nate maghrebian. Armenian: Փյունիկյան գիշերաչղջիկ. Azerbaijani: Siçanqulaq gecə şəbpərəsi. Basque: Saguzar arratoi-belarri mairutar. Belarusian: Начніца фінікійская, Начніца магрыбская. Bosnian: Punski šišmiš. Breton: Gousperell ar Magreb. Bulgarian: Магребски нощник. Castilian (Spain): Murciélago ratonero moruno. Catalan (Spain): Ratpenat rater africà. Croatian: Sjevernoafrički oštrouhi šišmiš. Czech: Netopýr punský. Danish: Mahgreb museøre. Dutch: Fenicische vale vleermuis. English: Maghrebian Mouse-eared Bat, Felten's Myotis. Estonian: Vahemere lendlane. Finnish: Tunisiansiippa. French: Murin du Maghreb. Frisian: Maghreb mûsearflearmûs. Galician (Spain): Morcego rateiro africano. Georgian: მაღრიბული მღამიობი. German: Punisches Mausohr, Maghreb-Mausohr. Greek: Τρανομυωτίδα της Καρχηδόνας. Hungarian: Magrebi denevér. Irish Gaelic: Ialtóg luch-chluasach Mhaigribeach. Italian: Vespertilio maghrebino. Latvian: Pūnijas naktssikspārnis. Lithuanian: Finikinis pelėausis. Luxembourgish: Maghreb-Mausouer. Macedonian: Магребски ноќник. Maltese: Farfett il-Lejl Widnet il-ġurdien ta' Maghreb, Farfett il-Lejl Widnet il-Gurdien. Montenegrin: Punski večernjak. Norwegian: Mahgrebmusøre. Polish: Nocek punicki. Portuguese: Morcego-rato do Magrebe. Rhaeto-Romance: Vespertil ureglia-mieur punic. Romanian: Liliacul din Maghreb. Russian: Ночница финикийская. Serbian: Магребски велики вечерњак [= Magrebski veliki večernjak]. Scottish Gaelic: Ialtag luch-chluasach Mhaigribeach. Slovak: Netopier magrebský. Slovenian: Punski netopir. Swedish: Medelhavsmusöra. Turkish: Mahrep Farekulaklı

Yarasası. Ukrainian: Нічниця магрибська. Welsh: Ystlum clustlydan Maghreb.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Ruedi (2020: 4) indicated that fossils from Morocco, attributed to *Myotis blythii* by Ouahbi *et al.* (2003: 281, 284) and Aouraghe *et al.* (2010: 322) should be assigned to *M. punicus*.

CONSERVATION STATUS:
Global Justification
Juste and Paunović (2016a) reports that insufficient information about population dimension and demographic trends to make an assessment. It is probably declining but needs further research.

Assessment History
Global
2016: DD ver 3.1 (2001) (Juste and Paunović, 2016a). 2008: NT ver 3.1 (2001) (Aulagnier *et al.*, 2008c; IUCN, 2009). 2004: DD ver 3.1 (2001) (Aulagnier and Juste, 2004; IUCN, 2004).

Regional
In the Maltese Island *Myotis punicus* is listed as Vulnerable (VU) (Baron and Vella, 2010).

Legal Status
Aulagnier *et al.* (2008c) [in IUCN (2009)] report that it is protected by national legislation in its European range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention, in parts of its range where these apply. It is included in Annex IV of the EU Habitats and Species Directive, and some habitat protection may be provided through Natura 2000.

MAJOR THREATS:
Human disturbance is a major threat, as colonies are located in tourist areas, in caves that are well known and popular. Changes in land management and agricultural pollution are also threats (Aulagnier *et al.*, 2008c; IUCN, 2009).

Juste and Paunović (2016a) report that in the African part of the range, the cave habitat where the species roosts is being destroyed by fires and vandalism. In North Africa the species is collected for traditional medicinal use (Aulagnier *et al.*, 2008c; IUCN, 2009; Juste and Paunović, 2016a).

The species is a cave or tree rooster, its water stress and long-distance dispersal were found to be the major risk factors related to climatic change (Sherwin *et al.*, 2012: 174).

CONSERVATION ACTIONS:
Juste and Paunović (2016a) reports that no conservation actions are in place and further research into population trends, establishment and management of protected areas, education, and implementation of national-scale legislation are needed.

While Aulagnier *et al.* (2008c) [in IUCN (2009)] report that there are ongoing project for the conservation of this species. Appropriate conservation measures include fencing cave entrances (but not gating) and obtaining legal protection for the species.

In North Africa further research into population trends, establishment and management of protected areas, education, and implementation of national-scale legislation are needed (Aulagnier *et al.* (2008c) [in IUCN (2009)).

Biollaz *et al.* (2010) suggest that special care is needed for the Sardinian population as an important source of genetic diversity.

GENERAL DISTRIBUTION:
Myotis punicus occurs in North-west Africa (Morocco, Algeria, Tunisia, and to extreme northwestern Libya) and on the Mediterranean islands of Corsica (France), Sardinia (Italy), and Malta (including Gozo [Baron and Borg, 2013: 407]; Ruedi, 2023: 399).

Native: Algeria; Libyan Arab Jamahiriya; Malta; Morocco (Benda *et al.*, 2004d; 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 361; Dbiba *et al.*, 2025: 8); Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867, 2019b: 26; Ruedi, 2023: 400).

BIOGEOGRAPHY:
Biollaz *et al.* (2010: 8)'s study suggests that the islands (Corsica and Sardinia) were colonized by *M. punicus* in a stepping-stone manner and predates human colonization. Mitochondrial analysis revealed that the insular populations were well differentiated from the mainland, with mean haplotypes and nucleotide diversities decreasing from Tunisia to Sardinia, and from Sardinia to Corsica. While a Baysian and ML trees showed that the Corsican haplotypes are nested within the Sardinian ones, suggesting that the Corsica might have been colonized from Sardinia (Biollaz *et al.*, 2010: 8). Compared with the North African populations, the two islands harbour significant lower allelic richness as well as observed and expected heterozygosities, which could reflect recent population crashes or a bottleneck during the colonization of the islands (Biollaz *et al.*, 2010). The Sardinian and Corsican populations were estimated to date back to the

early and mid-Pleistocene, respectively (Biollaz *et al.*, 2010). During the glacial episodes that punctuated this period, low sea levels exposed land that was previously underwater. Geographical distances between the islands and the mainland were thus reduced with the emergence of land bridges between some of the islands, favouring island colonization, with the first the colonization of Sardinia from North Africa and then the colonization of Corsica from Sardinia. As the Ice Age ended, sea levels rose and isolated the two islands, explaining the strong reduction of gene flow currently observed (Biollaz *et al.*, 2010).

The large divergence between the Moroccan and Tunisian populations suggest that both populations had been isolated since the Pleistocene (Biollaz *et al.*, 2010), despite current nuclear gene flow, no female exchange seems to have occurred since then. The confinement of Moroccan populations in the High Atlas Range and the philopatric behaviour of females could have enhanced the isolation of these populations, explaining the low haplotype diversity (Biollaz *et al.*, 2010). In North Africa, poor nuclear differentiation between colonies associated with a strong mitochondrial differentiation suggested current male-biased dispersal on the continental area.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Dietz and von Helversen (2004) and Baron (2012: 1) mention the following external characters: large size (comparable to *M. myotis*), the wing membrane starting at the base of the toes, a lancet shaped tragus and distinct dorsal (light brown) and ventral (white) fur coloration.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^3/_3$, $C^3/_3$ = 38 teeth and all the lower molars are myotodont (Ruedi, 2020: 7).

ECHOLOCATION:
For this species, Disca *et al.* (2014: 226) report two call types: A - FM APMF, with the following parameters: F_{start}: 79.2 ± 16.4 kHz, F_{end}: 25.0 ± 2.1 kHz, F_{peak}: 37 ± 7.9 kHz, bandwidth: 54.2 ± 15.5 kHz, duration: 5.5 ± 0.6 ms; B - FM APBF, with the following parameters: F_{start}: 77.3 ± 6.6 kHz, F_{end}: 20.2 ± 1.2 kHz, F_{peak}: 32.0 ± 5.2 kHz, bandwidth: 57.1 ± 7.1 kHz, duration: 8.6 ± 0.6 ms.

Ruedi (2023: 410) mention a F_{start}: 60.42 ± 15.65 (60 - 75) kHz, F_{end}: 27.07 ± 2.26 (20 - 30) kHz, F_{max}: 35.82 ± 4.21 (30 - 40) kHz, duration: 3.62 ± 0.96 (5 - 10) ms.

Ait-Abdesselam *et al.* (2025: 40) reported an F_{end} value of 25.3 kHz for Algerian bats.

MOLECULAR BIOLOGY:
Karyotype
Baker *et al.* (1974: 706) mentioned 2N = 44 and FN = 50 with a medium-sized submetacentric X and an acrocentric Y for "*Myotis blythii*" from Tunisia, whereas Ruedi (2023: 405), referring to the same publication, mentioned a FN value of 54. The latter divided the autosomes into three pairs of large and one pair of small metacentrics, and 17 pairs of submetacentric or acrocentric chromosomes.

Genetics
See Castella *et al.* (2000) and Biollaz *et al.* (2010).

Ruedi (2020: 10) refers to Biollaz *et al.* (2010), who found clear differences in the mitochondrial control region (HVII) of bats from the Mediterranean islands and those from northern Africa, where the latter differed by nine to ten mutations from the insular haplotypes.

ROOST:
Benda *et al.* (2014c: 38-39) reported that, in Libya, these bats are only found in ruins, which might serve as temporary roosts or perhaps as maternity roost.
Kowalski *et al.* (1986) [in Ruedi (2023: 407)] reported this species to occupy the same cave in northern Algeria throughout the year, although with in much smaller numbers during winter. In September-October the bats leave their summer roosts and move to alternative, colder roosts.

DIET:
Ahmim and Moali (2011: 45, 48) found that the diet of *M. punicus* in Algeria consisted of 96.06 % of insects, 2.82 % of chilopods, and 1.12 % of spiders. Among the insects, Diptera (46.32 %), Lepidoptera (20.33 %), and Hemiptera (10.16 %) were found most frequently in the bat's guano.

On Malta, Baron and Borg (2013: 415) report that the major food sources are Orthoptera (65 %), Lepidoptera (20 %), and Coleoptera (15 %), whereas on Corsica, the Orthoptera only account for 36 %.

In Libya, Benda *et al.* (2014c: 44) analyses two groups of pellets. One set (from one individual) contained only large spiders (Aranea), while the other consisted primarily of Coleoptera (Scarabaeidae: Melolonthinae), which were supplemented by solifuges (Solpugida), cockroaches (Blattodea) and small scorpions (Scorpionida).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 77 minutes, and the digestibility rate about 79.9 %.

PREDATORS:
Ruedi (2023: 408) mentioned that skulls of *M. punicus* were found in owl pellets of *Bubo ascalaphus* Savigny, 1809, *Strix aluco* Linnaeus, 1758, *Tyto alba* (Scopoli, 1769), and *Athene noctua* (Scopoli, 1769). Other predators include the horseshoe whip snake *Hemorrhois hippocrepis* (Linnaeus, 1758), and possibly martens (*Martes* spp.), genets (*Genetta genetta*) and cats (*Felis* spp.).

Rihane *et al.* (2024: 224) counted three *Myotis punicus* prey items in pellets of a Magreb Owl (*Strix mauritanica* (Witherby, 1905)).

POPULATION:
Structure and Density
Over 10,000 individuals, found in large colonies (300 - 500 individuals) (Juste and Paunović, 2016a). On Corsica, there are around 4,000 individuals in four colonies. The total population size on Corsica, Sardinia and Malta is estimated at between 7,000 and 9,000 individuals. This is a cave dwelling species, therefore there are few colonies. On Malta, over 50 % of the population was lost between the latter half of the 1980s and the early 1990s. Numbers appear to have stabilised at 400 - 450 individuals (Borg, 2002, J.J. Borg *unpubl. data* [in Aulagnier *et al.* (2008c) in IUCN (2009)]).

Trend
2016: Unknown (Juste and Paunović, 2016a).
2008: Decreasing (Aulagnier *et al.*, 2008c; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
At Sabratha (Libya), Benda *et al.* (2014c: 40) collected a pregnant female on 2 April and a juvenile female on 14 April. Dalhoumi *et al.* (2019a: 158) reported about 50 neonates in a cave in Tunisia on 19 May. Ruedi (2023: 407) mentioned births between April and early June.

In the Maghreb, *M. punicus* can form maternity colonies of a few thousands' specimens (Ruedi, 2020: 14).

MATING:
Ruedi (2020: 11) mentioned that adult males hold small territories near nurseries and start to attrack females starting in August.

PARASITES:
Aellen (1955b) mentioned the following nycteribid and streblid flies occurring on "*Myotis oxygnathus*" from Morocco and Algeria: *Nycteribia (Nycteribia) latreillei* (Leach, 1817), *Nycteribia (Nycteribia) schmidli* Schiner, 1853, *Nycteribia (Acrocholidia) vexata* Westwood, 1835, *Penicillidia dufouri* (Westwood, 1835), *Penicillidia conspicua* Speiser, 1901, and *Nycteribosca kollari* (Frauenfeld, 1855).

Bruyndonckx *et al.* (2010) collected *Spinturnix myoti* (Kolenati, 1856) in 11 colonies in North Africa, Corsica and Sardinia. These mites were also collected by Thiévent *et al.* (2020: 2) from bats from Morocco and Tunisia. Three of the seven Moroccan and two of the three Tunisian mites they examined were infected by Chlamydiae bacteria.

From Libya, Benda *et al.* (2014c: 44) reported the following ectoparasites: Nycteribiidae: *Nycteribia vexata* Westwood, 1835, *Nycteribia latreillii* (Leach, 1817); Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856); Macronyssidae: *Steatonyssus occidentalis* (Ewing, 1933); Ischnopsyllidae: *Rhinolophopsylla unipectinata* (Taschenberg, 1880).

From Algeria, Bendjeddou *et al.* (2013: 325) reported the following ectoparasites:
Nycteribiidae: *Penicillidia dufouri* (Westwood, 1825), *Phthiridium biarticulatum* Hermann, 1804; Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856); Ixodidae: *Rhipicephalus sanguineus* (Latreille, 1806).

Bendjeddou *et al.* (2016a: 109) added *Ixodes vespertilionis* Koch, 1844.

Bendjeddou *et al.* (2017: 15) mentioned the following species from Algeria: Nycteribiidae: *Nycteribia (Nycteribia) latreillii* (Leach, 1817) and *Phthiridium biarticulatum* Hermann, 1804; Streblidae: *Brachytarsina (Brachytarsina) flavipennis* Macquart, 1851 and Arachnida: *Spinturnix myoti* (Kolenati, 1856) and *Ixodes vespertilionis* Koch, 1844.

Bendjoudi *et al.* (2019: 71) furthermore reported the nycteriibid *Nycteribia pedicularia* Latreille, 1805.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Ixodidae: *Ixodes vespertilionis* Koch, 1844; Macronyssidae: *Rhipicephalus sanguineus* s.l., *Steatonyssus occidentalis*

(Ewing, 1933); Nycteribiidae: *Nycteribia latreillii* (Leach, 1817), *Nycteribia pedicularia* Latreille, 1805, *Nycteribia schmidlii schmidlii* Schiner, 1853, *Nycteribia vexata* Westwood, 1835, *Penicillidia conspicua* Speiser, 1901, *Penicillidia dufourii* (Westwood, 1834), *Phthiridium biarticulatum* (Hermann, 1804); Spinturnicidae: *Spinturnix myoti* (Kolenati, 1856); and Streblidae: *Brachytarsina flavipennis* Masquart, 1851;

Blackwell (1980: 145) and Haelewaters *et al.* (2017: Suppl.) mention the presence of the Nycteribiid bat-fly *Nycteribia vexata* Westwood, 1835 on "*M. oxygnathus*" in Tunisia, which in turn was infected by the fungus *Arthrorhynchus nycteribiae* (Peyritsch) Thaxter (see also de Groot *et al.*, 2020: Suppl.)..

VIRUSES:
Coronaviridae - Coronaviruses
Alphacoronavirus
Ar Gouilh *et al.* (2018: 92) reported the EPI 9 virus from Tunisia (3 infected out of 8 bats).

Rhabdoviridae
Lyssavirus
Serra-Cobo *et al.* (2018: 2) tested 63 Algerian bats for European bat lyssavirus type 1 and found one being seropositive. This was also the case for 15 out of 262 Moroccan bats.

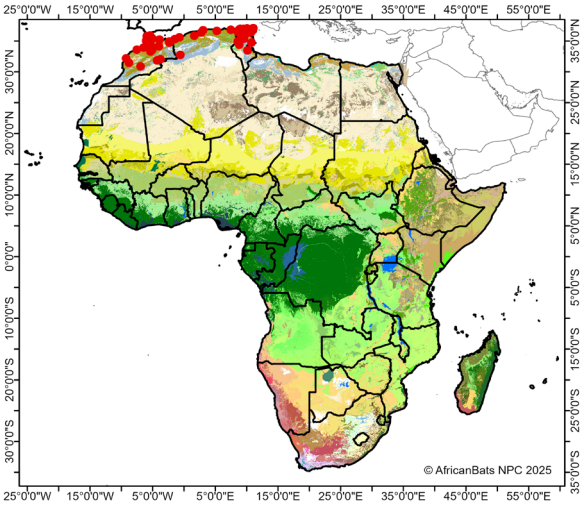

Figure 276. Distribution of *Myotis (Myotis) punicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Libya, Morocco, Tunisia.

Myotis (Myotis) zenatius Ibáñez, Juste, Salicini, Puechmaille and Ruedi, 2019

2019. *Myotis escalerai cabrerae* Çoraman, Mayer and Dietz, in: Çoraman et al., J. Biogeogr., 46 (2): 350. Publication date: 28 January 2019. Type locality: Morocco: Sous_Massa region: Wim Timdouine cave: near Agadir [30 40 49 N 09 20 42 W, 1340 M]. Holotype: ZMB 107229: ♀, tissue. - Etymology: In honour of Angel Cabrera, who described *M. escalerai* from Spain.

*2019. *Myotis zenatius* Ibáñez, Juste, Salicini, Puechmaille and Ruedi, in: Juste et al., Acta Chiropt., 20 (2): 293, 295, figs 3C, 5D (for 2018). Publication date: 30 January 2019. Type locality: Morocco: Tanger-Tétouan-Al Hoceima region: Mizou Cave [c. 35 30 42 N 05 19 53 W, 330 m]. Holotype: EBD 29831M: ad ♂, skull and alcoholic. Collected by: Irene Salicini, Carlos J. Ibáñez Uargui and Javier Juste; collection date: 18 July 2011; original number: 110718MspB12. Paratype: EBD 26020M: ♀, skull and alcoholic. Collection date: 10 June 2002; original number: MNA-56. Paratype: EBD 26023M: ♂, skull and alcoholic. Collection date: 11 July 2002; original number: MNA-15. Paratype: EBD 29826M: ad ♀, skin and skull. Collected by: Irene Salicini, Carlos J. Ibáñez Uargui and Javier Juste; collection date: 18 July 2011; original number: MspB6. Paratype: EBD 29829M: ad ♂, skull and alcoholic. Collected by: Irene Salicini, Carlos J. Ibáñez Uargui and Javier Juste; collection date: 18 July 2011; original number: Msp7. Paratype: EBD 29830M: ad ♀, skull and alcoholic. Collected by: Irene Salicini, Carlos J. Ibáñez Uargui and Javier Juste; collection date: 18 July 2011; original number: Msp11. - Etymology: "*zenatius*" refers to "Zanatah", a little known Berber tribe that lived in the Maghreb region in the Middle Ages (see Juste *et al.*, 2019: 297).

? *Myotis (Myotis) zenatius:* (Current Combination).

TAXONOMY:
Simmons and Cirranello (2023b: 79) did not assign this species to a subgenus ("unassigned").

The specimens forming this taxon were formerly included in *Myotis nattereri* (e.g., Brosset, 1963: 440; Gaisler, 1983: 362; Gaisler, 1984: 89; Kowalski *et al.*, 1986: 185; Aulagnier and Thevenot, 1986: 44; Benda *et al.*, 2004d: 19; Dieuleveut, 2010: 37). Various authors (e.g., García-Mudarra *et al.*, 2009: 442; Puechmaille *et al.*, 2011a: 225; Salicini *et al.*, 2011: 890; 2012: 1185), however, found differences between the European representatives of *M. nattereri* and the animals from northern Africa and assigned the latter tentatively to "*Myotis* sp. B".

Based on DNA, Çoraman *et al.* (2019: 350) indicated that "*Myotis* sp. B" is clearly distinct, both in mitochondrial and nuclear markers from *M. nattereri*, and suggests that this taxon should be considered as a subspecies of *Myotis escalerai*, for which they propose the name *Myotis escalerai cabrerae* Çoraman, Mayer and Dietz 2018. The paper only contains a short paragraph on the proposed name, where as the

"description" itself is in the online supplement and is also restricted to a single sentence. The description is not supported by the designation of a physical museum specimen, but rather a DNA (tissue) sample, which according to the ICZN (http://iczn.org/content/can-dna-be-type-specimen) should nevertheless be acceptable.

Juste *et al.* (2019) compared physical specimens of "*Myotis* sp. B" with *M. escalerai* from the Iberian Peninsula and found a number of differences (including a much darker dorsal fur), which led them to describe a new species: *Myotis zenatius*.

As these two publications suggest a name for the populations previously assigned to "*Myotis* sp. B" (see Salicini *et al.*, 2011; 2012) the priority principle comes into play. Both papers were published in early 2019:

1) "*Myotis zenatius* Ibáñez, Juste, Salicini, Puechmaille and Ruedi, 2019" was published in "Acta Chiropterologica, 20 (2): 225 - 300, 2018", the front page of which indicates "December 2018", but the BioOne website (https://bioone.org/journals/Acta-Chiropterologica/volume-20/issue-2/15081109ACC2018.20.2.001/Two-New-Cryptic-Bat-Species-within-the-Myotis-nattereri-Species/10.3161/15081109ACC2018.20.2.001.full) mentions 14 February 2019 as date. Furthermore, the paper header mentions: "Version of Record, published online January 30, 2019 with fixed content and layout in compliance with Art.8.1.3.2.ICZN and registered in Zoobank with LSID urn:lsid:zoobank.org:pub:2348ACBD-2ECC-4A80-8EA4-E3DF05C878E3". This suggest that 30 January is to be considered as date of publication.

2) "*Myotis escalerai cabrerae* Çoraman, Mayer and Dietz, 2018" was published in "Journal of Biogeography, 46 (2): 343 - 354, 2019". Here the Wiley Online Library website (https://onlinelibrary.wiley.com/loi/13652699) mentions "February 2019" as publication date for the issue and for the paper itself (https://onlinelibrary.wiley.com/doi/10.1111/jbi.13509), it mentions "First published: 28 January 2019". The fact that the authors mention "2018" in the header of their description should be ignored.

ICZN article 21.9. mentions "Works issued on paper and electronically. A name or nomenclatural act published in a work issued in both print and electronic editions takes its date of publication from the edition that first fulfilled the criteria of publication of Article 8 and is not excluded by Article 9."

The members of our "Taxonomic Advisory Committee" [Petr Benda, Gábor Csorba, Peter Taylor, Stéphane Aulagnier] indicated that a description published in an online (part of the) paper without a ZooBank number (a requirement since 2012; IUCN, 2012: 1) is invalid for taxonomic purposes [="*nomen nudum*"]. ZooBank currently contains urn:lsid:zoobank.org:pub:A4A8BF4B-D592-485C-9E02-DC2A0B7C94F8 for the paper by Çoraman et al. and mentions publication date "February 2019". This agrees with the remark made in IUCN (2012: 3): "The following are examples of inadmissible errors: An author, in preparing a manuscript for publication, states that day's date for the registration date, intending to register it later that day but forgetting to do so. The author discovers the omission after the work is published and immediately registers it; because registration occurred after publication, the work is not available."

The problem was also signalled by Ruedi *et al.* (2019), who indicated that the new names proposed by Çoraman *et al.* (2019) (besides *M. escalerai cabrerae*, they also introduced *M. nattereri helverseni*) do not follow several mandatory rules imposed by the Code, they are declared unavailable and are not to be used for further taxonomy studies.

As such, we accept the name *Myotis zenatius* proposed in Juste *et al.* (2019) for this taxon.

COMMON NAMES:
Castilian (Spain): Murcielago ratonero Zenate. English: Zenati myotis. French: Murin Zenati. German: Zenati Mausohr.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Probably endemic to the Mediterranean region of Morocco and Algeria, and possibly Tunisia (Juste *et al.*, 2019: 296; Dbiba *et al.*, 2025: 8).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Ischnopsyllidae: *Ischnopsyllus hispanicus* Jordan, 1942; and Spinturnicidae: *Spinturnix mystacina* (Kolenati, 1857).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Morocco.

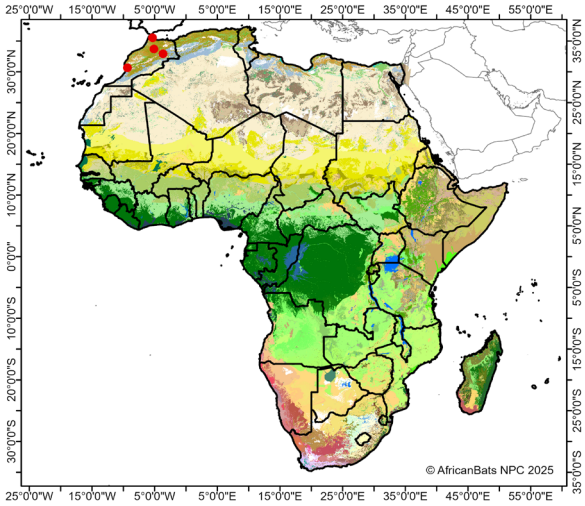

Figure 277. Distribution of *Myotis (Myotis) zenatius*.

Subfamily Scotophilinae Van Cakenberghe and Seamark, 2008

1866. *Scotophili* A. Murray, The geographical distribution of mammals, 238. - Comments: Type genus: *Scotophilus* Leach, 1821. Introduced as "section". Synonymized with the Nycticeiini tribe by McKenna and Bell (1997: 320) (see Jackson and Groves, 2015: 276).
1866. *Scotophilina* J. E. Gray, Ann. Mag. nat. Hist., er 3, 17 (98): 90.
1987. *Scotophilini* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 278. Publication date: 30 July 1987. - Comments: Type genus: *Scotophilus* Leach, 1821. Introduced as tribe, and originally included the genera *Scotomanes* Dobson, 1875 [including *Scoteinus* Dobson, 1875] and *Scotophilus* Leach, 1821. The rank was recognized by Hoofer and Van Den Bussche (2003: 38), but synonimized with the Nycticeiini tribe by McKenna and Bell (1997: 320) (see Jackson and Groves, 2015: 276).
2006. *Philisinae* Horáček, Fejfar and Hulva, Lynx, 37: 145. - Comments: Type genus: *Philisis* Sigé, 1985.
*2008. *Scotophilinae* Van Cakenberghe and Seamark, African Chiroptera Report, 238. Publication date: 1 July 2008. - Comments: Type genus: *Scotophilus* Leach, 1821. Following the principle of typification. (Current Combination).

TAXONOMY:
Known genera of the subfamily Scotophilinae: †***Scotophilisis*** Horácek, Fejfar and Hulva 2006; †***Vampyravus*** Schlosser, 1910; ***Scotophilus*** Leach 1821.

COMMON NAMES:
Czech: mračníkové.

†Genus ***Scotophilisis*** Horácek, Fejfar and Hulva, 2006

*2006. *Scotophilisis* Horáček, Fejfar and Hulva, Lynx, ns37: 131, 140. - Comments: Type species - *Scotophilisis libycus* Horácek, Fejfar and Hulva, 2006. The publication might date from 2007, since the paper was only received on 8 December 2006. - Etymology: Combination of the extant genus *Scotophilus* Leach, 1821 and a Palaeogene genus *Phylisis* Sigé, 1985, as this new genus is supposedly related to the stem line (Horáček *et al.*, 2006). (Current Combination).
2014. *Scotiphilisis:* Ravel, Adaci, Bensalah, Mahboubi, Mebrouk, Essid, Marzougui, Ammar, Charruault, Lebrun, Tabuce, Vianey-Liaud and Marivaux, J. Syst. Palaeontol., 13 (8): 694. Publication date: 21 August 2014. (Lapsus).

TAXONOMY:
Currently recognized species of the genus *Scotophilisis*: †***libycus*** Horácek, Fejfar and Hulva, 2006.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Time frame - Early Miocene (Burdigalian).

†***Scotophilisis libycus*** Horácek, Fejfar and Hulva, 2006

*2006. *Scotophilisis libycus* Horáček, Fejfar and Hulva, Lynx, ns 37: 131, 140, figs 1 - 3. Type locality: Libya: MS2: Jebel Zelten [28 28 N 20 00 E]. Holotype: NMP NMPC/OF.J.Zel./Chil.. Right mandible with M_1 and M_2 and alveoli of I_1 to P_4 and M_3. - Comments: Early Miocene, MN4-5. (Current Combination).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS: Timeframe: Middle Miocene (Langhian - Brown *et al.*, 2019: Suppl.).

Genus ***Scotophilus*** Leach, 1821

*1821. *Scotophilus* Leach, Trans. Linn. Soc. Lond., 13 (1): 69, 71. Publication date: 23 May - 21 June 1821 [Goto Description]. - Comments: Type species: *Scotophilus kuhlii* Leach, 1821 (According to Meester *et al.*, 1986: 59 "=juvenile *Vespertilio temmincki* Horsfield"). Not *Scotophilus* Swainson, 1836 (Aves, Strigiformes, Strigidae). Not *Scotophilus* Meinert, 1870 (Arthropoda, Chilopoda, Geophilomorpha, Dignathodontidae). Not *Scotophilus* Hesse, 1881 (Crustacea, Maxillopoda, Cyclopodea, Family incertae sedis) (see Jackson and Groves, 2015: 272). - Etymology: From the Greek "*σκόοτος*", meaning "darkness" and "*φίλος*", meaning "loving" (see Palmer, 1904: 627). - ZooBank: EE74E9E4-260A-48A5-9CD7-C690F661AF90. (Current Combination).
1831. *Pachyotus* J. E. Gray, Zool. Misc., 1: 38. Publication date: 1831 [Goto Description]. - Comments: Type species: *Scotophilus kuhlii* Leach, 1821. - Etymology: From the Greek "*παχύς*" meaning thick and "*ούς*" or "*ώτός*", meaning ear (see Palmer, 1904: 495).
1842. *Nicticejus* Rüppell, Mus. Senckenberg., 3 (2): 157, 188. - Comments: Type species: *Nycticejus leucogaster* Cretzschmar, 1826.
1981. *Scotophilous:* Demeter, Vertebr. Hung., 20: 135. (Lapsus).
2013. *Scatphalous:* McCulloch, Barcoding of South African bat species and evaluation of their natural exposure to lyssaviruses, 159. Publication date: July 2013. (Lapsus).
2018. *Schotophilus:* Leopardi, Holmes, Gastaldelli, Tassoni, Priori, Scaravelli, Zamperin and De Benedictis, Infec. Gen. Evol., 58: 284. Publication date: 30 January 2018. (Lapsus).
2018. *Scotophilis:* Adams and Kwiecinski, Diversity, 10 (3) 103: 4. Publication date: 18 September 2018. (Lapsus).
2019. *Scroptophilus:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).
? *Scotophilus sp. B156*
? *Scotophilus sp. clade 3 TD-2019*
? *Scotophilus sp. clade 4 TD-2019*
? *Scotophilus sp. clade 7 TD-2019*
? *Scotophilus sp. DMR-2017*
? *Scotophilus sp. IVK-2011*

TAXONOMY:

Bronner *et al.* (2003) states that the taxonomy of African *Scotophilus* remains problematic. Three species, differing mainly in body size, probably occur in the [southern African] subregion, but species limits and phylogenetic inter-relationships are unclear (Meester *et al.*, 1986). Ellerman *et al.* (1953) referred to the largest species as *gigas*, but Robbins (1978a) showed that in describing *gigas*, Dobson (1875a) had in fact re-described *nigrita*, the name used by Ellerman *et al.* (1953) for the medium-sized species. Koopman (1982) accepted *nigrita* as a senior synonym of *gigas*, but argued that *nigrita* is a *nomen dubium* and should therefore not be used; a position later recanted (Koopman, 1993a, 1994). Since *nigrita* was no longer available for the medium-sized species, Robbins (1978a) used *dinganii* as the next valid name. Koopman (1975, 1978), however, regarded *leucogaster* as a senior synonym of *dinganii*, but later revised this opinion and recognised these as discrete species (Koopman, 1993a). Shortly thereafter he reverted to his earlier treatment and again listed *dinganii* under *leucogaster* (Koopman, 1994).

Ellerman *et al.* (1953) referred to the smallest of the three species in the [southern African] subregion as *viridis*, containing two subspecies (*S. v. viridis* and *S. v. damarensis*), which they recognised as distinct from *borbonicus* on Reunion Island. Hill (1980) regarded these taxa as conspecific and, therefore, used *borbonicus* as the prior name for this taxon. Corbet and Hill (1980) followed Koopman (1975) in confining *borbonicus* to Madagascar and Reunion, and thus once again recognised *viridis* as a mainland species, a treatment followed by Swanepoel *et al.* (1980) and Koopman (1982). Robbins *et al.* (1985) followed suit, but also listed *leucogaster* to accommodate *damarensis*, which they considered distinct from *viridis*, a treatment endorsed by Corbet and Hill (1992). Koopman (1993a) considered *damarensis* synonymous with *viridis*, but subsequently recognised both of these as only subspecies of *borbonicus* (Koopman, 1994).

Vallo *et al.* (2010: 303) indicate that several unrelated mitochondrial lineages occur within *S. dinganii*, but also that the African *Scotophilus* as a whole is in need of more detailed investigation and formal revision of systematics.

For a discussion on the names introduced by Brooks and Bickham, see Vallo and Van Cakenberghe (2017: 6).

Demos *et al.* (2018: 10) used multi-locus coalescent delimitation methods and concluded that 15 different species may occur in continental Africa, keeping in mind that large parts of the continent are seriously undersampled.

Prié *et al.* (2016) report on the echolocation characteristics of a "Chiroptera sp. 1" from Réunion, which they believe to be a *Scotophilus*. However, due to the terrible physical status and the taxonomic uncertainty of the *S. borbonicus* specimen(s) collected on the island, they feel it impossible to use the name *borbonicus* for these "Chiroptera sp. 1" specimens. Additional acoustic and distributional information on this species is provided by Augros (2017).

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Scotophilus*: ***altilis*** G.M. Allen, 1914; ***andrewreborii*** Brooks and Bickham, 2014; ***borbonicus*** (E. Geoffroy Saint-Hilaire, 1803); ***colias*** Thomas, 1904; *collinus* Sody, 1936 – Sabah, western Java, Bali, Lombok, Flores, Lembata, Timor, Semanu and Roti Isls (Indonesia) (Simmons, 2005: 466); ***dinganii*** (A. Smith, 1833); ***ejetai*** Brooks and Bickham, 2014; *heathii* (Horsfield, 1831) – Afghanistan to southern China, including Hainan Isl, south to Sri Lanka, Vietnam, Cambodia, Thailand and Burma (Simmons, 2005: 466); *kuhlii* Leach, 1821 – Bangladesh, Pakistan to Taiwan, south to Sri Lanka, Burma, Cambodia, western Malaysia, Java, Bali, Nusa Tenggara (Indonesia), southeast to Philippines and Aru Isls (Indonesia) (Simmons, 2005: 466); ***leucogaster*** (Cretzschmar, 1830); ***livingstonii*** Brooks and Bickham, 2014; ***marovaza*** Goodman, Ratrimomanarivo and Randrianandrianina, 2006; ***nigrita*** (Schreber, 1774); ***nigritellus*** de Winton, 1899; ***nucella*** Robbins, 1983; ***nux*** Thomas, 1904; ***robustus*** A. Milne-Edwards, 1881; ***tandrefana*** Goodman, Jenkins and Ratrimomanarivo, 2005; ***trujilloi*** Brooks and Bickham, 2014; ***viridis*** (Peters, 1852).

Common Names:

Czech: mračníkové, mrakolibové. English: Yellow bats, House bats, Brown bats. French: Scotophiles. German: Hausfledermäuse. Italian: Scotòfili.

Detailed morphology:

Baculum

Hill and Harrison (1987).

Molecular Biology:

Karyotype

Volleth *et al.* (2006) reported 2*n* = 36, FN = 50, BA = 18, a submetacentric X and a submetacentric Y chromosome for a male *S. leucogaster* from Burkina Faso. Recently, Eick *et al.* (2007) reported 2*n* = 36, FN = 50, BA = 16, a metacentric X chromosome and an acrocentric Y chromosome for South African specimens of *S. dinganii*.

For an Ethiopian bat (either *S. dinganii* or *S. viridis*); Tolera *et al.* (2021: 127) reported 2n = 36 and FN = 56. The autosomal chromosomes included three pairs of large metacentrics, two pairs of medium metacentrics and 11 (5 + 6?) pairs of acrocentrics. The X and Y chromosomes consist of a medium sized metacentric and a small sized acrocentric, but it was not possible to determine which was the X and the Y.

Genetics

See Hoofer and Van Den Bussche (2003) for a *S. borbonicus* from Kenya.

Habits:

Foord *et al.* (2018: 5) indicate that clutter-edge bats such as *Scotophilus* spp. may commute up to 3 km between roosts and feeding areas, but generally use a smaller core area.

Rainho *et al.* (2023: 7) assigned the *Scotophilus* bats in Meru county (Kenya) to a medium-to-high flying bats guild occurring at altitudes between 3 and 15 m.

Diet:

Jacobs (2000: 201) reported the following proportions of prey categories for 32 "*Scotophilus borbonicus*" specimens: Lepidoptera (13.8 ± 23.0), Coleoptera (37.4 ± 38.1), Isoptera (15.8 ± 28.7), Hymenoptera (11.5 ± 26.0), Diptera (7.5 ± 23.1), Hemiptera (13.4 ± 29.8), and unknown (0.6 ± 2.0).

Reproduction and ontogeny:

van der Merwe and Rautenbach (1988: 321) described the placenta of the lesser yellow house bat ("*S. borbonicus*") as antimesometrial discoidal, deciduate and hemodichorial. van der Merwe and Rautenbach (1990: 540) reported that this bat commonly gives birth to twins and occasionally even triplets. van der Merwe *et al.* (1988: 551) found that insemination, ovulation and fertilization take place in autumn. The embryonic growth is soon retarded, but not arrested and the embryo remains in the morula stage for 6 to 8 weeks, followed by a blastocyst stage of about two months.

In the same species, van der Merwe and Rautenbach (1989: 83) found that spermatogenesis was prolonged and extended over 8 months, coinciding with spring, summer and autumn.

The above information might pertain to either *S. leucogaster* or *S. viridis*.

PARASITES:
PROTOZOA
Espinosa-Álvarez *et al.* (2018: 572, Suppl.) reported new trypanosomes (*Trypanosoma vespertilionis*-like G1 and *Trypanosoma* sp. HochG3) from *Scotophilus* bats collected in Guinea-Bissau.

DIPTERA
Nycteribiidae
Basilia ansifera Theodor, 1956 mainly a West African species, reaching Lake Victoria in the east and Lake Nyasa in the south, nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110).

Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on *Scotophilus* sp.: *Basilia (Basilia) ansifera* Theodor, 1956 and *Basilia (Paracyclopodia) bouvieri* (Falcoz, 1924), *Basilia (Basilia) robusta* Theodor, 1956 has been found on *Scotophilus* clade 4 (although this might have been erroneous). *Basilia (Paracyclopodia) bouvieri* (Falcoz, 1924) has been reported from a "*Scotophilus nigrita*", which might be either a true *nigrita* or a *S. dinganii*.

SIPHONAPTERA
Ischnopsyllidae
The genus *Scotophilus* was reported by Beaucournu and Kock (1996) as the first African host (in Eritrea) for *C. brockmani* Rothschild, 1915.

VIRUSES:
Togaviridae
Alphavirus
Chikungunya virus
Isolates from Senegal in 1962, from the salivary glands of *Scotophilus* sp. were reported by Bres and Chambon (1963).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Ghana, Guinea, Kenya, Madagascar, Malawi, Mali, Mozambique, Namibia, Nigeria, Rwanda, Senegal, South Africa, South Sudan, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Scotophilus 'incertae-sedis'

? *Scotophilus sp.:*

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

Scotophilus altilis G.M. Allen, 1914

*1914. *Scotophilus altilis* G.M. Allen, Bull. Mus. comp. Zool., 58 (7): 350. Publication date: July 1914. Type locality: Sudan: Blue Nile province: north of [Er] Roseires: Aradeiba [12 25 N 34 20 E]. Holotype: MCZ 14463: ad ♂, skin and skull. Collected by: Glover Morrill Allen and The Phillips Sudan Expedition; collection date: 22 January 1913; original number: 73. See Helgen and McFadden (2001: 147). Paratype: FMNH 34161: ad ♂, skin and skull. Collected by: Glover Morrill Allen; collection date: 6 January 1913; original number: 22. Formely MCZ 14462. Paratype: MCZ 14610: ad ♂, alcoholic (skull not removed). Paratype: MCZ 14611: ad ♂, alcoholic (skull not removed). See Helgen and McFadden (2001: 147).

TAXONOMY:
Traditionally considered a synonym of *Scotophilus leucogaster*, but see Vallo *et al.* (2019: 148) who found that there is a 10% genetic difference for *cytb* between *S. leucogaster* and specimens from southwestern Ethiopia and southern South Sudan. These latter specimens were also slightly smaller and had a slightly different ventral colour. Additionally, two nuclear markers (*zfy* and *fgb7* also showed similar differences.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Democratic Republic of the Congo, Ethiopia, Kenya, South Sudan, Sudan (Vallo *et al.*, 2019: 151).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

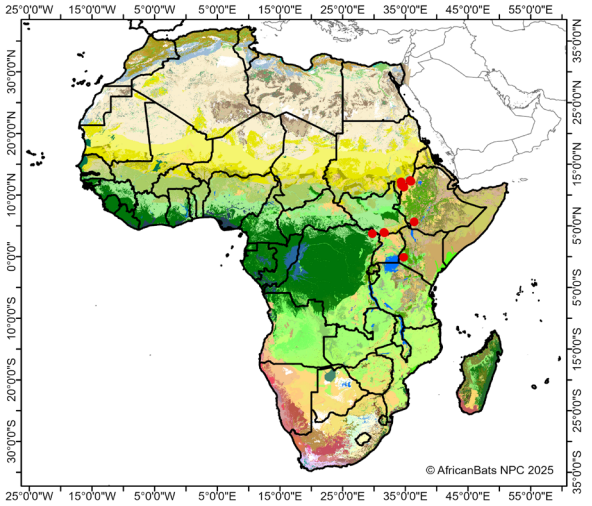

Figure 278. Distribution of *Scotophilus altilis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Ethiopia, Kenya, South Sudan, Sudan.

Scotophilus andrewreborii Brooks and Bickham, 2014

*2014. *Scotophilus andrewreborii* Brooks and Bickham, Occ. Pap. Mus. Texas Tech Univ., 326: 1, 8, fig 2. Publication date: 26 June 2014. Type locality: Kenya: Nakuru district, 12 km S, 4 km E Nakuru [00 24 S 36 07 E]. Holotype: CM 98049: ad ♂, skin and skull. Collected by: Dr. Kimberlyn ("Kim") Nelson; collection date: 7 October 1985; original number: 217. Muscle tissue sample TK 33143. Paratype: CM 98048: ad ♀, skin and skull. Collected by: Dr. Kimberlyn ("Kim") Nelson; collection date: 7 October 1985; original number: 214. Muscle tissue sample TK 33140. Demos *et al.* (2018) identified this specimen as *Scotophilus livingstonii* and Goodman *et al.* (2020: Suppl.) considered it a paratype of *S. livingstonii*. As it doesn't represent the first species and was not designated as a paratype of the second, its status as "paratype" should be ignored. Paratype: CM 98050: ad ♂, skin and skull. Collected by: Dr. Kimberlyn ("Kim") Nelson; collection date: 8 October 1985; original number: 219. Muscle tissue sample TK 33149. - Etymology: In honor of Andrew N. Rebori (1948 - 2011), who unknowingly touched the lives and inspired many individuals, including many museum professionals. He always maintained a keen interest in animals, especially bats, which exemplified his spirit and attitude toward life, 'Take flight every new day!' (see Brooks and Bickham, 2014: 8).

TAXONOMY:
Brooks and Bickham (2014) described four new species in the genus *Scotophilus*. However, they did not compare them with a number of already described taxa such as *colias* Thomas, 1904 or *flavigaster* Heuglin, 1861, which make the validity of (some of) these names doubtful.

The analyses performed by Demos *et al.* (2018: 2) confirmed the validity of the taxon, but these authors also indicate that they cannot vouch for the validity of the name with respect to older taxa that would have nomenclatural priority. Benda *et al.* (2025: 32) consider *andrewreborii* to be a synonym of *Scotophilus colias*.

COMMON NAMES:
Chinese: 安氏黄蝠. English: Andrew Rebori's House Bat. German: Andrews Hausfledermaus

CONSERVATION STATUS:
Global Justification
This species is known from at least six widely distributed localities in Kenya including several protected areas (Brooks and Bickham, 2014) and occurs in close association with human altered landscapes, roosting in buildings (Monadjem, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2017a).

Regional
None known.

MAJOR THREATS:
Brooks and Bickham (2014) report that the major threat is persecution of roosting sites.

CONSERVATION ACTIONS:
This species is known to occur in Tsavo National Park and may occur in other protected areas in Kenya (Monadjem, 2017a).

GENERAL DISTRIBUTION:
Brooks and Bickham (2014: 8) indicate that the type series was collected in two localities in Kenya, and that there are at least five other Kenyan localities where this species occurs.

ROOST:
Jackson *et al.* (2023: 5) reported three roosts in buildings in Kenya, of which two were shared with another bat species.

POPULATION:
Structure and Density
Population size is not known but is presumably large since it occurs in anthropomorphic environments (Monadjem, 2017a).

Trend
2016: Unknown (Monadjem, 2017a).

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023: 75) reported *Basilia (Paracyclopodia) bouvieri* (Falcoz, 1924) on bats from the Marsabit National Park (Kenya).

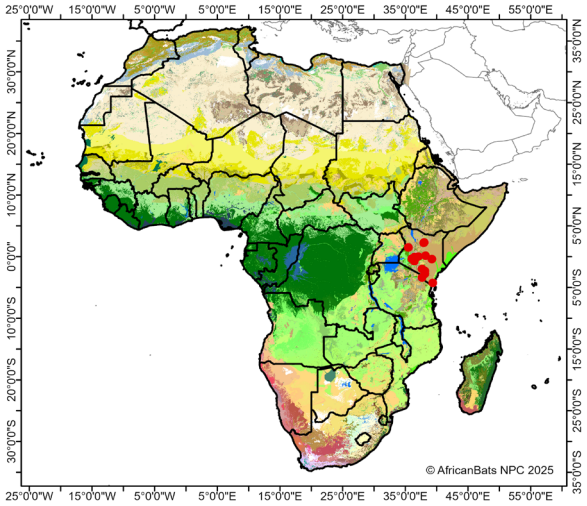

Figure 279. Distribution of *Scotophilus andrewreborii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Scotophilus borbonicus (E. Geoffroy St.-Hilaire, 1803)

*1803. *Vespertilio borbonicus* E. Geoffroy Saint-Hilaire, Catalogue des Mammifères du Muséum national d'Histoire naturelle, Paris, 55. Type locality: Réunion: Ile Bourbon [=Réunion Island]. [Goto Description]. Lectotype: RMNH MAM.28508: ad ♂, mounted skin (skull not removed). "Individu adulte monté, figuré dans la Mammalogie de Temminck, T.H. Pl. XLVII, fig. 6. Bourbon. Du voyage de M. Macé": see Goodman *et al.* (2005b: 871).
. - Etymology: Refering to "Ile Bourbon" where the type specimen was collected.
1855. *N[ycticejus] borbonicus:* Giebel, Die Säugethiere, 928. (Name Combination).
? *Scotophilus borbonicus:* (Name Combination, Current Combination).
? *Scotophilus cf. borbonicus:*

TAXONOMY:
The authorship and date of this name was fixed to E. Geoffroy St.-Hilaire (1803) by Opinion 2005 (Case 3022) (see Anonymus, 2002b: 154).

Included equivocally in *leucogaster* by Hayman and Hill (1971: 50 - 51), but see Koopman (1975: 414 - 416). Hill (1980) considered African *viridis* and *damarensis*, and possibly *leucogaster* to be conspecific with *borbonicus*; but Robbins *et al.* (1985) rejected any affinity with African mainland species. Also see comment under *leucogaster* and genus. Koopman (1986) included *viridis*, *damarensis*, and *nigritellus* (but not *leucogaster*) in this species.

As the lectotype (RMNH MAM.28508) is collected on the east coast of Africa, rather than on La Réunion and its mitochondrial sequence is similar to *S. trujilloi* captured in Kenya, this might lead to priority issues and taxonomic ambiguity. To resolve potential taxonomic problems, Goodman *et al.* (2020: 41) propose to consider the name *S. borbonicus* a nomen dubium. Recent inventories on La Réunion failed to find any *Scotophilus*, which led Goodman *et al.* (2020: 46) to conclude that if specimens are captured on the island, they might potentially represent a (new) separate species.

COMMON NAMES:
Czech: mračník réunionský, netopýr zelený. English: Lesser Yellow Bat, Lesser Yellow House Bat, Madagascar Yellow House Bat, Bourbon Bat. French: Scotophile de Bourbon, Scotophile de Madagascar, Petite Chauve-souris jaune des maisons, chauve-souris des Hauts, Scotophile de la Réunion. German: Réunion-Hausfledermaus, Bourbonische Schwirrfledermaus. Portuguese: Morcego amarelo pequeno.

CONSERVATION STATUS:
Global Justification
There have been exhaustive surveys of Réunion (e.g., Moutou, 1982) and this species has not been recorded for nearly 140 years. Abhaya and Probst (1999: 54) refer to Coquerel (1864) as one of the last to report on this species on Réunion ("Autrefois très commun sur l'île; très rare aujourd'hui.").

There is, however, not enough information to determine its taxonomic status, as the holotype is badly damaged and other possible specimens cannot be reliably assigned to this species. If the taxonomic status of this species is confirmed, then the species may qualify for a higher threat category and may well be extinct (Andriafidison *et al.*, 2008j; IUCN, 2009; Andriafidison *et al.*, 2019).

Assessment History
Global
2018: DD ver 3.1 (2001) (Andriafidison *et al.*, 2019). 2008: DD ver 3.1 (2001) (Andriafidison *et al.*, 2008j; IUCN, 2009). 2004: CR A1c ver 2.3 (1994) (IUCN, 2004). 2002: CR: A1c (Mickleburgh *et al.*, 2002a: 22).

Jones *et al.* (2009b: 507) assessed its status as Critically endangered - A1c. Conenna *et al.* (2017: Suppl.) assessed it as Data Deficient (DD).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Andriafidison *et al.*, 2008j; IUCN, 2009).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008j) [in IUCN (2009)] and Andriafidison *et al.* (2019) report that there are no conservation measures in place.

GENERAL DISTRIBUTION:
This holotype was described from two specimens from La Réunion and one of these was designated as the lectotype but is now in very poor condition (Goodman *et al.*, 2005a). In Madagascar, it is known only from a single specimen collected in 1868, at Sarodrano, near Toliara in the south (Goodman *et al.*, 2005a). The identity of the Madagascar specimen cannot be confirmed due to absence of reliable material from La Réunion. The area near Sarodrano has been relatively well surveyed recently, but no new specimens were obtained (Goodman *et al.*, 2005a).

Records from Mauritius (Mascarene Islands) are erroneous, see Cheke and Dahl, 1981: 217, Moutou, 1982: 44).

Native: Madagascar (?); Réunion.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 10.4 Pa, aspect ratio 7.5 for a wingspan of 34 cm and a wing area of 151 cm^2 and a body mass of 16 g, although this is probably not for "*borbonicus*" as recognized here.

ECHOLOCATION:
During their field work on Réunion, Barataud and Giosa (2013) captured some echolocation calls of two unidentified bats, which were neither *Mormopterus francoismoutoui* nor *Taphozous mauritianus*. The signals for one of these ("Chiroptera sp1" - QFC = 60 kHz, FM = 61 kHz) were very similar to those of Madagascan and African continental *Scotophilus*, which lead them to hypothesize that "Chiroptera sp1" might possibly be *S. borbonicus*.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003) for the results of a specimen from Kenya (which most probably represents a different species).

HABITAT:
Maillard (1862: 158) indicated that this species usually lived in forests and also near the coast of Réunion.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 120 minutes, and a digestibility rate of about 75.4 %.

POPULATION:
Structure and Density
This species was considered to be relatively common in the early 19th Century on La Réunion; however, it was not recorded in the 20th century or 21st century (Cheke and Dahl, 1981).

Trend
2018: Unknown (Andriafidison *et al.*, 2019). 2008: Unknown (Andriafidison *et al.*, 2008j; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

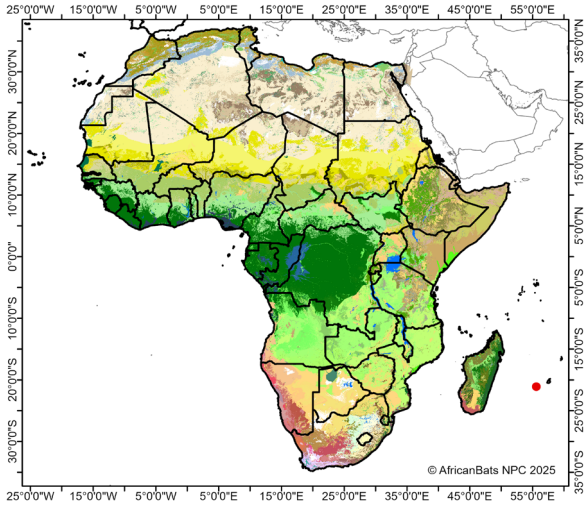

Figure 280. Distribution of *Scotophilus borbonicus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Réunion.

Scotophilus colias Thomas, 1904

*1904. *Scotophilus nigrita colias* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (75): 207. Publication date: 1 March 1904. Type locality: Kenya: Fort Hall [=Muranga] [00 43 S 37 09 E]. [Goto Description]. Holotype: NHMUK 1902.7.6.11: ad ♂. Collected by: Mrs. Hildegarde Beatrice Hinde; collection date: 25 January 1902; original number: 107. Presented/Donated by: Mrs. Hildegarde Beatrice Hinde.

1958. *Scotophilus nigrita coreas:* Eisentraut, Veröff. Überseemus. Bremen, (A) 3: 23. - Comments: Lapsus for *colias* (see Kock, 1969a: 193). (Lapsus).

2014. *S[cotophilus] colias:* Vallo, Benda, Červený and Koubek, Mammalia, 79 (2): 225. Publication date: 19 June 2014. (Name Combination).

2015. *Scotophilus colias:* Kassahun, Sadlova, Benda, Kostalova, Warburg, Hailu, Baneth, Volf, Votypka, Acta Trop., 150: 168. Publication date: 29 July 2015. (Current Combination).

TAXONOMY:
In their study on Arabian *Scotophilus*, Vallo *et al.* (2011c: 359) tentatively suggested to use the name *S. colias* for the East African yellow-bellied house bat as these bats clearly differ from the typical *S.dinganii* from southern Africa. This view was confirmed by Vallo and Van Cakenberghe (2017: 7) and Cosentino *et al.* (2023b: Suppl.), and followed by Wilson and Mittermeier (2019), Azami-Conesa *et al.* (2021) and Marsh *et al.* (2022).

Two other names were recently introduced by Brooks and Bickham (2014) for eastern African forms: *andrewreborii* and *ejetai*. However, they omitted any of the other *Scotophilus* names previously proposed from that area. Benda *et al.* (2025: 103) tentatively reject these names until further data confirm they represent different taxa.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Eritrea, Ethiopia, Kenya, Somalia (?), South Sudan (?), Northern Tanzania (?), Uganda (?), Yemen. (see Benda *et al.*, 2025: 102).

PARASITES:
PROTOZOA
Kassahun *et al.* (2015: 168) examined 12 Ethiopian *S. colias* specimens and found one (out of 11 from Metu) infected with *Leishmania* parasites (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 5).

ARACHNIDA
Spinturnicidae
Orlova *et al.* (2024: 151) referred to Zumpt and Till (1954), who described *Spinturnix scotophili* from a "*Scotophilus murinoflavus*".

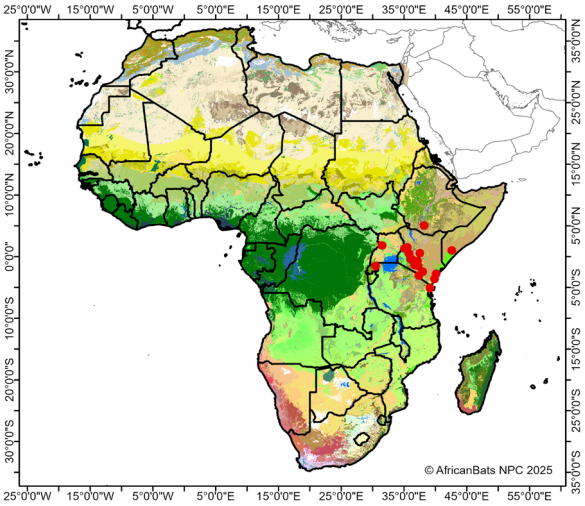

Figure 281. Distribution of *Scotophilus colias*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Ethiopia, Kenya, Rwanda, Somalia, Tanzania, Uganda.

Scotophilus dinganii (A. Smith, 1833)

1832. *Vespertilio epichrysus* Temminck, in: Smuts, Enumer. Mamm. Capensium, 106. Type locality: South Africa: Cape Town [33 56 S 18 28 E]. - Comments: Allen (1939a) and Ellerman *et al.* (1953) regard this taxon as unidentifiable, besides which it appears to fall outside the known range of the species as a whole (see Roberts, 1951: 90); Meester *et al.*, 1986: 60), who include it with a question mark). However, if valid, this is the senior name for the species. Dobson (1878: 303) mentions *Vespertilio epichrysus* (Temminck, Monogr. Mamm., 2: 208) with a question mark in the synonymy of *Vespertilio* [=*Myotis*] *emarginatus*.

*1833. *Vespertilio Dinganii* A. Smith, S. Afr. Quart. J., ser 2, 1 (2): 59. Publication date: November 1833. Type locality: South Africa: Port Natal [=Durban] & Delagoa Bay [=Maputo], btwn. [Goto Description]. - Etymology: In honour of Dingane (or Dingan / Dingaan), king of the Zulus (1795 - 1840) (see Lanza *et al.*, 2015: 487).

*1846. *Vesperugo Dinganii* Sundevall, Öfvers. kongl. Sv. Vet.-Akad. Förhandl., 3 (4): 119. Type locality: South Africa: Gauteng: Magaliesberg [25 46 00 S 27 40 00 E, 1350 m]. [Goto Description]. Neotype: NRM 651065: ad, skin only. Collected by: Johan August Wahlberg; collection date: 18 April 1841. Robbins *et al.* (1985: 65) mention that "The second specimen, NHRM 1065, is a mounted skin only. Based on the locality given by Sundevall (1846), the specimen from Caffer could be considered as the holotype of *Scotophilus dinganii* (Sundevall). To clarify the problem, we designate the Caffer specimen as the lectotype of *Scotophilus dinganii* (Sundevall)." However, as the name *Scotophilus dinganii* is based on *Vespertilio dinganii* A. Smith, 1833, this specimen can not be a lectotype as it wasn't part of the original material. It therefore should be considered a neotype as suggested by Kearney *et al.* (2010: 22). The latter authors, however, selected the wrong specimen [NRM 1064]. - Comments: Sundevall (1846: 119) mentioned the locality as "interior of Caffraria", but the type specimen in the NRM .

1852. *Nycticejus planirostris* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 65, pl; 17, fig 1, a-e. Publication date: 1852. Type locality: Mozambique: Lower Zambesi River: Tete [16 10 S 33 35 E, 230 m]. [Goto Description]. Holotype: ZMB 527: ad ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1845. See Turni and Kock (2008) [=An 16363].

1855. *N[ycticejus] Dingani:* Giebel, Die Säugethiere, 927. (Name Combination).

1906. *Scotophilus nigrita herero* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (98): 174. Publication date: 1 February 1906. Type locality: Namibia: Ovamboland: Olifants Vlei [18 00 S 17 30 E]. [Goto Description]. Holotype: NHMUK 1907.1.1.449: ad ♀, skin and skull. Collected by: Mr. Charles John Andersson; collection date: 8 August 1859; original number: 260. Formerly in Tomes collection. - Comments: Ellerman *et al.* (1953) point out that the type locality is not in Damaraland, as claimed by Thomas for both *herero* and *damarensis*: see Meester *et al.* (1986: 60).

1914. *Vespertilio dinyani:* Rothschild, Bull. Entom. Res., 5 (1): 41. Publication date: April 1914. (Lapsus).

1921. *Scotophilus nigrita dingani:* Kershaw, Durban Mus. Novit., 3 (1): 29. (Name Combination, Alternate Spelling).

1946. *Scotophilus nigrita pondoensis* Roberts, Ann. Transv. Mus., 20 (4): 304. Type locality: South Africa: Transkei, Western Pondoland: Port St.Johns [31 27 S 29 33 E]. [Goto Description]. Holotype: SAMC 6858: Collected by: Captain Guy Chester Shortridge; collection date: 22 August 1902.

1951. *Vespertilio epichrysurus:* Roberts, Mammals of South Africa, 90. (Lapsus).

1953. *Scotophilus nigrita dingaanii:* Lawrence and Loveridge, Bull. Mus. comp. Zool., 110 (1): 6. (Lapsus).

2001. *scotophilus nigrata:* Lameed, Biodiversity, 8 (4): 8. - Comments: We can not exclude that this might be a synonym for *S. nigrita*. (Lapsus).

2019. *Scroptophilus dinganii:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

2025. *Scotophilus diaganii:* Ngene, Okwuonu, Ogbonna, Ukwueze and Ejere, Caryologia, 78 (1): 3. Publication date: 1 October 2025. (Lapsus).

? *Scotophilus cf. dinganii:*

? *Scotophilus dingani:* (Alternate Spelling).

? *Scotophilus dinganii colias:* (Name Combination).

? *Scotophilus dinganii dinganii:* (Name Combination).

? *Scotophilus dinganii herero:* (Name Combination).

? *Scotophilus dinganii:* (Name Combination, Current Combination).
? *Scotophilus nigrita dinganii:* (Name Combination).
? *Scotophilus nigrita nigrita:* (Name Combination).
? *Scotophilus nigrita:*

TAXONOMY:



Figure 282. *Scotophilus dinganii*.

Placed in *leucogaster* by Koopman (1975: 414 - 416, as *nigrita*; 2004ah: 11) and Koopman *et al.* (1978: 4 - 5); but see also Schlitter *et al.* (1980).

See also the discussion under the genus and under *nigrita* and *leucogaster*.

In their study on Arabian *Scotophilus*, Vallo *et al.* (2011c: 359) tentatively suggest to use the name *S. colias* for the East African yellow-bellied house bat as these bats clearly differ from the typical *S. dinganii* from southern Africa.

Trujillo *et al.* (2009: 554) found several divergent cytochrome *b* lineages in *S. dinganii*, suggesting that cryptic species might be present in different geographic areas southern Africa, eastern Africa, Ghana to Kakamega Forest (Kenya).

Decher *et al.* (2021: 271) suggest that the West African specimens probably represent *S. livingstonii* rather than *S. dinganii* as one of the paratypes of the former was collected in Legon (Ghana). However, we believe that further examination of additional specimens is needed to evaluate the status of the West African specimens.

COMMON NAMES:
Afrikaans: Geel Dakvlermuis. English: Yellow House Bat, Dingan's Bat, Dingaan's House Bat, Yellow-bellied House Bat, Dingaan's Yellow Bat, African Yellow Bat, African Yellow House Bat. French: Scotophile africain, Chauve-souris jaune des maisons, Scotophile à ventre jaune. German: Gelbbäuchige Hausfledermaus, Natalischen Schwirrfledermaus, Flachschnauzigen Schwirrfledermaus. Italian: Scotòfilo di Dìngan. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego caseiro amarelo. Tshokwe (Angola): Kafukufuku.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
This species has been recovered from the upper Pleistocene in South Africa, at Border Cave (Avery, 1991: 6), and Wonderwerk (Avery and Avery, 2011: 19).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Griffin, 2008a; IUCN, 2009; Monadjem and Griffin, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Griffin, 2017a). 2008: LC ver 3.1 (2001) (Griffin, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Griffin, 2004b; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016s). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Griffin, 2008a; IUCN, 2009; Monadjem and Griffin, 2017a).

CONSERVATION ACTIONS:
Griffin (2008a) [in IUCN (2009)] and Monadjem and Griffin (2017a) report that in view of the species wide range it is believed to be present in many protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Scotophilus dinganii is widely distributed in sub-Saharan Africa. It ranges from Senegal and the Gambia in the west, through West Africa and parts of Central Africa, to Sudan, Eritrea, Djibouti and Ethiopia in the east, from here it ranges south through much of East Africa and southern Africa, being recorded as far south as eastern South Africa, Lesotho and Swaziland. For South Africa, Babiker Salata (2012: 49) found that its

distribution is strongly associated with the mean temperature of the coldest quarter.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,251,825 km^2.

Native: Angola (Crawford-Cabral, 1989; Cotterill, 2004a: 262; Monadjem *et al.*, 2010d: 573; Taylor *et al.*, 2018b: 63); Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 573); Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 626); Burundi; Cameroon; Central African Republic; Congo (Bates *et al.*, 2013: 337); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Dowsett *et al.*, 1991: 259; Van Cakenberghe *et al.*, 1999; Monadjem *et al.*, 2010d: 573); Côte d'Ivoire; Djibouti (Pearch *et al.*, 2001: 398); Eritrea; Eswatini (Monadjem *et al.*, 2010d: 574, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 131); Gambia; Ghana; Guinea; Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 71); Kenya; Lesotho; Liberia; Malawi (Ansell and Dowsett, 1988: 38; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 573); Mali; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 573; Monadjem *et al.*, 2010c: 384); Namibia (Monadjem *et al.*, 2010d: 573); Nigeria; Rwanda; Saudi Arabia; Senegal; Sierra Leone; Somalia; South Africa (De Graaf, 1960; Monadjem *et al.*, 2010d: 573); Sudan; Tanzania (Stanley and Goodman, 2011: 45); Togo; Uganda; Yemen (Benda *et al.*, 2011b: 42); Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 574); Zimbabwe (Monadjem *et al.*, 2010d: 574).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

Vomeronasal complex
In this species, the VNC is bar-shaped in cross section (Smith *et al.*, 2024: 9).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 12.4 Pa, aspect ratio 7.3 and tip shape index of 7.71 for a wingspan of 37 cm and a wing area of 190 cm^2 and a body mass of 24 g.

In their study on rewarming along an altitudinal gradient in the RSA, Marsden *et al.* (2022: 5) found that the rewarming rate of these bats decreased with increasing altitude.

ECHOLOCATION:
See Taylor (1999b) and Taylor *et al.* (2005).

Jacobs *et al.* (2007a) recorded the peak echolocation frequency (33.4 ± 1.4 kHz) for individuals from St. Lucia, KwaZulu Natal, South Africa. Schoeman and Waddington (2011: 291) mention a peak frequency of 33.9 ± 1.1 kHz and a duration of 4.1 ± 0.7 ms for specimens from Durban, South Africa.

Taylor *et al.* (2013b: 17) recorded the following parameters for 7 calls from Soutpansberg, South Africa: F_{max}: 51.6 ± 8.19 (42.1 - 65.2) kHz, F_{min}: 33.1 ± 0.79 (31.6 - 34.1) kHz, F_{knee}: 36.4 ± 1.10 (34.4 - 37.4) kHz, F_{char}: 33.8 ± 1.03 (31.9 - 35.3) kHz, duration: 3.4 ± 0.66 (2.7 - 4.6) ms.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg range (RSA): F_{min}: 32 - 34 kHz, F_{char}: 32 - 35 kHz, F_{knee}: 34 - 37 kHz, slope: 287 - 588 OPS, duration: 3 - 5 ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 36 (34 - 37) kHz. From Maroua, Cameroon, Manga Mongombe (2012: 79) and Bakwo Fils *et al.* (2018: 4) reported for 19 calls a call type of FM/QCF and the following parameters: F_{max}: 58.5 ± 8.9 (49.4 - 84.8) kHz, F_{min}: 52.6 ± 6.2 (46.7 - 69.5) kHz, F_{mean}: 55.6 ± 7.5 (48.1 - 77.0) kHz, F_{knee}: 58.5 ± 8.9 (49.4 - 84.0) kHZ, F_{char}: 52.7 ± 6.2 (46.8 - 69.5) kHz, and duration: 0.88 ± 0.92 (0.73 - 1.02) ms.

132 calls of 5 bats from KwaZulu-Natal and Eastern Cape (RSA) reported by Moir (2020: 30) and Moir *et al.* (2021a: 371) had the following parameters: F_{max}: 53.63 ± 8.39 (51.57 - 74.49) kHz, F_{min}: 34.68 ± 1.58 (33.15 - 36.94) kHz, F_{char}: 34.68 ± 1.58 (33.15 - 36.94) kHz, F_{knee}: 35.33 ± 1.72 (33.57 - 37.95) kHz, and duration: 2.65 ± 0.52 (2.30 - 3.55) ms.

Eisenring *et al.* (2016: SI 2) report on two calls from *S. nigrita* from the Aberdares Range in Kenya with the following characteristics: PF: 36.8 ± 3.3 (34.5 - 39.2), HF: 57.3 ± 12.4 (48.5 - 66.1), LF: 29.8 ± 0.4 (29.5 - 30.1), DT: 0.1 ± 0.0 (0.1 - 0.1) DF: 27.5 ± 12.9 (18.4 - 36.6), IPI: 1.1 ± 0.4 (0.9 - 1.4). As they compare their values with those presented by Fenton (1975), Fenton and Bell (1981) and O'Shea and Vaughan (1980), these values are probably also for *S. dinganii*.

From Swaziland, the following parameters were reported by Monadjem *et al.* (2017c: 179): F_{min}: 33.2 ± 1.26 (30.3 - 34.7) kHz, F_{knee}: 36.4 ± 1.61 (32.1 - 38.6) kHz, F_c: 33.7 ± 1.44 (30.3 - 35.6)

kHz, and duration: 3.8 ± 0.94 (2.6 - 6.1) ms. The calls were detectable up to a distance of 20 m.

Adams and Kwiecinski (2018: 4) recorded the following characteristics for four calls of bats from the Kalahari Desert: F_{char}: 33.9 ± 2.4 kHz, F_{max}: 40.9 ± 2.1 kHz, F_{min}: 33.4 ± 2.0 kHz, duration: 3.3 ± 0.9 ms.

Four calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 41.28 ± 5.17 kHz, F_{min}: 33.95 ± 1.18 kHz, F_{knee}: 35.71 ± 1.49 kHz, F_{char}: 34.39 ± 1.46 kHz, slope: 39.62 ± 32.49 OPS, duration: 3.77 ± 1.67 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 33.6 kHz and duration: 4.9 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 10 bats: F_{max}: 47.09 ± 7.53 kHz, F_{min}: 31.86 ± 6.25 kHz, F_{knee}: 36.27 ± 1.63 kHz, F_{char}: 33.43 ± 1.26 kHz, slope: 363.33 ± 166.43 OPS, duration: 3.52 ± 2.09 ms. 11 calls recorded by Cory-Toussaint and Taylor (2022: Table S1) at the Venatia mine had a duration of 4.24 ± 1.06 ms, F_{min}: 32.23 ± 1.78 kHz, F_{max}: 38.28 ± 3.11 kHz, F_{knee}: 35.03 ± 0.80 kHz and F_{char}: 33.30 ± 0.82 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 26 *Scotophilus dinganii* calls from the Kruger Park (RSA): F_{min}: 32.3 ± 1.1 (30.1 34.7) kHz, Duration: 3.7 ± 0.9 (2.2 5.8) ms, F_{max}: 53.6 ± 8.1 (40.2 64.8) kHz, F_{knee}: 35.0 ± 2.3 (31.6 42.1) kHz, F_{char}: 33.0 ± 1.2 (30.4 35.9) kHz.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 33.00 ± 1.20 kHz, F_{max}: 53.60 ± 8.10 kHz, F_{min}: 32.30 ± 1.10 kHz.

86 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 32 - 34 kHz, F_{max}: 42 - 65 kHz, F_{char}: 32 - 35 kHz, F_{knee}: 34 - 37 kHz and duration 3 - 5 ms.

Parker (2022: 20) reported F_{min}: 31.72 ± 2.70 kHz, F_{char}: 35.05 ± 1.42 kHz and F_{max}: 41.34 ± 3.48 kHz for 15 passes at Mountain Zebra National Park (RSA).

For 40 calls from 2 *Scotophilus dinganii* females from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 33.06 ± 1.34 kHz, F_{knee}: 37.53 ± 3.30 kHz, F_{min}: 32.55 ± 1.31 kHz, F_{max}: 57.44 ± 9.68 kHz, Bandwidth: 24.89 ± 9.23 kHz, Duration: 2.96 ± 0.55 ms. 38 calls from 4 males showed the following values: F_{char}: 32.71 ± 1.48 kHz, F_{knee}: 36.87 ± 2.92 kHz, F_{min}: 32.20 ± 1.40 kHz, F_{max}: 63.03 ± 10.10 kHz, Bandwidth: 30.84 ± 9.61 kHz, Duration: 3.06 ± 0.66 ms.

In Benin, Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 55) reported F_{char}: 33.00 ± 1.20 kHz, F_{max}: 53.60 ± 8.10 kHz and F_{min}: 32.30 ± 1.10 kHz.

Taylor-Boyd *et al.* (2025: 116) report the following values for 16 calls for Zambian *Scotophilus dinganii*: Interpulse interval: 73.8 ± 20.4 (43.1 - 112.0) ms; F_{max}: 37.7 ± 2.6 (32.2 - 43.3) kHz; Start slope: -15.1 ± 2.8 (-10.4 - -21.0) kHz/ms; End slope: -6.7 ± 3.2 (-10.5 - -9.8) kHz/ms; Ledge duration: 0.4 ± 0.1 (0.3 - 0.5) ms.

Molecular Biology:

Karyotype

Peterson and Nagorsen (1975), Schlitter *et al.* (1980) and Ruedas *et al.* (1990) all reported 2*n* = 36. However, while Schlitter *et al.* (1980) reported FN = 52, BA = 18, an acrocentric X chromosome, and a metacentric Y chromosome, Ruedas *et al.* (1990) reported FN = 50, BA = 16, a submetacentric X chromosome, and a telocentric Y chromosome. Eick *et al.* (2007) reported the following autosomal pairs: seven meta- to submetacentric, nine acrocentric, and one subtelocentric. One homologue of the smallest acrocentric pairs showed a small heterochromatic short arm in one specimen, resulting in a subtelocentric state (Eick *et al.*, 2007). The diploid chromosome number (2*n*) is 36, the fundamental number of autosomal arms (Fna) is 50 (Eick *et al.*, 2007). The X chromosome is a medium-sized metacentric and the Y chromosome a small, probably acrocentric, partly heterochromatic chromosome (Eick *et al.*, 2007).

Ngene *et al.* (2025: 6) reported *2n* = 36 and FN = 45 for Nigerian bats.

Genetics

See Hoofer and Van Den Bussche (2003) for the results of a specimen from Tanzania.

Habitat:

In southern Africa, this species is found in Savanna habitats (80 %; Cooper-Bohannon *et al.*, 2016: Table S2).

HABITS:
Scotophilus dinganii is gregarious, roosting in small groups of up to 12 individuals (Skinner and Smithers, 1990).
Thermoregulation - See Jacobs *et al.*, 2007b).

ROOST:
Type - Buildings (Skinner and Smithers, 1990). In KwaZulu Natal, South Africa, Jacobs *et al.* (2007b), found *S. dinganii* roosted in the roofs of buildings in the crevices between the roof (either made of asbestos, clay tiles, or corrugated metal sheets) and the brickwork of the walls. Jacobs *et al.* (2007b) did not find any relationship between aspect and roost selection, or any relationship that the bats preferred roosts which received the direct rays of the afternoon sun. Monadjem *et al.* (2010b: 74) found that they roosted in *Combretum imberbe* trees.

Microclimate - Jacobs *et al.* (2007b) found that the temperature of building roosts appeared to track ambient temperature with a slight lag (see also Marroquin and Muñoz-Garcia, 2023: 9)..

Happold and Happold (2023: 172) mention that these bats sometimes roost singly, but more often they are found in groups of up to 20 animals, and more than one group can occupy the same roof, but at different places.

DIET:
On the Umbilo River (KwaZulu Natal, RSA), Naidoo *et al.* (2011: 26) found the diet to contain the following volume percentages during summer: Lepidoptera (17.5 ± 15.9), Coleoptera (81.9 ± 16.6), and Diptera (0.6 ± 1.3). And during winter: Lepidoptera (24.9 ± 12.9), Coleoptera (66.4 ± 21.7), and Diptera (8.9 ± 8.7).

Taylor *et al.* (2017b: 245, 252 - 254) reported the following 23 food items in the Limpopo province (RSA): five insect orders: Lepidoptera (*Toxocampinae tathorhynchus* + *Achrosis* sp. + *Isturgia roraria* + *Sena* sp. + *Sena prompta* + *Cortyta canescens* + *Pandesma robusta* + *Pericyma atrifusa* + *Argyrogrammatini*sp. + *Spodoptera exigua* + *Maurilia arcuata* + unmatched), Orthoptera (Tettigoninae + unmatched), Hemiptera (*Nezera viridula* + *Macrorhaphis acuta* + unmatched), Coleoptera (unmatched) and Blattodea (unmatched).

Weier *et al.* (2019c: 6) investigated droppings from this species in the Levubu region (Limpopo, RSA) and found DNA sequences of: Lepidoptera: *Cryptophlebia peltastica* (Meyrick, 1921) and *Thaumatotibia batrachopa* (Meyrick, 1908); Hemiptera: *Bathycoelia distincta* Distant, 1878 and *Nezara viridula* (Linnaeus, 1758).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 143 minutes, and a digestibility rate of about 73.6 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) and the African harrier-hawk (*Polyboroides typus* Smith, 1829) as diurnal avian predators. Malan *et al.* (2022: 167) also mentioned 41 individuals found in pellets of South African Bat hawks.

Mumford (1980: 11) observed a *Scotophilus dinganii* being caught by an African goshawk (*Accipiter tachiro* (Daudin, 1800)) in Kenya.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Griffin, 2008a; IUCN, 2009; Monadjem and Griffin, 2017a).

Trend
2016: Unknown (Monadjem and Griffin, 2017a).
2008: Unknown (Griffin, 2008a; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Jacobs *et al.* (2007b) found that bats roost exit times were variable, but most left their roost for the first time on a particular day between 17h15 and 18h00 and returned between 18h45 and 19h15 (remaining out of the roost on average for about 1hr).

REPRODUCTION AND ONTOGENY:
van der Merwe *et al.* (2006) reported, from examination of serially sectioned reproductive tracts of females, that *S. dinganii* is monoestrous species and that insemination, ovulation and fertilization take place during mid to late autumn (April to May), Kruger-NP., South Africa. Early embryonic development of normally two embryos (one in each uterine horn) was retarded and implantation delayed until mid-winter (July), when the blastocysts implanted (van der Merwe *et al.*, 2006). van der Merwe (2006) found *S. dinganii* in the Kruger-N.P., South Africa to be seasonally monestrus, carrying a single foetus in each of the two uterine horns of the bicornute uterus. The amnion in *S. dinganii* was a schizamnion, and van der Merwe (2006) deduced that its formation was preceded by cavitation of the inner cell mass, with formation of the definitive amniotic cavity, where the floor of the cavity eventually formed the

embryonic disc and its roof the ectodermal part of the true or definitive amnion.

van der Merwe and Rautenbach (1990: 540) reported that *S. dinganii* commonly gives birth to twins and occasionally even triplets (= polytocy, see Garbino *et al.*, 2021: Suppl.).

In Malawi, births occurred early in the wet season (Happold and Happold, 1990b: 568).

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births taking place between November and December.

Two pregnant females were reported from Sierra Leone on 7 April and 29 May by Weber *et al.* (2019: 27).

PARASITES:

BACTERIA

Dietrich *et al.* (2016b: 3) found one out of 12 bats from Rocktail Bay (RSA) to be positive for *Rickettsia*. Also from the RSA, Dietrich *et al.* (2018a: 4) reported the presence of *Leptospira borgpetersenii*.

PROTOZOA

Clément *et al.* (2019a: 5) reported on two southern African bats, which were both infected by *Trypanosoma vespertilionis*_likeG1_AF3.

HEMIPTERA

Cimicidae

Cacodmus sparsilis Rothschild, 1914 was described from one female specimen taken from a "*Vespertilio dinyani*" at Durban, South Africa (Haeselbarth *et al.*, 1966: 10, referred to as *Scotophilus nigrita*). *Stricticimex transverses* Ferris and Usinger, 1957 recorded from Windhoek, Namibia (Haeselbarth *et al.*, 1966: 14). Kock *et al.* (1998b: 237) reported *Cacodmus sparsilis* Rothschild, 1914 too, but also *Aphrania* cf. *barys* Jordan and Rothschild, 1912.

DIPTERA

Nycteribiidae

Basilia bouvieri (Falcoz, 1924) from Tanzania, Sudan, Senegal and Sierra Leone (Haeselbarth *et al.*, 1966: 111), referred to as *Scotophilus nigrita*).

SIPHONAPTERA

Ischnopsyllidae

(*Chiropteropsylla brockmani* Rothschild, 1915 was reported on *Scotophilus dinganii flavigaster* from Eritrea by Beaucournu and Kock (1996).

ARACHNIDAI

Spinturnicidae

Orlova *et al.* (2024: 151) mentioned this species (as *Scotophilus nigrita*) as host for *Spinturnix scotophili* Zumpt and Till, 1954.

Trombiculidae

Stekolnikov (2018a: 134) reported the presence of *Ericotrombidium scotophilum* (Vercammen-Grandjean and Langston, 1976) from "*Scotophilus nigrita*" from Pietermaritzburg, RSA. Zajkowska *et al.* (2018: 199) [referring to Anciaux de Faveaux (1971)] mentioned *Microtrombicula scotophili* Vercammen-Grandjean, 1965 and *Schoutedenichia trombiculoides* Vercammen-Grandjean, 1958 from a "*Scotophilus dinganii colias*" from Sudan.

VIRUSES:

Coronaviridae - Coronaviruses

SARS-CoV

Müller *et al.* (2007b) tested between 1986 to 1999, for antibody to SARS-CoV in sera in five individuals from Limpopo Province, South Africa, none were tested positive (0/5). One out of 14 (7.1 %) Kenyan bats tested by Tao *et al.* (2017: Suppl.) was positive for CoV. Only one of the 29 Congolese bats examined by Kumakamba *et al.* (2021: 7) tested positive for coronaviruses.

Montecino-Latorre *et al.* (2022: 5) mention the CoV as Eidolon bat coronavirus/Kenya/KY24/2006.

Flaviviridae

Pegivirus (BPgV)

1 of 2 Kenyan specimens examined by Quan *et al.* (2013: Table S5) (50.0 %) was infected by clade G type *Pegivirus*.

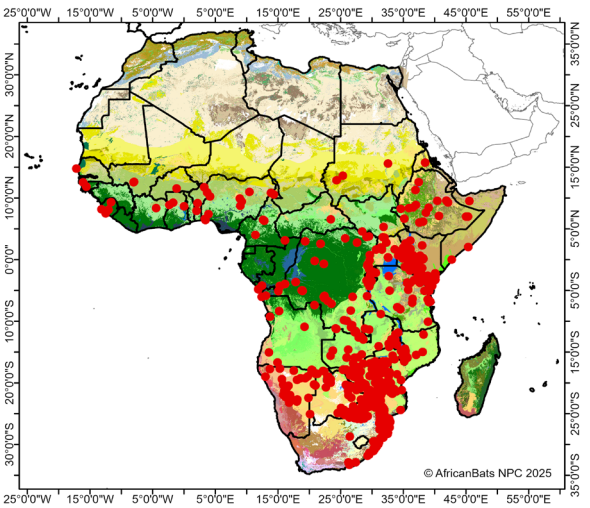

Figure 283. Distribution of *Scotophilus dinganii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Eritrea, Eswatini, Ethiopia, Ghana, Guinea-Bissau, Kenya, Malawi, Mali, Mozambique, Namibia, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Uganda, Zambia, Zimbabwe.

Scotophilus ejetai Brooks and Bickham, 2014

*2014. *Scotophilus ejetai* Brooks and Bickham, Occ. Pap. Mus. Texas Tech Univ., 326: 1, 14, fig 5. Publication date: 26 Jun 2014. Type locality: Ethiopia: Orimaya region: Dogy River Bridge [08 21 43 N 35 53 02 E, 1390 m]. Holotype: BRTC 57950: ad ♂, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 23 February 2001; original number: 10310. Muscle tissue sample AK 21235. Paratype: BRTC 57954: ad ♀, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 21 February 2001; original number: 10292. Tissue sample AK 21213. Paratype: CM 114043: ad ♀, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 2 April 1995; original number: 9986. Tissue sample SP 13027. - Etymology: In honour of Dr. Gebisa Ejeta, distinguished professor of plant breeding & genetics and international agriculture at Purdue University (see Brooks and Bickham, 2014: 14).

TAXONOMY:
Brooks and Bickham (2014) described four new species in the genus *Scotophilus*. However, they did not compare them with a number of already described taxa such as *colias* Thomas, 1904 or *flavigaster* Heuglin, 1861, which make the validity of (some of) these names doubtful. Benda *et al.* (2025: 32) consider *ejetai* to be a synonym of *Scotophilus colias*.

COMMON NAMES:
English: Ejeta's House Bat. German: Äthiopische Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Assessed as Least Concern as this species is known from at three widely distributed localities in Ethiopia (Brooks and Bickham, 2014), and possibly occurs widely throughout the country (Largen *et al.*, 1974) and may occur in protected areas (Monadjem, 2017b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2017b).

Regional
None known.

MAJOR THREATS:
The major threat is persecution at roosting sites (Monadjem, 2017b).

CONSERVATION ACTIONS:
Monadjem (2017b) report that this species is not currently known to occur in any protected areas. However, other medium-sized *Scotophilus* species in eastern and southern Africa occur in close association with human-altered landscapes and if this is the case with *S. ejetai*, then it is unlikely to need specific protection.

GENERAL DISTRIBUTION:
Known from three localities in Ethiopia.

Native: Ethiopia.

POPULATION:
Trend: 2016: Unknown (Monadjem, 2017b).

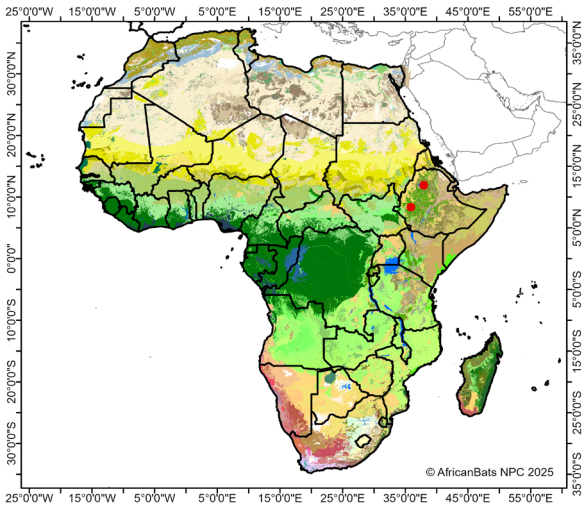

Figure 284. Distribution of *Scotophilus ejetai*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

Scotophilus leucogaster (Cretzschmar, 1826)

*1826. *Nycticejus leucogaster* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 71, pl 28a, 1, 2. Publication date: 1826. Type locality: Sudan: Kordofan province: Brunnen Nedger [=Nedger Wel; Bir Nedger]:. [Goto Description]. Lectotype: SMF 4309: Collected by: Wilhem Peter Edward Simon Rüppell. Mertens (1925: 22) old catalog II.O.1.b. Paralectotype: RMNH MAM.27432: ad, skin and skull. Collected by:

Wilhem Peter Edward Simon Rüppell. Mertens (1925: 22) mentions SMF 4309 (old catalog II.O.1.b, coll. E. Rüppell, 1825) as lectotype).
The RMNH catalog mentions two numbers: 27432.a (skull + loose bones) and 27432.b (mounted skin). - Comments: The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831". - Etymology: From the masculine Greek adjective "*λευκος*" (leukós), meaning "white" and the feminine Greek substantive "*γαστήρ*" (gastér), meaning "stomach", referring to the relatively light belly colour of the type specimen (see Lanza *et al.*, 2015: 487).

1861. *Nycticejus flavigaster* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 5, 14. Publication date: 1861. Type locality: Eritrea: Kérén [ca. 15 45 N 38 20 E]. [Goto Description]. Syntype: SMNS 983: ad ♂, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294). Syntype: SMNS 983a: ad ♀, skull and alcoholic. Collected by: Martin Theodor von Heuglin; collection date: 1861. See Dieterlen *et al.* (2013: 294).

1861. *Nycticejus murino-flavus* Heuglin, Nov. Act. Acad. Cæs. Leop.-Carol., 29 (8): 5, 15. Publication date: 1861. Type locality: Eritrea: near Massaua [=Massawa]: M'kullu [15 38 N 39 24 E]. [Goto Description]. Holotype: [Unknown] |TS294|: ad ♂.

1878. *Scotophilus borbonicus:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 260. Publication date: 15 June 1878. - Comments: .

1906. *Scotophilus damarensis* Thomas, Ann. Mag. nat. Hist., ser 7, 17 (98): 175. Publication date: 1 February 1906. Type locality: Namibia: Ovamboland: Olifants Vlei [18 00 S 17 30 E]. [Goto Description]. Holotype: NHMUK 1907.1.1.463: ad ♂, skin and skull. Collected by: Mr. Charles John Andersson; collection date: 10 August 1859; original number: 276. Received in the Tomes collection. - Comments: Included in *borbonicus* by Meester *et al.* (1986: 61), in *viridis* by Koopman (1993a: 228), but in *leucogaster* by Simmons (2005).

1938. *[Pachyotus] altilis:* Frechkop, Exploration du Parc National Albert, 53.

2019. *Scroptophilus leucigaster:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

? *Scotophilus borbonicus damarensis:* (Name Combination).

? *Scotophilus cf. leucogaster:*

? *Scotophilus leucogaster damarensis:* (Name Combination).

? *Scotophilus leucogaster leucogaster:* (Name Combination).

? *Scotophilus leucogaster:* (Name Combination, Current Combination).

? *Scotophilus nigrita leucogaster:* (Name Combination).

? *Scotophilus viridis damarensis:*

TAXONOMY:



Figure 285. *Scotophilus leucogaster*

Does not include *damarensis*, see Koopman (1986); but see Robbins *et al.* (1985). Herkt *et al.* (2017: Appendix S9) found that *damarenis* occupies a noticeably different ecological niche as compared with the northern populations of *leucogaster*.

Included *nucella*; but see Robbins *et al.* (1985).

For scope of this species see Koopman (1975: 414 - 416); as *nigrita*) and Koopman *et al.* (1978: 4 - 5). However Robbins (1978a: 212 - 213) has shown that the name *nigrita* was misapplied to another species, for which the next available name was *dinganii*, and which would be included in *leucogaster* if Koopman (1975)'s reasoning were followed. However Schlitter *et al.* (1980) listed *dinganii* as distinct from *leucogaster*, as did Robbins *et al.* (1985). See Koopman (1986).

COMMON NAMES:

Chinese: 白腹黄⚲ . Czech: mračník bělobřichý, netopýr bělobřichý. English: Lesser Yellow House Bat, White-bellied House Bat, White-bellied Yellow Bat, Cretzschmar's Brown Bat. French: Scotophile à ventre blanc. German: Weißbäuchige Hausfledermaus, Weissbauchige Schwirrfledermaus, Gelbbauchige Schwirrfledermaus, Olivenbraune Schwirrfledermaus. Italian: Scotòfilo panciabianca.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Griffin, 2008b; IUCN, 2009; Monadjem and Griffin, 2017b).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem and Griffin, 2017b). 2008: LC ver 3.1 (2001) (Griffin, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Griffin, 2004a; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Taylor *et al.*, 2016e).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Griffin, 2008b; IUCN, 2009; Monadjem and Griffin, 2017b).

CONSERVATION ACTIONS:
Griffin (2008b) [in IUCN (2009)] and Monadjem and Griffin (2017b) reports that in view of the species wide range it is presumably present in many protected areas. No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Scotophilus leucogaster has been recorded in much of West Africa (including northern parts of Cameroon, Nigeria, Benin, Togo, Ghana, Côte d'Ivoire, Sierra Leone, and Guinea, much of Senegal, Gambia, and Burkina Faso, and southern parts of Mali and Niger). There are isolated records from southwestern Mauritania, as well as western parts of the Central African Republic. The eastern parts of the distribution include records from Sudan, and the northern parts of Uganda and Kenya. Further south this species is found in Mozambique, Angola and Namibia, Zambia, northern Botswana, and northern South Africa.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 426,596 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 575; Taylor *et al.*, 2018b: 60); Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 575); Burkina Faso (Kangoyé *et al.*, 2015a: 626); Cameroon; Central African Republic; Chad; Côte d'Ivoire; Ethiopia (Benda *et al.*, 2020: 2587); Gambia; Ghana; Guinea (Ziegler *et al.*, 2002: 78); Guinea-Bissau (Vaughan *et al.*, 1997b; Robbins *et al.*, 1985; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 70); Kenya; Mali (Meinig, 2000: 105); Mauritania; Mozambique (Monadjem *et al.*, 2010d: 575; Monadjem *et al.*, 2010c: 385); Namibia (Monadjem *et al.*, 2010d: 575); Niger; Nigeria; Senegal; Saudi Arabia; Sierra Leone; South Africa (Monadjem *et al.*, 2010d: 575); Sudan; Togo; Uganda (Kityo and Kerbis, 1996: 62); Yemen; Zambia (Monadjem *et al.*, 2010d: 575); Zimbabwe (Monadjem *et al.*, 2010d: 575).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Leblanc and Taupin (2004: 26) refers to Fahr (2001), who reported an albino specimen found in the Nuba mountains of Sudan.

DETAILED MORPHOLOGY:
Brain
Amrein *et al.* (2007), from specimens collected from Bénin, reported that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus was found to be absent. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. Amrein *et al.* (2007) furthermore detected few DCX positive cells in the rostral migratory stream and the olfactory bulb. Hippocampal granule cells were homogeneously positive for NeuroD (Bigalke, 1968).

SEXUAL DIMORPHISM:
In Burkina Faso, Kangoyé *et al.* (2015a: 626) found the averages of the body measurements (except 3ph2) to be larger in females than in males, but the averages of the cranial measurements were larger in males.

ECHOLOCATION:
12 FM/QCF type calls from Maroua (Cameroon) were reported by Manga Mongombe (2012: 79) and Bakwo Fils *et al.* (2018: 4) with the following parameters: F_{max}: 55.7 ± 4.3 (48.5 - 64.1) kHz, F_{min}: 50.6 ± 3.0 (46.1 - 56.3) kHz, F_{mean}: 53.2 ± 3.6 (47.3 - 59.3) kHz, F_{knee}: 55.7 ± 4.3 (48.5 - 64.1) kHz, F_{char}: 50.7 ± 3.0 (46.1 - 55.0) kHZ, and duration: 0.81 ± 0.23 (0.44 - 1.00) ms.

Thiagavel *et al.* (2017: Suppl.) mention a F_{peak} of 46.27 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype
Ngene *et al.* (2025: 6) reported 2n = 36 and FN = 54 for Nigerian bats.

See also discussion in generic account.

Genetics
See Hoofer and Van Den Bussche (2003) for the results of a specimen from Kenya.

HABITAT:
In southern Africa, it occurs in Savanna (89 %) and SW arid (10 %) habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

ROOST:
Happold and Happold (2023: 173) indicate that these bats roosted in groups of up to nine individuals.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 127 minutes, and a digestibility rate of about 74.7 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Griffin, 2008b; IUCN, 2009; Monadjem and Griffin, 2017b).

Trend
2016: Unknown (Monadjem and Griffin, 2017b).
2008: Unknown (Griffin, 2008b; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

PARASITES:
PROTOZOA
From Burkina Faso, Thiombiano *et al.* (2023: 4) reported that five out of 29 Scotophilus leucogaster bats was carrying *Trypanosoma* cf. *vespertilionis* parasites.

ACARI
Dermanyssidae
Zumpt and Till (1954: 50) reported the presence of *Steatonyssus nyassae* (Hirst, 1922) on a "*Scolophilus murinoflavus*" from near Torit, South Sudan.

Spinturnicidae
Orlova *et al.* (2024: 151) mentioned this species as host for *Spinturnix scotophili* Zumpt and Till, 1954.

Trombiculidae
Stekolnikov (2018a: 114) reported *Schoutedenichia (Schoutedenichia) trombiculoides* Vercammen-Grandjean, 1958 and *Microtrombicula scotophili* Vercammen-Grandjean, 1965 from *S. leucogaster leucogaster* from South Sudan.

HEMIPTERA
Cimicidae
Szentiványi *et al.* (2022 12) reported *Aphrania elongata* Usinger, 1966 from a Mauritanian bat.

DIPTERA
Nycteribiidae
Dick *et al.* (2023: 75) mentioned that *Basilia (Paracyclopodia) bouvieri* (Falcoz, 1924) had been reported from Senegal and Uganda.

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
In Nigeria during June 2008, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs, none tested positive.
The viruses found in bats from Cameroon were assigned to the subgenus *Nobecovirus* by Motayo *et al.* (2020: 4).

Rhabdoviridae
Lyssavirus - Rabies related viruses
In Nigeria during June 2008, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluorescent antibody testing.

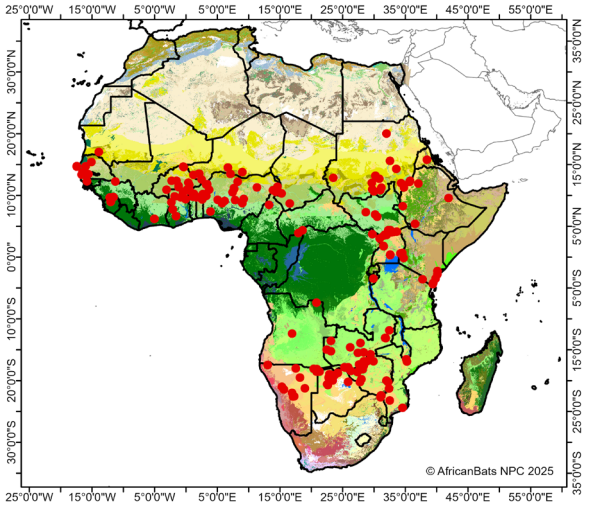

Figure 286. Distribution of *Scotophilus leucogaster*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Côte d'Ivoire, Eritrea, Ethiopia, Ghana, Guinea-Bissau, Kenya, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Scotophilus livingstonii Brooks and Bickham, 2014

2011. *S[cotophilus] aff. dinganii:* Vallo, Benda and Reiter, Afr. Zool., 48 (2): 350. Publication date: October 2011. (Name Combination).

*2014. *Scotophilus livingstonii* Brooks and Bickham, Occ. Pap. Mus. Texas Tech Univ., 326: 1, 11, fig 4. Publication date: 26 June 2014. Type locality: Kenya: Western province: Kakamega district: Ikuywa River Bridge, 6.5 km S, 19 km E Kakamega [00 13 N 34 55 E]. Holotype: CM 98051: ad ♂, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 8 November 1985; original number: 7394. Muscle tissue sample TK 33534. Paratype: CM 98053: ad ♀, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 8 November 1985; original number: 7396. Muscle tissue sample TK 33536. Paratype: USNM 412150: ad ♀, skin and skull. Collected by: Bruce Joliffe Hayward; collection date: 22 July 1967; original number: 4135. Collected at University of Ghana Botanical Garden (5º40'N, 10º12'W [sic]), Legon, Eastern (Greater Accra) Region, Ghana (Brooks and Bickham, 2014: 13). - Etymology: In honour of David Livingstone (1813 - 1873) (see Brooks and Bickham (2014: 13).

? *Scotophilus dinganii:* (Name Combination).

TAXONOMY:

Brooks and Bickham (2014) described four new species in the genus *Scotophilus*. However, they did not compare them with a number of already described taxa such as *colias* Thomas, 1904 or *flavigaster* Heuglin, 1861, which make the validity of (some of) these names doubtful.

The analyses performed by Demos *et al.* (2018: 2) confirmed the validity of the taxon, but these authors also indicate that they cannot vouch for the validity of the name with respect to older taxa that would have nomenclatural priority.

COMMON NAMES:

Chinese: 利文斯顿黄蝠. English: Livingstone's House Bat. German: Livingstone-Hausfledermaus.

CONSERVATION STATUS:

Global Justification

This species is assessed as Least Concern (LC ver 3.1 (2000)) as it is known from two extremely widely distributed localities in Kenya and Ghana (Brooks and Bickham, 2014), and the species is likely to occur in between. More research is needed across its region and requires examination of existing museum material to determine its full distribution (Monadjem, 2017c).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem, 2017c).

Regional

None known.

MAJOR THREATS:

The major threat is persecution of roosting sites (Monadjem, 2017c).

CONSERVATION ACTIONS:

Monadjem (2017c) report that this species is not currently known to occur in any protected area, but specimens of *Scotophilus* within the range of this species have been recorded from several protected areas.

GENERAL DISTRIBUTION:

This species is known from SW Kenya and SE Ghana, with a gap of about 4,000 km between them. Benda *et al.* (2023a: 27) report this species from Benin.

POPULATION:

There is no information about population size, but it is presumably large since it occurs over a large area and in anthropogenic environments (Monadjem, 2017c).

Trend:- 2016: Unknown (Monadjem, 2017c).

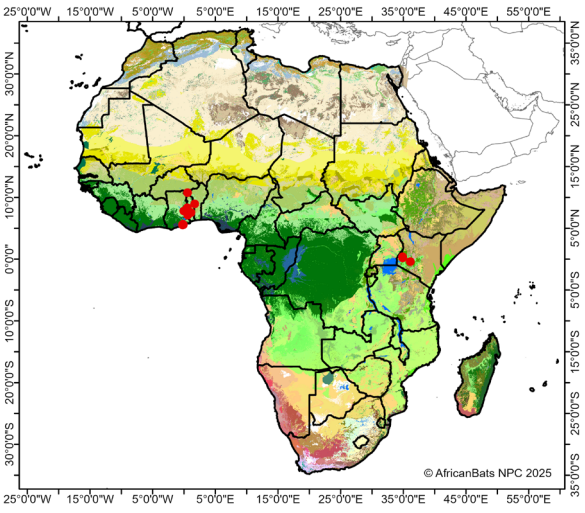

Figure 287. Distribution of *Scotophilus livingstonii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

Benin, Ghana, Kenya, Togo.

Scotophilus marovaza Goodman, Ratrimomanarivo and Randrianandrianina, 2006

2005. *Scotophilus nov. sp.:* Ratrimamanarivo and Goodman, ABCN, 6: 4.

*2006. *Scotophilus marovaza* Goodman, Ratrimomanarivo and Randrianandrianina, Acta Chiropt., 8 (1): 23, figs 2 - 5. Type locality: Madagascar: Mahajanga province: Marovaza [14 56 S 47 16 E, 5 m]. Holotype: FMNH 184050: ad ♂, skull and alcoholic. Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 11 December 2004. Paratype: FMNH 184051: Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 21 - 22 April 2005. locality: Madagascar: Province de Mahajanga - Marovaza [14 56 S 47 16 E, 5 m asl]. Paratype: FMNH 184052: Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 21 - 22 April 2005. Locality: Madagascar: Province de Mahajanga - Marovaza [14 56 S 47 16 E, 5 m asl]. Paratype: FMNH 184085: Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 21 - 22 April 2005. Locality: Madagascar: Province de Mahajanga - Marovaza [14 56 S 47 16 E, 5 m asl]. Paratype: FMNH 184086: Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 21 - 22 April 2005. Locality: Madagascar: Province de Mahajanga - Marovaza [14 56 S 47 16 E, 5 m asl]. Paratype: MNHN ZM-MO-1984-433: Collected by: Steven M. Goodman and Fania H. Ratrimomanarivo; collection date: 29 April 1869. Paratype: UADBA 46965: Collected by: Richard K.B. Jenkins; collection date: 24 November 2004; original number: RBJ 215. Locality: Madagascar: Antafinimihakatra, Parc National d' Ankarafantsika [16 16 S 46 48 E). - Comments: Publication date: prior to 15 May 2006. - Etymology: The name of the type locality (Marovaza) is placed in apposition to the generic name (Goodman *et al.*, 2006b). (Current Combination).

TAXONOMY:
See Goodman *et al.* (2006b).

COMMON NAMES:
Czech: mračník Goodmanův. English: Marovaza House Bat, Marovaza Yellow Bat. French: Scotophile de Marovaza. German: Marovaza-Hausfledermaus.

ETYMOLOGY OF COMMON NAME:
Refers to the name of the type locality (Marovaza).

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) because it is widely distributed in lowland areas of western Madagascar, there are no major threats, and its survival is not dependent on the conservation of intact forests (Jenkins *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017o).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017o). 2008: LC ver 3.1 (2001) (Jenkins *et al.*, 2008b; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Jenkins *et al.* (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017o) report that there are no major threats known. It is a widely distributed species and is tolerant of habitat disturbance (Goodman *et al.*, 2006b; Rakotoarivelo and Randrianandrianina, 2007).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017o) report that given the wide distribution of this species and occurrence in heavily disturbed habitats there are no pressing conservation measures. However, it should be noted that prevalence for synanthropic roosts does not automatically indicate a bat species is not of conservation concern. Furthermore, it should be noted that *S. marovaza* was not found in many of the sites surveyed for bats in western Madagascar (Goodman *et al.*, 2005a) which included areas from where it is suspected of being present (Goodman *et al.*, 2006b). Additional field studies are therefore needed to define its range, local abundance and habitat needs, but this is not a conservation priority (Goodman *et al.*, 2006b).

GENERAL DISTRIBUTION:
Scotophilus marovaza is known from a wide area of western Madagascar from near Morondava in the south, to the holotype locality at Marovaza in the north near Mahajanga (Goodman *et al.*, 2006b; Rakotoarivelo and Randrianandrianina, 2007). Goodman *et al.* (2006b) suspect that *S. marovaza* is distributed across much of western lowland Madagascar although specimen evidence for this is still lacking (Goodman *et al.*, 2005a). Current records are from below 200 m.

Native: Madagascar (Goodman *et al.*, 2006b).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Goodman *et al.* (2006b).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Goodman *et al.* (2006b).

DETAILED MORPHOLOGY:
Baculum
Rakotondramanana and Goodman (2017: 64) mention that the baculum is a flat triangular structure, with a rounded, expanded proximal portion and which gradually tapers to a rounded distal tip; length: 1.60 ± 0.155 (1.47 - 1.77) mm, width: 0.99 ± 0.071 (0.93 - 1.07) mm.

Other

For a description of the crania, teeth, ears and tragus see Goodman *et al.* (2006b).

ECHOLOCATION:
Kofoky *et al.* (2009: 384) reported the calls of nine individuals, characterized by broadband steep FM followed by QCF, and emitted low duty cycle calls with a maximum energy at about 45.9 kHz.

HABITAT:
It is known from dry forests, fragmented forests and anthropogenic savannas in proximity of forests (Goodman *et al.* (2006b; Garbutt, 2022: 103).

Ravelomanantsoa *et al.* (2019: 110) caught it over a pool surrounded by banana trees.

ROOST:
The type specimen was collected day roosting in dry palm leaves (*Bismarckia nobilis*) forming the roof of a building (Goodman *et al.*, 2006b).

DIET:
Diet primarily consisting of beetles (Coleoptera - 73.8 %), although bugs (Hemiptera - 15.0 %), moths (Lepidoptera - 9.8 %) and ants (Hymenoptera - 8.7 %) are also consumed in smaller numbers (Ravelojaona, 2017 [in Garbutt (2022: 103); Goodman *et al.* (2022: 1906].

PREDATORS:
Goodman *et al.* (2015c: 78) found the remains of one individual in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

POPULATION:
Structure and Density
There is very little information on this species. Only singletons are known from two of the four sites from which it has been recorded (Goodman *et al.*, 2006b). It has been found in small roosting colonies (< 5 individuals) in huts made from palm leaves (Ratrimomanarivo and Goodman, 2005).

Trend
2016: Unknown (Monadjem *et al.*, 2017o). 2008: Unknown (Jenkins *et al.*, 2008b; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
See Goodman *et al.* (2006b).

PARASITES:
BACTERIA
Gomard *et al.* (2016: 5) found the single specimen they tested to be positive for *Leptospira*.

DIPTERA
Nycteribiidae
Wilkinson *et al.* (2016) reported the presence of *Basilia (Paracyclopodia)* sp. Ramasindrazana *et al.* (2017: Suppl.) refer to this bat fly as "*Basilia* sp. 2". Szentiványi *et al.* (2019a: Suppl.) indicated that these flies were, in turn, infected by bacteria belonging to: Enterobacteriales, *Wolbachia* sp., *Bartonella* sp.

ANTHROPOPHILOUS:
Known to roost in the palm roofs of houses (Goodman *et al.*, 2006b).

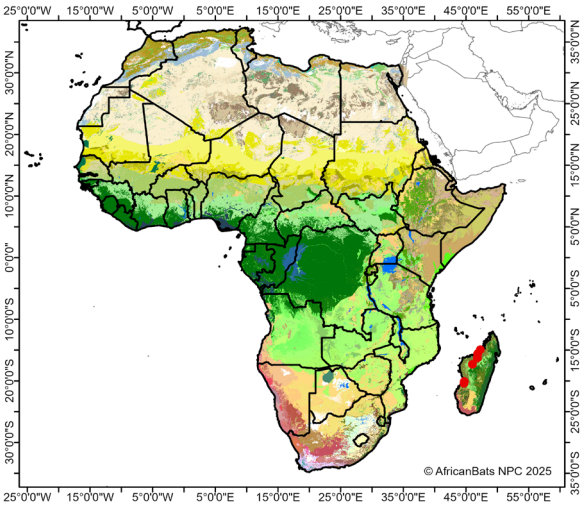

Figure 288. Distribution of *Scotophilus marovaza*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Scotophilus nigrita (Schreber, 1774)

*1774. *Vespertilio Nigrita* Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, 1 (8): pl 58 + 1 (9): 171. Publication date: 1774. Type locality: Senegal: "Senegal". [Goto Description]. - Etymology: Lanza *et al.* (2015: 493) state: "From the scientific Latin *nigritus*, diminutive of the masculin Latin adjective *niger* (nìger) 'black', (masculine *nigrìtus*; feminin *nigrita*, neuter *nigrìtum*), referring to the blackish uropatagial colour of the type specimen: 'Die Schwanzhaut ist schwärzlich' (Schreber 1774). Note that Schreber erroneously used a feminine adjective with the masculine gender noun *Vespertilio*, unless he did not consider *nigrita* as a noun in apposition (noun seemingly non-existent even in the post-classic Latin; instead, there exists in classic Latin the noun *nigritia*, meaning 'black or blackish colour').
.

1855. *N[ycticejus] nigrita:* Giebel, Die Säugethiere, 928. (Name Combination).

1875. *Scotophilus gigas* Dobson, Ann. Mag. nat. Hist., ser 4, 16 (92): 122. Publication date: 1 August 1875. Type locality: Nigeria: Western region: Lagos [06 27 N 03 23 E]. [Goto Description]. Holotype: NHMUK 1872.10.24.5: ad ♀, skull and alcoholic.

1965. *Scotophilus alvenslebeni* Dalquest, J. Mamm., 46 (2): 254, 258. Publication date: May 1965. Type locality: Mozambique: S bank Save River: Zinave National Park [ca. 21 26 S 33 52 E]. [Goto Description]. Holotype: KU 105222: ad ♂, skin and skull. Collected by: Prof. Dr. Walter Woelber Dalquest; collection date: 9 October 1963; original number: MWUC 18767. See Jones and Genoways (1969: 132). - Comments: Type locality originally as "S Bank Save River, bei Zinave, 212 km SSW Beira": see Kock (1969a: 204). - Etymology: In honour of Baron Werner von Alvensleben, in partial recognition of his labors in behalf of our work in Mozambique (see Dalquest, 1965: 258).

2016. *Scotophilus nigritta:* Mikula, Morelli, Lučan, Jones and Tryjanowski, Mammal Rev., Suppl Data. Publication date: 20 January 2016. (Lapsus).

? *Scotophilus nigrita alvenslebeni:* (Name Combination).

? *Scotophilus nigrita nigrita:* (Name Combination).

? *Scotophilus nigrita:* - Comments: . (Name Combination, Current Combination).

TAXONOMY:

For a review of this species see Robbins (1978a). The identity of this species is clear and *nigrita* is the senior synonym of *gigas* (although the latter name still persists in recent literature, e.g., Ospina-Garcés *et al.* (2018: 1615)). Most specimens called *nigrita* prior to 1978 should be called *dinganii* (see Robbins, 1978a: 212 - 213).

Based on cytochrome *b*, Vallo *et al.* (2014: 225) found *N. nigrita* to be paraphyletic with respect to the other continental African species *S. colias, S. dinganii, S. nigritellus* and *S. viridis*. They also found that cytochrome *b* from West and Southern African *S. nigrita* specimens differed between 7.6 and 8.1 %, which suggest that *S. nigrita* might differ on specific level from *alvenslebeni*. However, they (p. 229) find it too preliminary to officialize this split, and suggest further, more extensive genetic sampling and morphological analyses.

See Lanza *et al.* (2015: 493)'s remark on the taxon's suffix in the synonymy list above.

COMMON NAMES:

Afrikaans: Groot geel dakvlermuis. Castilian (Spain): Murciélago Amarillo. Chinese: 非洲大黄蝠. Czech: mračník olbřímí. English: Giant House Bat, Giant Brown House Bat, Brown House Bat, Great Brown House Bat, Giant Yellow House Bat, Schreber's Yellow Bat, Geat Brown Bat, Giant Brown Bat, Senegal Bat, Schreber's Brown Bat. French: Grand scotophile africain. German: Riesen-Hausfledermaus, Hundkopf-Schwirrfledermaus. Italian: Scotòfilo scùro. Portuguese: Morcego gigante amarelo das casas.

ETYMOLOGY OF COMMON NAME:

Most of the colloquial names refer to its colour (yellow) and being a House bat. The colloquial name Schreber's Yellow bat refers to J. von Schreber, who originally described the species (Taylor, 2005).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Cotterill, 2008d; IUCN, 2009; Monadjem and Cotterill, 2017a).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem and Cotterill, 2017a). 2008: LC ver 3.1 (2001) (Cotterill, 2008d; IUCN, 2009). 2004: NT ver 3.1 (2001) (Cotterill, 2004d; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: NT D2 ver 3.1 (2001) (Fernsby *et al.*, 2016). 2004: considered a vagrant not assessed, not recorded in SA (Friedmann and Daly, 2004).

MAJOR THREATS:

This species is threatened by the conversion of its habitat to agricultural use in parts of its range (Cotterill, 2008d; IUCN, 2009; Monadjem and Cotterill, 2017a).

CONSERVATION ACTIONS:

Cotterill (2008d) [in IUCN (2009)] and Monadjem and Cotterill (2017a) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Management of protected areas is necessary.

GENERAL DISTRIBUTION:

Scotophilus nigrita has been recorded as scattered records from West, East, and south-east Africa. It has been reported from Senegal, Côte d'Ivoire, Ghana, Togo, Nigeria and Cameroon in West Africa, from central Sudan, and from western Democratic Republic of the Congo, western Kenya and Tanzania, south to

Mozambique, Malawi, eastern Zimbabwe and north-eastern South Africa.

Native: Benin (Benda *et al.*, 2023a: 27); Cameroon (Bakwo Fils *et al.*, 2012: 55); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 575); Côte d'Ivoire; Ghana; Kenya; Malawi (Ansell and Dowsett, 1988: 37; Monadjem *et al.*, 2010d: 575); Mozambique (Dalquest, 1965; Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 575); Nigeria; Senegal; South Africa (Monadjem *et al.*, 2010d: 575); Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 63); Zimbabwe (Cotterill, 1996a; Monadjem *et al.*, 2010d: 575).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to O'Shea and Vaughan (1980), Amador *et al.* (2019), Mendes (2011)] mention a wing loading value of 5.2 Pa, aspect ratio 6.7 for a wingspan of 58 cm and a wing area of 507 cm^2 and a body mass of 27 g.

ECHOLOCATION:
Thiagavel *et al.* (2017: Suppl.) mention a peak frequency of 32.85 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 294 minutes, and a digestibility rate of about 66.8 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the African goshawk (*Accipiter tachiro* (Daudin, 1800)) preying upon *S. nigrita*. They also mention this bat to be a possible prey of the Lanner falcon (*Falco biarmicus* Temminck, 1825), Peregrine falcon (*Falco peregrinus* Tunstall, 1771), and Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850).

POPULATION:
Structure and Density
It appears to be a rare, or rarely recorded, species (Cotterill, 2008d; IUCN, 2009; Monadjem and Cotterill, 2017a).

Trend
2016: Decreasing (Monadjem and Cotterill, 2017a). 2008: Decreasing (Cotterill, 2008d; IUCN, 2009).

PARASITES:
PROTOZOA
Baleela *et al.* (2020: 360) reported *Leishmania donovani* from a *S. nigrita* specimen from Sudan.

ARACHNIDA
Spinturnicidae
Orlova *et al.* (2024: 151) reported this species (as *Scotophilus gigas)* as host for *Spinturnix scotophili* Zumpt and Till, 1954.

HEMIPTERA
Cimicidae
Kock *et al.* (1998b: 236) reported the presence of *Cacodmus villosus* (Stål, 1855), explicitly confirming the bat's identity.

VIRUSES:
Nairoviridae (formerly included in Bunyaviridae)
Nairovirus
Qalyub virus was reported by Luis *et al.* (2013: suppl.).

Coronaviridae - Coronaviruses
SARS-CoV
In Nigeria during June 2008, Quan *et al.* (2010) screened the gastrointestinal tissue for the presence of coronaviruses by PCRs, none tested positive.

Flaviviridae
Flavivirus
The presence of Dakar bat virus was mentioned by Luis *et al.* (2013: Suppl.), Blitvich and Firth (2017: 3), Willoughby *et al.* (2017: Suppl.).

Rhabdoviridae
Lyssavirus - Rabies related viruses
In Nigeria during June 2008, Quan *et al.* (2010) did not detect any lyssavirus-specific antigens from the brains by use of direct fluorescent antibody testing.

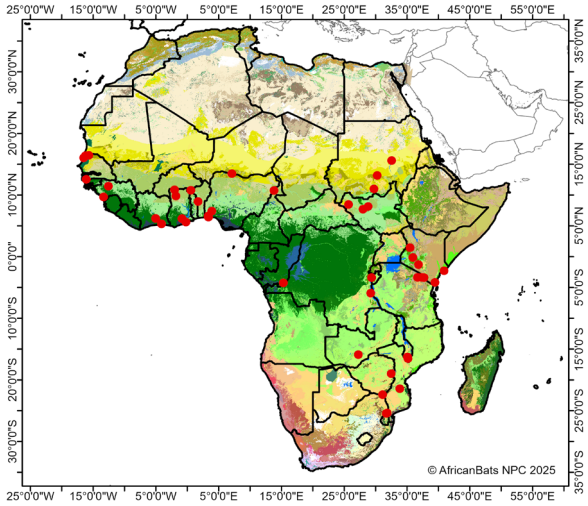

Figure 289. Distribution of *Scotophilus nigrita*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Burundi, Cameroon, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Guinea, Kenya, Malawi, Mozambique, Niger, Nigeria, Senegal, South Africa, South Sudan, Sudan, Tanzania, Togo, Zambia, Zimbabwe.

Scotophilus nigritellus de Winton, 1899

1899. *Scotophilus nigritellus* de Winton, Ann. Mag. nat. Hist., ser 7, 4 (23): 355. Publication date: 1 November 1899. Type locality: Ghana: Gambaga [10 32 N 00 26 W]. [Goto Description]. Holotype: NHMUK 1899.6.15.9: ad ♂. Collected by: Captain W. Giffard; collection date: 9 January 1899.
2014. *Scotophilus cf. nigritellus/sp. n.* Vallo, Benda, Červený and Koubek, Mammalia, 79 (2): 227. Publication date: 19 June 2014. (Name Combination).
? *Scotophilus leucogaster nigritellus:*
? *Scotophilus viridis nigritellus:* (Name Combination).

TAXONOMY:
This small sized *Scotophilus* has been included in *leucogaster* (Robbins *et al.*, 1985) or *viridis*, but see Vallo and Van Cakenberghe (2017) and Demos *et al.* (2018)

Vallo *et al.* (2011a: 45) showed that their cytochrome *b* analyses indicated that *S. viridis* contains two paraphyletic lineages, differing by about 12 %. They indicated that the greenish-yellow specimens from West Africa could be reliably identified with *S. nigritellus*. mtDNA analyses performed by Trujillo *et al.* (2009: 553) confirm that *S. viridis* is distinct from *S. nigritellus*, as suggested by Grubb *et al.* (1998).

Vallo *et al.* (2012: 5), who analyses the cytochrome *b* gene of West African "*S. nigritellus*" specimens, found that two paraphyletic lineages were present (agreeing with the belly colour of the specimens), with a genetic divergence ranging between 12.3 and 13.5 %. The white bellied lineage differed only 2.6 to 2.8 % from *S. leucogaster*. Their analysis of the *zfy* gene (zinc finger protein on the Y-chromosome) indicated that the white bellied lineage differed by 10 substitutions from the yellow bellied lineage, and that the white bellied lineage furthermore differed by 9 substitutions from *S. leucogaster*. Vallo *et al.* (2012: 10) concluded that the yellow bellied form agrees with the form *S. nigritellus* described by de Winton in 1899 but were unable to provide a name for the white bellied form.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Scotophilus nigritellus is widespread in West Africa, ranging from Senegal and Gambia to northern Cameroon and the Central African Republic.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2015a: 626); Cameroon; Central African Republic; Chad; Côte d'Ivoire; Gambia; Ghana; Guinea-Bissau (Peters, 1870; Seabra, 1900a; Rainho and Ranco, 2001: 72); Mali; Niger; Nigeria; Senegal; Togo.

ECHOLOCATION:
In Benin, the bat's call was categorized as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype by Roemer *et al.* (2021: Suppl.) [as "*Scotophilus viridis*"].

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Mali, Niger, Nigeria, Senegal, Sierra Leone, The Gambia, Togo, Uganda.

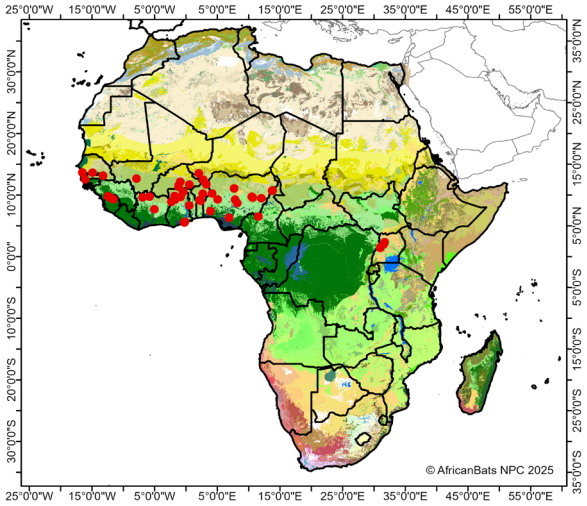

Figure 290. Distribution of *Scotophilus nigritellus*.

Scotophilus nucella Robbins, 1983

*1983. *Scotophilus nucella* Robbins, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., 273: 19. Type locality: Ghana: Eastern region: Nkawkaw, 1 mi N [06 33 N 00 44 W]. Holotype: USNM 412141: ad ♂, skin and skull. Collected by: Bruce Joliffe Hayward; collection date: 5 August 1967. - Etymology: *nucella* is a diminutive of *nux*. Following the rules for construction of a diminutive, the latin root of *nux* is used (=*nuc*). Although *Scotophilus* is masculine in gener, formation of a diminutive of a noun in apposition (*nux*) must retain the same gender as its root (*nuc*) which is feminine. The only ending then possible are *-ula* or *-ella*. (Current Combination).

TAXONOMY:
Included in *leucogaster* by Koopman (1993a: 227), Grubb *et al.* (1998: 91).

Vallo *et al.* (2016: 302) showed that cytochrome *b* sequences separated *S. nucella* 7.8 - 9.4 % from *S. nux* and puts both in a sister position. This was corroborated by the nuclear zinc finger protein gene on the Y-chromosome. Both species were separated from one another at the Pliocene-Pleistocene transition, some 2.5 MYA.

COMMON NAMES:
Czech: mračník guinejský. English: Lesser Nut-coloured House Bat, Rainforest House Bat, Robbins's House Bat, Robbin's House Bat, Nucella House Bat, Little Nut-coloured House Bat, Robbins's Yellow Bat. French: Scotophile de Robbins, Scotophile des hauteurs. German: Robbins Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status. The range is very poorly known, and it is unclear if the species is declining (Fahr, 2008o; IUCN, 2009; Fahr, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Fahr, 2019b). 2008: DD ver 3.1 (2001) (Fahr, 2008o; IUCN, 2009). 2004: VU A2a; B2ab(iii) ver 3.1 (2001) (Fahr, 2004b; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Fahr, 2008o; IUCN, 2009; Fahr, 2019b).

CONSERVATION ACTIONS:
Fahr (2008o) [in IUCN (2009)] and Fahr (2019b) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed.

GENERAL DISTRIBUTION:
Scotophilus nucella has only been recorded from southeastern Côte d'Ivoire, southern Ghana, and western Uganda close to the border with the Democratic Republic of the Congo, and Kambai Forest Reserve in the East Usambara Mountains of Tanzania (Cunneyworth, 1996b). Known from the high forest vegetation zone in Ghana (Decher and Fahr, 2007: 20) and Uganda, but it may occur in the high forest areas of West, Central and East Africa (Robbins, 1983a).

Native: Côte d'Ivoire; Ghana (Decher and Fahr, 2007: 20); Tanzania Cunneyworth, 1996b); Uganda.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 152 minutes, and a digestibility rate of about 73.0 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species. It is suspected to be declining as it appears that the species has not been collected since 1984 (Fahr, 2008o; IUCN, 2009; Fahr, 2019b).

Trend
2018: Unknown (Fahr, 2019b). 2008: Unknown (Fahr, 2008o; IUCN, 2009).

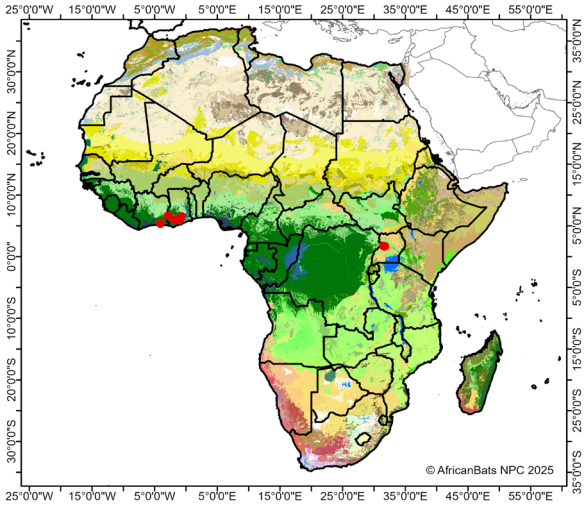

Figure 291. Distribution of *Scotophilus nucella*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Tanzania, Uganda.

Scotophilus nux Thomas, 1904

*1904. *Scotophilus nigrita nux* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (75): 208. Publication date: 1 March 1904. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1903.2.4.5: ad ♂. Collected by: George Latimer Bates Esq. - Etymology: From the Latin "*nux*" meaning nut.
1915. *Scotophilus nux:* Thomas, Ann. Mag. nat. Hist., ser 8, 16 (96): 468. Publication date: 1 December 1915. (Name Combination, Current Combination).
1938. *[Pachyotus] nux:* Frechkop, Exploration du Parc National Albert, 53. (Name Combination).
1938. *Pachyotus mux:* Frechkop, Exploration du Parc National Albert, 59. (Lapsus).
1938. *Pachyotus nigrita mux:* Frechkop, Exploration du Parc National Albert, 59. - Comments: Mentioned in the synonymy of *Pachyotus mux* (sic). (Lapsus).
1938. *Scotophilus nigrita mux:* Frechkop, Exploration du Parc National Albert, 59. - Comments: Mentioned in the synonymy of *Pachyotus mux* (sic). (Lapsus).
? *Scotophilus dinganii nux:* (Name Combination).
? *Scotophilus leucogaster nux:* (Name Combination).

TAXONOMY:
S. nux has been most often recognized as a subspecies of *nigrita*, when *nigrita* was used for the species now called *dinganii*; see Allen (1939a), Rosevear (1965), and Hayman and Hill (1971: 50). Koopman (1965: 4 - 5) listed it as a subspecies of *leucogaster*. Grubb *et al.* (1998: 90) include *nux* as a subspecies of *dinganii*.

Vallo *et al.* (2016: 306) found that the cyt-*b* of specimens from Guinea differs 3.4 - 4.5 % from that of conspecifics from other parts of Africa and therefore these specimens might probably be assigned to a separate subspecies.

COMMON NAMES:
Chinese: 喀麦隆黄蝠. Czech: mračník ořechový. English: Nut-coloured House Bat, Dark House Bat, Nut-colored Yellow Bat, Nux Yellow House Bat. French: Scotophile noisette, Scotophile nux. German: Nußfarbene Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008p; IUCN, 2009; Monadjem and Fahr, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Fahr, 2017c). 2008: LC ver 3.1 (2001) (Fahr, 2008p; IUCN, 2009). 2004: LC ver 3.1 (2001) (Fahr, 2004q; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species. Some populations may be impacted by general deforestation, however, this needs to be confirmed (Fahr, 2008p; IUCN, 2009; Monadjem and Fahr, 2017c).

CONSERVATION ACTIONS:
Fahr (2008p) [in IUCN (2009)] and Monadjem and Fahr (2017c) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas.

GENERAL DISTRIBUTION:
Scotophilus nux has been patchily recorded from West Africa (Sierra Leone, Guinea, Liberia Côte d'Ivoire, Ghana and Nigeria), Central Africa (Cameroon and Democratic Republic of the Congo) and East Africa (Uganda and Kenya), and is believed to likely occur more widely than is currently known. It is possibly present in Equatorial Guinea; however, this needs to be confirmed.

Native: Cameroon; Congo (Bates *et al.*, 2013: 337); Congo (The Democratic Republic of the); Côte d'Ivoire; Ghana (Decher and Fahr, 2007: 21); Guinea (Fahr *et al.*, 2006a: 74; Decher *et al.*, 2016: 274); Kenya; Liberia (Fahr, 2007a: 104); Nigeria; Rwanda; Sierra Leone; Uganda.

Presence uncertain: Equatorial Guinea.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
From western Uganda, Monadjem *et al.* (2011: 30) reported the following data: Fa: 55.6 mm, mass: 30 g, wing loading: 6.4 N/m^2, aspect ratio: 5.5.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Monadjem *et al.* (2011)] mention a wing loading value of 13.7 Pa, aspect ratio 5.5 for a wingspan of 34 cm and a wing area of 215 cm^2 and a body mass of 30 g.

ECHOLOCATION:
From western Uganda, Monadjem *et al.* (2011: 32) reported the following values: F_{min}: 40.71 kHz, F_{max}: 54.05 kHz, F_{char}: 43.01 kHz, F_{knee}: 45.07 kHz, and duration: 2.0 ms.

For a *S.* cf. *nux* specimen from Gabon, Peereboom and van Lieshout (2015: 6) mention F_{min}: 38.49 ± 0.83 (37.82 - 40.04) kHz, F_{max}: 59.45 ± 7.23 (52.54 - 75.79) kHz, $F_{min\ dom}$: 44.54 ± 1.91 (41.11 - 47.37) kHz, duration: 1.87 ± 0.30 (1.60 - 2.50) ms, interpulse interval: 57.08 ± 33.44 (16.20 - 108.60) ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 23 calls of 1 bat: F_{peak}: 43.7 ± 1.0 (42.7 - 44.9) kHz, F_{min}: 41.2 ± 2.8 (38.1 - 44.1) kHz, F_{max}: 75.1 ± 5.8 (71.5 - 83.8) kHz, duration: 2.0 ± 0.2 (1.7 - 2.2) ms.

Thiagavel *et al.* (2017: Suppl.) mention a peak frequency of 26.09 kHz.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 292. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1903.2.4.5, holotype of *Scotophilus nigrita nux* Thomas, 1904.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Monadjem *et al.* (2016y: 371) collected two specimens over water in a disturbed forest habitat on the Liberian side of Mount Nimba at 520 m.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 156 minutes, and a digestibility rate of about 72.7 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Fahr, 2008p; IUCN, 2009; Monadjem and Fahr, 2017c).

Trend
2016: Unknown (Monadjem and Fahr, 2017c).
2008: Unknown (Fahr, 2008p; IUCN, 2009).

VIRUSES:
Coronaviridae
Anthony *et al.* (2017b: Suppl.) mention the alphacoronavirus Predict_CoV_33.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Guinea, Kenya, Liberia, Nigeria, Sierra Leone, Uganda.

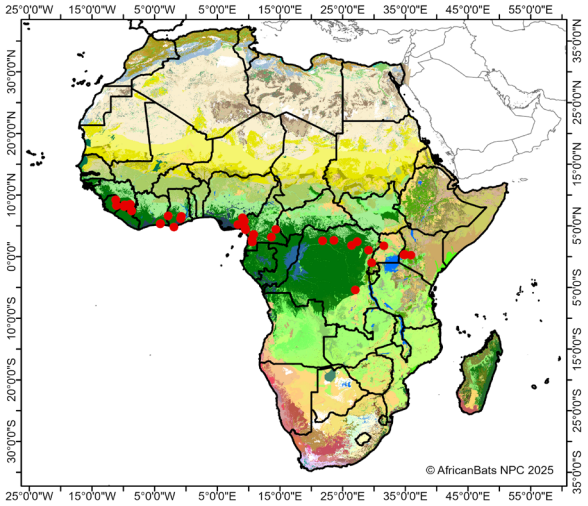

Figure 293. Distribution of *Scotophilus nux*.

Scotophilus robustus A. Milne-Edwards, 1881

*1881. *Scotophilus robustus* A. Milne-Edwards, C. R. séances Acad. Sci., Paris, 91: 1035. Publication date: 1881. Type locality: Madagascar: "Madagascar". [Goto Description]. Holotype: MNHN 218: ♀. Holotype: MNHN ZM-MO-1997-1833a: ad ♀, alcoholic (skull not removed). Collected by: Léon Humblot. Number 218 in Rode (1941: 248). See also Peterson *et al.* (1995: 112), Goodman *et al.* (2005b: 873). Paratype: MNHN ZM-MO-1997-1833b: ad ♀, alcoholic (skull not removed). Collected by: Léon Humblot. Number 218a in Rode (1941: 248). Goodman *et al.* (2005b: 873) additionally mention that the jar with the type specimen contains two specimens (1997-1883a and 1997-1883b), but that not can be determined which of the two is the holotype. - Comments: Goodman *et al.* (2005b: 873) mention "entre Foulpointe et le lac d'Alaoutre" in the central portion of het eastern humid forest as type locality. Goodman *et al.* (2005b: 873) also mention that the jar with the type specimen contains two specimens (1997.1883a and 1997.1883b), but that not can be determined which of the two is the holotype. (Current Combination).
? *Scotophilus nigrita robustus:* (Name Combination).

TAXONOMY:
Recognized as a subspecies of *nigrita* (when *nigrita* was used for the species now called *dinganii*) by Hayman and Hill (1971: 50). However, Robbins *et al.* (1985) considered it specifically distinct from *dinganii* and *borbonicus*.

COMMON NAMES:
Czech: mračník statný. English: Malagasy Large House Bat, Robust House Bat, Robust Yellow Bat. French: Scotophile de Madagascar, Chauve-souris domestique malgache, Grande scotophile de Madagascar, Scotophile robuste. German: Madagaskar-Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) as although the species is not thought to be abundant and has not often been recorded, the available information indicates that the species is widespread across Madagascar occurring in a wide variety of habitats, including in human habitations. While the threats affecting the species are imperfectly known, there is no reason to expect that the species is currently undergoing a decline that would warrant listing in a threatened category (Andriafidison *et al.*, 2008k; IUCN, 2009; Monadjem *et al.*, 2017bx).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017bx). 2008: LC ver 3.1 (2001) (Andriafidison *et al.*, 2008k; IUCN, 2009). 1996: LR/nt ver 2.3 (1994).

Regional
None known.

MAJOR THREATS:
Andriafidison *et al.* (2008k) [in IUCN (2009)] and Monadjem *et al.* (2017bx) report that the major threats to this species are not well known. This species uses forest habitat, but it also occurs outside of forested areas. There is one reported occurrence of this species being hunted by food by local people, but there is no evidence that this constitutes a major threat (Goodman *et al.*, 2008d).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008k) [in IUCN (2009)] and Monadjem *et al.* (2017bx) report that this species

is known from a number of protected areas across Madagascar and does not appear to require specific conservation measures but, like many other Malagasy bats that are not considered to be threatened, there is a lack of basic natural history data.

GENERAL DISTRIBUTION:
Scotophilus robustus is endemic to the island of Madagascar, where it is broadly distributed from the coast to the highland plateau up to 1,400 m in Tsinjoarivo (Goodman *et al.*, 2005a). This species is rarely recorded, but as more surveys are conducted it is likely that this species will be found to have a wider distribution.

Native: Madagascar (Russ *et al.*, 2001).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
S. robustus is the largest vespertilionid bat occurring on Madagascar (Garbutt, 2022: 103).

DETAILED MORPHOLOGY:
Baculum
This bone has a flat triangular structure, with a distinct indentation to the proximal margin (Rakotondramanana and Goodman, 2017: 64); length: 2.02 ± 0.048 (.94 - 2.09) mm, width: 1.18 ± 0.096 (0.98 - 1.29) mm.

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls which were characterized by a broadband steep FM followed by a QCF calls at low duty cycle. The fundamental was always the most intense with peak energy at about 38.1 kHz.

Hending *et al.* (2023: 372) mention the following values: F_{peak}: 38.6 ± 3.0 kHz, duration: 12 ± 5 ms, and interpulse interva: 115 ± 40 ms.

HABITAT:
Ravelomanantsoa *et al.* (2019: 110) indicated that this large species occurs in wet and dry deciduous forests. It is known for inhabiting human constructions. They also caught it near the base of a *Ficus cocculifolia* and near a *Mangifera indica* plantation.

ROOST:
Roosts are found around habitation and in natural sites (Garbutt, 2022: 103).

DIET:
The following prey volume percentages were reported from the faeces of 2 *S. robustus* specimens by Rakotondramanana *et al.* (2015: 74): Coleoptera: 14.5 ± 20.51; Lepidoptera: 50.0 ± 70.71; Homoptera: 8.0 ± 11.31; Blattoidea: 27.5 ± 38.90. Expressed as frequency percentages, the values are: Coleoptera: 50.0 ± 70.71; Lepidoptera: 50.0 ± 70.71; Homoptera: 60.0 ± 42.43; Blattoidea: 50.0 ± 70.71.

Rasoanoro *et al.* (2015: 63) found that Coleoptera formed about 68 % of the diet, whereas sampling in the feeding area revealed that only 3 % of the available prey consisted of Coleoptera. They indicated that - at least in the hot season - *S. robustus* is a Coleopteran specialist. The droppings of three bats contained the following volume percentages of prey types: Aranea: 5.7 ± 0.33, Coleoptera: 68.0 ± 10.08, Diptera: 1.9 ± 1.88, Homoptera: 2.1 ± 2.06, Hymenoptera: 8.7 ± 3.87, Lepidoptera: 9.1 ± 4.50, and Orthoptera: 4.3 ± 2.15.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 145 minutes, and a digestibility rate of about 73.4 %.

PREDATORS:
Razakaratrimo *et al.* (2019: 114) mention the bat hawk (*Macheiramphus alcinus anderssoni* (Gurney, 1866)).

POPULATION:
Structure and Density
A number of bat surveys have failed to locate this species (Goodman *et al.*, 2005b; Robinson *et al.*, 2006; Rakotoarivelo and Randrianandrianina, 2007) and it appears not to be locally abundant (Andriafidison *et al.*, 2008k; IUCN, 2009; Monadjem *et al.*, 2017bx).

Trend
2016: Unknown (Monadjem *et al.*, 2017bx).
2008: Unknown (Andriafidison *et al.*, 2008k; IUCN, 2009).

PARASITES:
HAEMOSPORIDA
Rasoanoro *et al.* (2021: 4) report the presence of a new, unidentified *Polychromophilus* in a single representative of this bat species.

DIPTERA
Nycteribiidae
Duron *et al.* (2014: 2108) refer to a *Basilia* nov. sp. collected from this bat species.

Wilkinson *et al.* (2016) reported the presence of *Basilia (Paracyclopodia)* sp., which was carrying *Bartonella* bacteria, as well as Enterobacteriales. Ramasindrazana *et al.* (2017: Suppl.) refer to the bat fly as "*Basalia* sp. 1". They also mention (p. 6) a *Basilia (Paracyclopodia) madagascarensis*, which was collected from a "*Scotophilus borbonicus*" from Nosy Be, but this bat most

probably should be assigned to *S. robustus*. Szentiványi *et al.* (2019a: Suppl.) furthermore indicated that a new bat fly (Basilia nov. spec.) found on a *S. robustus* bats, was parasitized by an *Arsenophonus* sp. Bacteria.

VIRUSES:
Flaviviridae
Flavivirus
Dakar Bat Virus (DBV)
Isolated from salivary glands (Coulanges *et al.*, 1974; Rousset and Andrianarivelo, 2003).

UTILISATION:
See Goodman *et al.* (2008d).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

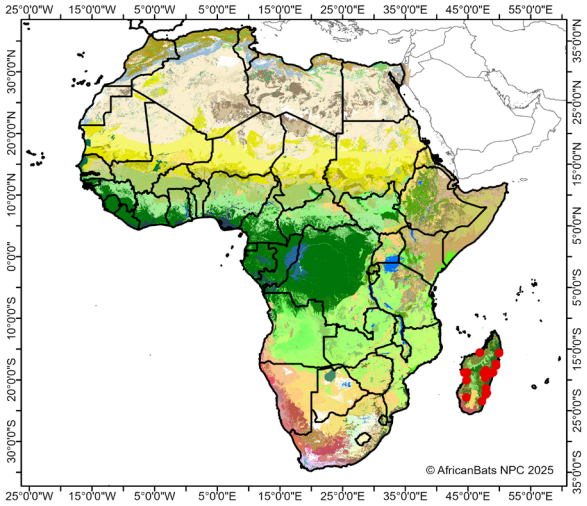

Figure 294. Distribution of *Scotophilus robustus*.

Scotophilus tandrefana Goodman, Jenkins and Ratrimomanarivo, 2005

*2005. *Scotophilus tandrefana* Goodman, Jenkins and Ratrimomanarivo, Zoosystema, 27 (4): 867, 875, figs 3 - 5. Type locality: Madagascar: Mahajanga province: just outside the Parc national de Bemaraha: 1.8 km SE Bekopake and 0.6 km NE Andadoany [19 08 S 44 49 E, 50 m]. Holotype: UADBA 46923: ad ♂, skull and alcoholic. Collected by: Richard K.B. Jenkins and Fania H. Ratrimomanarivo; collection date: 27 July 2003; original number: RBJ 161. - Etymology: From the Malagasy meaning "from the west" (see Goodman *et al.*, 2005b: 875). (Current Combination).

TAXONOMY:
Goodman *et al.* (2005b) described this species based on three specimens which were collected in 1868, 1869 and 2003 (the latter being designated as the holotype). One of these (the specimen collected in 1869) was later reassessed as *S. marovaza* (Goodman *et al.*, 2006b).

Trujillo *et al.* (2009: 553) indicate that inferred phylogenies do not support the separation of *S. tandrefana* and *S. marovaza* as the cytochrome *b* phylogeny only reveals a genetic divergence of 0.6 %, a level indicative of within-species divergence. This might indicate that cytochrome *b* is not representative or that the separation between the two taxa occurred too recent to be already reflected in that gene.

COMMON NAMES:
Czech: mračník madagaskarský. English: Malagasy Western house bat, Western Yellow Bat, Malagasy Yellow Bat, Western House Bat. French: Scotophile d'Andadoany, Scotophile de l'ouest de Madagascar. German: Westliche Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) as the species is known from only two specimens (one collected as recently as 2003) and there is no information on its population status or threats (Jenkins *et al.*, 2008c; IUCN, 2009; Jenkins *et al.*, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jenkins *et al.*, 2019b).
2008: DD ver 3.1 (2001) (Jenkins *et al.*, 2008c; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The major threats to this species are not known (Jenkins *et al.*, 2008c; IUCN, 2009; Jenkins *et al.*, 2019b).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008c) [in IUCN (2009)] and Jenkins *et al.* (2019b) report that this species has been recorded from near Parc National Tsingy de Bemaraha and the managed forest of Kirindy CFPF (Goodman *et al.*, 2005a), but evidence is lacking that it actually roosts or feeds in these forests.

GENERAL DISTRIBUTION:
Scotophilus tandrefana is endemic to Madagascar where it is known from two localities below 100 m: near Parc National Tsingy de Bemaraha in the west and Sarodrano in the south (Goodman *et al.*, 2005a). Photographs and

forearm measurements of an individual from Kirindy (CFPF) forest in the west represents the third known locality for this species (Goodman *et al.*, 2005a).

Native: Madagascar.

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls from a single individual in a flight cage, which emitted broadband FM/QCF calls at low duty cycle with frequency containing most energy at about 48.2 kHz.

HABITAT:
This species occurs In dry forests and forest edges including grassland (Garbutt, 2022: 103).

POPULATION:
Structure and Density
There are no data on the population of this species and all existing information is based on two specimens that were collected in 1868 and 2003 (Goodman *et al.*, 2005b; 2006b).

Trend
2018: Unknown (Jenkins *et al.*, 2019b). 2008: Unknown (Jenkins *et al.*, 2008c; IUCN, 2009).

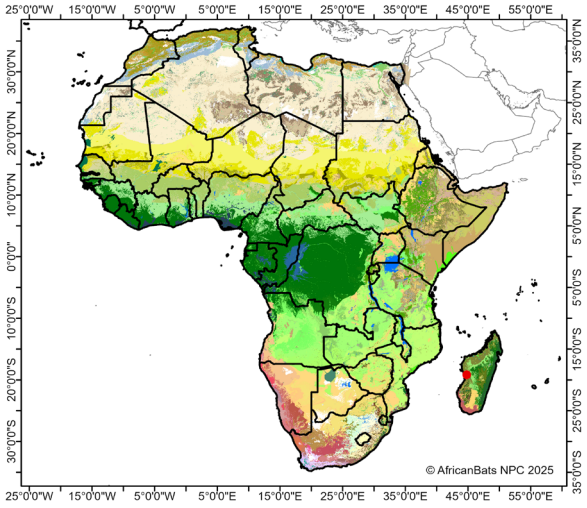

Figure 295. Distribution of *Scotophilus tandrefana*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Madagascar.

Scotophilus trujilloi Brooks and Bickham, 2014

*2014. *Scotophilus trujilloi* Brooks and Bickham, Occ. Pap. Mus. Texas Tech Univ., 326: 1, 16, fig 6. Publication date: 26 Jun 2014. Type locality: Kenya: Coastal province: Kwale district: Moana Marine Station, 1 km S, 2 km E Ukunda [04 18 S 39 35 E]. Holotype: CM 98038: ad ♂, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 18 October 1985; original number: 7086. Muscle tissue sample TK 33263. Paratype: CM 98040: ad ♀, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 18 October 1985; original number: 7087. Tissue sample TK 33266. Paratype: CM 98041: ad ♀, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 18 October 1985; original number: 7090. - Etymology: In honour of Dr. Robert Trujillo (b. 1975), who's ground-breaking doctoral dissertation on the molecular systematics of *Scotophilus* paved the way for the description of the four cryptic species described in this paper (Trujillo 2005; Trujillo *et al.* 2009) (see Brooks and Bickham (2014 18).

TAXONOMY:
Brooks and Bickham (2014) described four new species in the genus *Scotophilus*. However, they did not compare them with a number of already described taxa such as *colias* Thomas, 1904 or *flavigaster* Heuglin, 1861, which make the validity of (some of) these names doubtful.

The analyses performed by Demos *et al.* (2018: 2) confirmed the validity of the taxon, but these authors also indicate that they cannot vouch for the validity of the name with respect to older taxa that would have nomenclatural priority. Benda *et al.* (2025: 104) consider this name tentatively as valid, at least for the series of NMW and NMP specimens from Kenya.

Musila *et al.* (2018a: 29) indicate that *trujilloi* should be used for the Kenyan animals formerly included in *S. viridis*.

COMMON NAMES:
Chinese: 特鲁黄蝠. English: Trujillo's House Bat. German: Trujillos Hausfledermaus.

CONSERVATION STATUS:
Global Justification
Assessed as Least Concerned (LC ver 3.1 (2001) as this species is from five samples from coastal Kenya (Brooks and Bickham, 2014). Further research is required to verify the taxonomy of this taxon (Monadjem, 2017d).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem, 2017d).

Regional
None known.

MAJOR THREATS:
The major threat is persecution of roosting sites (Monadjem, 2017d).

CONSERVATION ACTIONS:
Monadjem (2017d) reported that this species is known to occur in the Shimba Hills National Park and may occur in the other protected areas in Kenya.

ECHOLOCATION:
Musila *et al.* (2018c: 43) [referring to Monadjem *et al.* (2010d)] mention a shallow frequency modulated call, with a peak frequency of 40 kHz and a bandwidth of 25 kHz, but Monadjem *et al.* (2010d: 528) had these parameters assigned to *S. viridis*.

POPULATION:
There is no information about population size and trend (Monadjem, 2017d).

Trend:- 2016: Unknown (Monadjem, 2017d).

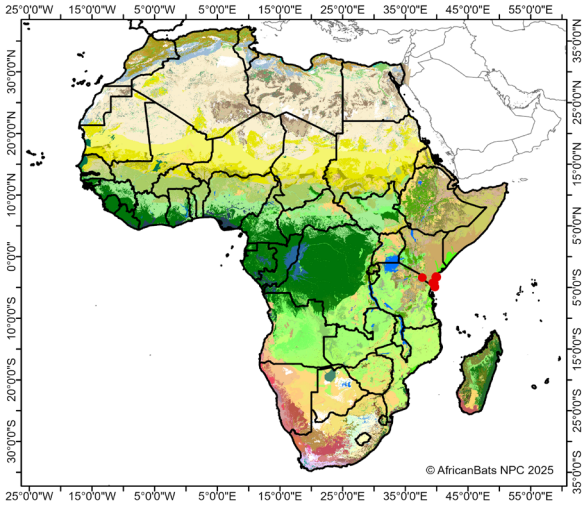

Figure 296. Distribution of *Scotophilus trujilloi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Tanzania.

Scotophilus viridis (Peters, 1852)

*1852. *Nycticejus viridis* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 67, pl 17, fig 2, a-e. Publication date: 1852. Type locality: Mozambique: Mozambique Island [15 S 40 42 E]. [Goto Description]. Holotype: ZMB 73610: ad ♂, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: March 1845. Formerly ZMB 526 [=An 16362]; see Turni and Kock (2008: 53). - Etymology: From the masculine Latin adjective *viridis*, meaning "green", referring to the body colour: "Die Farbe der Rückseite ist ein schönes dunkles Olivengrün, die Haare der Bauchseite sind grünlichgelb" (Peters (1852: 68) (see Lanza *et al.*, 2015: 498).

1984. *Scotophilus borbonicus viridis:* Aggundey and Schlitter, Ann. Carnegie Mus., 53 (5): 121, 138. Publication date: 19 April 1984. (Name Combination).

2018. *Scotophilus viridus:* Adams and Kwiecinski, Diversity, 10 (3) 103: 1. Publication date: 18 September 2018. (Lapsus).

2019. *Scroptophilus borbonicus:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

2019. *Scroptophilus vividis:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

? *Scotophilus cf. viridis*

? *Scotophilus leucogaster viridis:* (Name Combination).

? *Scotophilus viridis viridis:* (Name Combination).

? *Scotophilus viridis:* (Name Combination, Current Combination).

TAXONOMY:
Included in *leucogaster* by Hayman and Hill (1971: 50) but see Koopman (1975: 414 - 416) and Schlitter *et al.* (1980). Included *damarensis* but see Robbins *et al.* (1985).

Vallo *et al.* (2011a: 45) showed that their cytochrome *b* analyses indicate that *S. viridis* contained two paraphyletic lineages, differing by about 12 %. They indicated that the greenish-yellow specimens from West Africa could be reliably identified with *S. nigritellus*. mtDNA analyses performed by Trujillo *et al.* (2009: 553) confirm that *S. viridis* is distinct from *S. nigritellus*, as suggested by Grubb *et al.* (1998). They also found that *S. viridis* s.s. is not monophyletic because it is found in 2 divergent clades; specimens from Kenya group with *S. dinganii* from South Africa, and specimens of *S. viridis* from South Africa group with *S. robustus* from Madagascar.

COMMON NAMES:
Afrikaans: Klein geel dakvlermuis. Czech: mračník zelený. English: Green House Bat, Greenish Yellow Bat, Lesser Yellow House Bat. French: Petit scotophile africain, Scotophile verdâtre. German: Grünliche Hausfledermaus, Olivengrüne Schwirrfledermaus. Italian: Scotòfilo vérde. Malawian: Liputiputi, Ndemiya, Namzeze.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a

more threatened category (Griffin, 2008c; IUCN, 2009; Monadjem and Griffin, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Griffin, 2017c). 2008: LC ver 3.1 (2001) (Griffin, 2008c; IUCN, 2009). 2004: LC ver 3.1 (2001) (Griffin, 2004c; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Richards *et al.*, 2016a). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species (Griffin, 2008c; IUCN, 2009; Monadjem and Griffin, 2017c).

CONSERVATION ACTIONS:
Griffin (2008c) [in IUCN (2009)] and Monadjem and Griffin (2017c) reports that there appear to be no direct conservation measures in place. It has been recorded from the Matusadona National Park in Zimbabwe, and likely is present in several other protected areas.

GENERAL DISTRIBUTION:
Scotophilus viridis is widespread in sub-Saharan Africa, ranging from Sudan and Ethiopia southwards through much of East Africa and southeastern Africa, being reported as far south as eastern South Africa and Swaziland. For South Africa, Babiker Salata (2012: 49) found that its distribution is strongly associated with the mean temperature of the coldest quarter.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 895,732 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 575); Botswana; Eswatini (Monadjem *et al.*, 2010d: 575, Monadjem *et al.*, 2021: 5); Ethiopia; Kenya; Malawi (Ansell and Dowsett, 1988: 38; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 575); Mozambique (Monadjem *et al.*, 2010d: 575; Monadjem *et al.*, 2010c: 385 as *S.* cf. *viridis*); Namibia; South Africa (De Graaf, 1960; Monadjem *et al.*, 2010d: 575); Sudan; Tanzania (Stanley and Goodman, 2011: 45) (including the islands of Pemba and Mafia [O'Brien, 2011: 290]); Zambia (Monadjem *et al.*, 2010d: 575); Zimbabwe (Cotterill, 2004a: 262; Monadjem *et al.*, 2010d: 575).

ECHOLOCATION:
See Taylor (1999b).

Schoeman and Waddington (2011: 291) mention a F_{peak} 46.9 ± 1.1 kHz and a duration of 2.9 ± 1.2 ms for *S.* cf. *viridis* specimens from St. Lucia Wetland Park, South Africa.

From Swaziland, Monadjem *et al.* (2017c: 179) reported F_{min}: 39.8 ± 1.33 (38.5 - 41.2) kHz, F_{knee}: 42.7 ± 1.05 (41.6 - 43.7) kHz, F_c: 40.1 ± 1.31 (38.8 - 42.4) kHz and duration: 3.5 ± 1.55 (2.0 - 5.0) ms. The calls could be detected up to a distance of 15 m.

Thiagavel *et al.* (2017: Suppl.) mention a peak frequency of 40.1 kHz.

In the Kalahari Desert, Adams and Kwiecinski (2018: 4) recorded three calls with the following parameters: F_{char}: 37.5 ± 1.6 kHz, F_{max}: 70.6 ± 6.6 kHz, F_{min}: 36.7 ± 1.8 kHz, duration: 4.3 ± 0.3 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 40 kHz and duration: 10 ms.

4 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 41 kHz, F_{max}: 57 kHz, F_{char}: 43 kHz, F_{knee}: 46 kHz and duration 4 ms.

From Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 10 calls: Interpulse interval: 58.3 ± 12.0 (39.3 - 77.3) ms; F_{max}: 48.3 ± 4.8 (42.2 - 58.3) kHz; Start slope: -16.7 ± 6.7 (-13.5 - -9.7) kHz/ms; End slope: -6.4 ± 3.0 (-1.2 - -9.6) kHz/ms; Ledge duration: 0.4 ± 0.0 (0.4 - 0.5) ms.

MOLECULAR BIOLOGY:
Karyotype
See discussion in generic account.

Genetics
See Hoofer and Van Den Bussche (2003) for the results of a specimen from Tanzania.

HABITAT:
In southern Africa, the species primarily occurs in Savanna (77 %) and Coastal mosaic (13 %) habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

HABITS:
Cotterill and Giddings (1987: 175) studied the activity patterns of *S. viridis* in Zimbabwe and found that most of the females were active between 7 and 9 p.m. (when there is a peak in

insect abundance)., whereas most of the males were active between 9 and 10 p.m.

ROOST:
Monadjem *et al.* (2010b: 74) found that they roosted in *Combretum imberbe* and *Acacia nigrescens* trees in Swaziland, where they found that 4 of the 5 radio tracked individuals roosted simultaneously in the same *Combretum imberbe* on a single night, and then one individual switched roosts to a different *Combretum imberbe* for two nights.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 125 minutes, and a digestibility rate of about 74.9 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the following diurnal avian predators: Red-necked falcon (*Falco ruficollis* Daudin, 1800), Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) [although the prey might have been a *S. nigrita*]; Grey-headed bushshrike (*Malaconotus blanchoti* Stephens, 1826).

POPULATION:
Structure and Density
This is a common species (Griffin, 2008c; IUCN, 2009; Monadjem and Griffin, 2017c).

Trend
2016: Unknown (Monadjem and Griffin, 2017c).
2008: Unknown (Griffin, 2008c; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

Delayed development (van der Merwe *et al.*, 1988).

VIRUSES:
Astroviridae
Neither of the two bats from Mozambique tested by Hoarau *et al.* (2018: 2) was positive for these viruses.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested [as *S. borbonicus*] between 1986 to 1999, for antibody to SARS-CoV in sera in one individual from Limpopo Province, South Africa, which turned out to be negative.

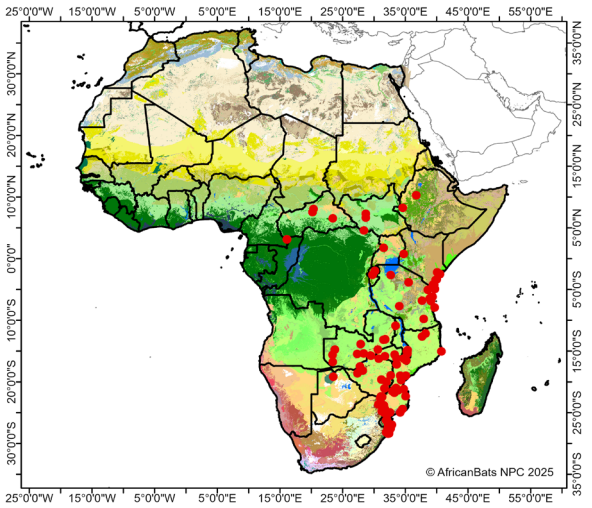

Figure 297. Distribution of *Scotophilus viridis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Central African Republic, Eswatini, Ethiopia, Kenya, Malawi, Mozambique, Rwanda, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

†Genus ***Vampyravus*** Schlosser, 1910

*1910. *Vampyravus* Schlosser, Zool. Anz., 35: xxx. (Current Combination).
1911. *Provampyrus* Schlosser, Beitr. Paläont. Geol. Öst.-Ung., 24: xxx. - Comments: This is possibly a synonym of *Vampyravus* Schlosser, 1910.

TAXONOMY:
The position of this genus is still uncertain.

Sigé (1985) [in Ravel *et al.* (2014: 696)] found some similarities between the humerus (the only known specimen of this species) and the Natalidae, but Gunnell *et al.* (2009) indicated that the morphology of this bone was more compatible with that of the Emballonuridae and Rhinopomatidae.

Currently recognized species of the genus *Vampyravus*: †***orientalis*** Schlosser, 1910.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Time frame - Late Eocene, Early Oligocene (Rupelian).

†*Vampyravus orientalis* Schlosser, 1910

*1910. *Vampyravus orientalis* Schlosser, Zool. Anz., 35: xxx. Type locality: Egypt: Fayum: Jebel Qatrani Formation. Holotype: SMNS unnumbered |TS1092|. - Comments: This is a fossil form from Egypt's Lower Oligocene, of which the type (the right humerus) is in the collection of the SMNS. (Current Combination).

1911. *Provampyrus orientalis* Schlosser, Beitr. Paläont. Geol. Öst.-Ung. (Name Combination).

TAXONOMY:
Gunnell *et al.* (2008: 5) indicate that the holotype is from an unknown horizon in the Jebel Qatrani Formation. The humerus resembles in size to *Rousettus aegyptiacus* (49 mm) and could possible represent the same taxon as *Philisis sphingis*, only known from teeth.

Bown *et al.* (1982: 624) include this taxon in the "*Phyllostomatidae*?".

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Early Oligocene (Rupelian - 32.46 - 29 mya - Brown *et al.*, 2019: Suppl.).

Subfamily Vespertilioninae J. E. Gray, 1821

*1821. *Vespertilioninae* J. E. Gray, London Med. Repos., 15: 299. Publication date: 1 April 1821. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. (Current Combination).

1821. *Vespertilionini* J. E. Gray, London Med. Repos., 15: 299. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Originally included the genera *Megadermes* [sic = *Megaderma*] É. Geoffroy, 1810; *Rhynolophus* [sic = *Rhinolophus*] Lacépède, 1799; *Nycterus* [sic = *Nycteris*] É. Geoffroy and G. Cuvier, 1795; *Rhynopoma* [sic = *Rhinopoma*] É. Geoffroy, 1818; *Thaphosores* [sic = *Taphozous*] É. Geoffroy, 1818; *Vespertilio* Linnaeus, 1758; *Pecotus* [sic = *Plecotus* É. Geoffroy, 1818; and Barbastella *J. Gray*, 1821 (see Jackson and Groves, 2015: 271). Accepted as tribe by Koopman and Jones (1970: 27), McKenna and Bell (1997: 318), Hoofer and Van Den Bussche (2003: 38) and Simmons (2005: 484) (see Jackson and Groves, 2015: 271).

1865. *Nyctophilinae* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1865: 524. - Comments: Type genus: *Nyctophilus* Leach, 1821. Considered a valid subfamily by Hall and Kelson (1959: 201) [including *Antrozous*], Corbet and Hill (1992: 156), but see Hoofer and Van Den Bussche (2003: 1), who reject this (actually Peters uses "Nyctophili").

1878. *Vespertiliones* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 168. Publication date: 15 June 1878. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Dobson (1878: 168) introduced the name Vespertiliones in his key as "Group II" including the bats of the Vespertilioninae subfamily (see Jackson and Groves, 2015: 227). Originally included the genera *Vesperugo* Keyserling and Blasius, 1839 [= *Vespertilio* Linnaeus, 1758]; *Chalinolobus* Peters, 1865; *Scotophilus* Tomes, 1857; *Nycticejus* [sic = *Nycticeius*] Rafinesque, 1819; *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825]; *Harpiocephalus* J. Gray, 1842; *Vespertilio* Linnaeus, 1758; and *Kerivoula* J. Gray, 1842. Not Vespertiliones Pallas, 1767, nor Vespertiliones Peters, 1865.

1897. *Vespertilioninæ* Miller, N. Am. Fauna, 13: 41, 54. Publication date: 16 October 1897. - Comments: Type genus: *Vespertilio* Linnaeus, 1758. Originally included the genera *Dasypterus* Peters, 1870 [= *Lasiurus* J. Gray, 1831]; *Rhogeëssa* H. Allen, 1866; *Nycticeius* Rafinesque, 1819; *Lasiurus* J. Gray, 1831; *Vespertilio* Linnaeus, 1758; *Pipistrellus* Kaup, 1829; *Lasionycteris* Peters, 1865; and *Myotis* Kaup, 1829 (see Jackson and Groves, 2015: 270).

1942. *Nycticeini* Tate, Bull. Am. Mus. Nat. Hist., 80 (7): 280. Publication date: 27 November 1942. - Comments: type genus: *Nycticeius* Rafinesque, 1819. Introducted as tribe and originally included the genera *Scoteinus* Dobson, 1875 [= *Scotomanes* Dobson, 1875]; *Nycticeius* Rafinesque, 1819; *Rhogeëssa* H. Allen, 1866; *Baeodon* Miller, 1906 [= *Rhogeëssa* H. Allen, 1866]; *Scotoecus* Thomas, 1901; *Scotophilus* Leach, 1821; *Scotomanes* Dobson, 1875; and *Otonycteris* Peters, 1859 (see Jackson and Groves, 2015: 276).

1987. *Eptésiformes* Menu, Palaeovert., 17 (3): 78, 104, 134. Publication date: 31 March 1987. - Comments: Type genus: *Eptesicus* Rafinesque, 1820. Originally included the genera *Eptesicus* Rafinesque, 1820 and *Nycterikaupius* Menu, 1987. Emended by McKenna and Bell (1997: 318) as published as 'les eptésiformes' as it seems to meet the requirements of Article 11 of the Code (ICZN, 1985a: 19) (see Jackson and Groves, 2015: 271).. Jackson and Groves (2015: 271) erroneously mentioned the genus *Nyctalus* Bowdich, 1825 as type genus.

1987. *Leuconoïdes* Menu, Palaeovert., 17 (3): 77, 82. Publication date: 31 March 1987. - Comments: Type genus: *Leuconoe* Boie, 1830. Introduced without formal rank, and originally including the genera *Leuconöe* Boie, 1830 [= *Myotis* Kaup, 1829]; *Pizonyx* Miller, 1906 [= *Myotis* Kaup , 1829]; and *Perimyotis* Menu, 1984 [= *Pipistrellus* Kaup, 1829] (see Jackson and Groves, 2015: 271). Emended by McKenna and Bell (1997: 316) to 'les leuconoïdes" as it apparently meets the requirements of Article 11 of the Code (ICZN, 1985a: 19) (see Jackson and Groves, 2015: 271).

1987. *Néoeptésiformes* Menu, Palaeovert., 17 (3): 77, 123, 134. Publication date: 31 March 1987. - Comments: Type genus: *Nyctalus* Bowdich, 1825. Originally included the genera *Hypsugo* Kolenati, 1856; *Tylonycteris* Peters, 1872; and *Mimetillus* Thomas, 1904. Emended by McKenna and Bell (1997: 318) as published as 'les néoeptésiformes' as it seems to meet the requirements of Article 11 of the Code (ICZN, 1985a: 19) (see Jackson and Groves, 2015: 271)..

1987. *Nyctaliformes* Menu, Palaeovert., 17 (3): 77, 95, 133. Publication date: 31 March 1987. - Comments: Type genus: *Nyctalus* Bowdich, 1825. Its original rank was unclear, but it was ranked in the "Les Nyctaloïdes" and included the genera *Pipistrellus* Kaup, 1829; *Glischropus* Dobson, 1875; *Philetor* Thomas, 1902; *Scotoecus* Thomas, 1901; and *Nyctalus* Bowdich, 1825 (see Jackson and Groves, 2015: 274). Synonymized with

Vespertilioninae by McKenna and Bell (1997: 318), but with the tribe Pipistrellini by Jackson and Groves (2015: 274).

1987. *Nyctaloïdes* Menu, Palaeovert., 17 (3): 77, 94. Publication date: 31 March 1987. - Comments: Type genus: *Nyctalus* Bowdich, 1825. Originally, the rank was unclear, and it included the Nyctaliformes Menu, 1987, Eptésiformes Menu, 1987 and Néoeptésiformes Menu, 1987 (see Jackson and Groves, 2015: 274). McKenna and Bell (1997: 318) synonymized it with the subfamily Vespertilioninae, whereas Jackson and Groves (2015: 274) synonymized it with the tribe Pipistrellini.

2018. *Vespertilininae:* Foord, Swanepoel, Evans, Schoeman, Erasmus, Schoeman, Keith, Smith, Mauda, Maree, Nembudani, Dippenaar-Schoeman, Munyai and Taylor, PLoS ONE, 13(5): e0194336: 6. Publication date: 8 May 2018. (Lapsus).

2025. *Vespertilionae:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: 1. Publication date: 18 July 2025. (Lapsus).

TAXONOMY:

Bronner *et al.* (2003) state that the classification of the subfamily Vespertilioninae was historically based on facial shortening and dental reduction characters (Miller, 1907), and augmented by bacula morphology (Hill and Harrison, 1987). Interrelationships among *Eptesicus* and *Pipistrellus* species have long been contentious and have for the most part remained unresolved. The principal character used to diagnose these genera was the presence (*Pipistrellus*) or absence (*Eptesicus*) of the anterior upper premolar. However, this character is variable in both genera Wallin, 1969; Koopman, 1975; Heller and Volleth, 1984). Baculum morphology (Heller and Volleth, 1984; Hill and Harrison, 1987) and karyological properties (Heller and Volleth, 1984; Zima and Horáček, 1985) also vary markedly among species assigned to *Pipistrellus* using dental characters. Heller and Volleth (1984) concluded that the genus *Eptesicus* is characterised by a distinct karyotype of 2*n* = 50, and removed those taxa with 2*n* = >44 (*E. capensis* and some Australian species) from *Eptesicus* to *Pipistrellus*, a treatment they considered consistent with patterns of variation in baculum morphology.

After extensively reviewing variation in baculum morphology, Hill and Harrison (1987) divived *Pipistrellus* into seven subgenera. They transferred *anchietae* (see Kock (2001c: 246) for justification of spelling) to the subgenus *Hypsugo* and four African species of *Eptesicus* (*capensis, melckorum, zuluensis* and *rendalli*) to the subgenus *Neoromicia* within *Pipistrellus*. *Hypsugo* was subsequently raised to generic rank on the basis of detailed morphological and biochemical analyses (Horáček and Hanák, 1986; Ruedi and Arlettaz, 1991), a treatment supported also by cytogenetic evidence showing radical reorganization of the genome and karyotypic evolution in *H. anchietae* (Kearney *et al.*, 2002). Most of the other (extralimital) subgenera were subsequently also awarded full genus status, with the exception of *Pipistrellus* and *Neoromicia*. McBee *et al.* (1987) and Morales *et al.* (1991) provided further cytogenetic and electrophoretic evidence supporting the findings of Heller and Volleth (1984), but argued that further studies were needed to justify the inclusion of these species in *Pipistrellus*. Koopman (1993a), therefore, recognised *Neoromicia*, but retained it as a subgenus of *Eptesicus*.

Volleth and Heller (1994) subsequently published more karyotypic evidence supporting the inclusion of *Neoromicia* within *Pipistrellus*, a treatment formalised by Koopman (1994). Most recently, Volleth *et al.* (2001) showed that the four African species included in *Neoromicia* (*capensis, nanus, rendalli* and *zuluensis*) display karyotypic synapomorphies typical of the Vespertilionini, in contrast to the other African *Pipistrellus* that show cytogenetic traits characteristic of the Pipistrellini. *Neoromicia* should thus be elevated to full generic rank to avoid recognising a paraphyletic *Pipistrellus*. Cladistic analysis of chromosomal data (showing that the four *Neoromicia* species also share three Robertsonian fusions), and of baculum characters in southern African species, provide additional support for recognising *Neoromicia* as a distinct genus (Kearney *et al.*, 2002). Consequently, the genus *Eptesicus* in southern Africa is represented by only one species, namely *E. hottentotus*.

Using digenomic DNA, Roehrs *et al.* (2010: 1073) were able to distinguish 6 tribes in the Vespertilioninae: Antrozoini, Lasiurini, Scotophilini, Vespertilionini, and 2 new unnamed tribal clades, the perimyotine group and the hypsugine group. They were unable to confirm a Nycticeiini-Eptesicini group, nor were they able to separate the Plecotini.

Guan *et al.* (2025: 3) also recovered six tribes, with Scotophilini and Lasiurini forming the basal clade and Plecotini being sister to Vespertilionini, Pipistrellini and Eptesicini, whereby Vespertilionini is closer to Pipstrellini than to Eptesicini.

COMMON NAMES:

Czech: praví netopýři. Ukrainian: Лилики [= Lylyky]

HABITS:
Rainho *et al.* (2023: 7) assigned the *Pipistrellus, Afronycteris, Neoromicia* and *Nycticeinops* bats in Meru county (Kenya) to a medium-to-high-flying guild flying at altitudes between 2 and 10 m.

PARASITES:
DIPTERA
Nycteribiidae
Nycteribia tecta Theodor, 1957 (Haeselbarth *et al.*, 1966: 110 as *Eptesicus sp.*).

SIPHONAPTERA
Ischnopsyllidae
Dampfia grahami (Waterston, 1915) collected in the Free State and KwaZulu Natal, South Africa where the host is assumed to belong to the genus *Eptesicus* now possibly referring to *Neoromicia* (Haeselbarth *et al.*, 1966: 187).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Angola, Cameroon, Congo, Congo (Democratic Republic of the), Djibouti, Ghana, Kenya, Madagascar, Mali, Namibia, Rwanda, Senegal, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

TRIBE Nycticeiini Gervais, 1855

1855. *Nycticeiini* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud.Zool, Zool (Sec 7), Vol 1, pt 2: 71, footnote. Publication date: 23 July 1855. - Comments: Type genus: *Nycticeius* Rafinesque, 1819. Introduced as tribe (Nycticéins) and originally included the genera *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825] and *Nycticejus* [sic = *Nycticeius*] Rafinesque, 1819 (see Jackson and Groves, 2015: 275, who also recognized it as a valid tribe). (Current Spelling).

*1855. *Nycticeina* Gervais, in: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud, Zool (Sec 7), Vol 1, pt 2: 71, footnote. Publication date: 23 July 1855. - Comments: Type genus: *Nycticeius* Rafinesque, 1819. Introduced as tribe (Nycticéins) and originally included the genera *Atalapha* Rafinesque, 1814 [= *Nyctalus* Bowdich, 1825] and *Nycticejus* [sic = *Nycticeius*] Rafinesque, 1819 (see Jackson and Groves, 2015: 275).

1872. *Nycticejinae* Gill, Smiths. Misc. Coll., 11 (1): 17. Publication date: November 1872. - Comments: Type genus: *Nycticeius* Rafinesque, 1819. Introduced as subfamily but considered a synonym of the tribe Nycticeiini by Jackson and Groves (2015: 276).

Genus ***Cnephaeus*** Kaup, 1829

*1829. *Cnephæus* Kaup, Skizzierte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 103. Publication date: 1829. - Comments: Type species: *Vespertilio serotinus* Schreber, 1774. Considered a valid subgenus by Hoofer and Van Den Bussche (2003: 38), including *serotinus* and *hottentotus*.

TAXONOMY:
Artyushin *et al.* (2018: 475) indicated that the previously proposed inclusion of the Old World representatives of the subgenus *Cnephaeus* into the genus *Eptesicus* could not be confirmed by their analyses of five nuclear and one mitochondrial (cyt-*b*) genes.

Subsequently, Cláudio *et al.* (2023: 1) restricted the genus name *Eptesicus* to *E. fuscus* (Palisot de Beauvois, 1796) and *E. guadeloupensis* Genoways and Baker, 1975, both of them New World species. The next available generic name for the Old World taxa is *Cnephaeus* Kaup, 1829.

Currently, Simmons and Cirranello (2024a) do not recognize subgenera, but they recognize the following species in the genus *Cnephaeus*:
Subgenus *Cnephaeus* Kaup, 1829: *anatolicus* Felten, 1971 – Anatolia (Turkey), Cyprus, Lebanon to SW Iran; Kurdistan; ***bottae*** (Peters, 1869); *gobiensis* Bobrinskii, 1926 – Iran, northern Afghanistan, Kashmir, Pakistan and Nepal, southern Russia, Mongolia (Simmons, 2005: 454); ***hottentotus*** (A. Smith, 1833); ***isabellinus*** (Temminck, 1840); *japonensis* Imaizumi, 1953 – Honshû Isl (Japan) (Simmons, 2005: 455); *kobayashii* Mori, 1928 – Korea (Simmons, 2005: 455); *nilssonii* (Keyserling and Blasius, 1839) – western and eastern Europe to eastern Siberia and northwestern China, north beyond Artic Circle in Scandinavia, south to Bulgaria, Iraq, the Elburz Mtns (northern Iran), The Pamirs and western China (not Tibet), Korea, Hokkaido (Japan), Sakhalin Isl (Russia) (Simmons, 2005: 456); *ognevi* Bobrinskii, 1918 – Transcaucasia to Pakistan, Afghanistan and NW China; *pachyomus* (Tomes, 1857) – Afghanistan, Pakistan and NW India (Rajasthan, Kashmir); *pachyotis* (Dobson, 1871) – Bangladesh, northeastern India, Tibet (China), northern Burma, northern Thailand (Simmons, 2005: 456);

platyops (Thomas, 1901); *serotinus* (Schreber, 1774) – western Europe through Turkey and southern Asiatic Russia to Himalayas, Thailand and China, north to Korea, Taiwan, south England, most islands in Mediterranean, possibility north Africa (Simmons, 2005: 456); *tatei* Ellerman and Morrison-Scott, 1951 – northeastern India (Simmons, 2005: 456).
Subgenus *Rhinopterus* Miller, 1906: ***floweri*** (de Winton, 1901).

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Avery (2007: 619) reported on the presence of "*Eptesicus*" sp. in Pleistocene deposits at Wonderwerk Cave, South Africa.

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023) mentioned the following nycteribiid flies have been found on African "*Eptesicus*" sp.: *Basilia (Basilia) robusta* Theodor, 1956 and *Nycteribia schmidlii scotti* Falcoz, 1923. However, it is not clear whether these reports refer to what is currently considered *Cnephaeus*, *Neoromicia* or *Pseudoromicia* (or perhaps any other "little brown bat").

Cnephaeus bottae (Peters, 1869)

*1869. *Vesperus Bottae* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 406. Type locality: Yemen: "Yemen": Restricted to W Yemen, between Al Hudayda, Ta'izz and Al Mukha, according to Karami *et al.* (2009: 70). Holotype: MNHN ZM-MO-1987-297: ad, skull and alcoholic. Collected by: Dr. Paolo Emilio Botta; collection date: 1837. Number 212 in Rode (1941: 247). Rode (1941) mentions a male specimen, whereas Peters (1869a: 406) mentions a female. - Etymology: In honour of Paul-Emile Botta (1802 - 1870), who collected the type specimen (see Kozhurina, 2002: 14).
1887. *Vesperugo (Vesperus) Innesi* Lataste, Ann. Mus. civ. Stor. nat. Genova, ser 2, 4 (OS 24): 625, 2 text-figs. Publication date: 25 July 1887. Type locality: Egypt: Cairo [30 03 N 31 15 E]. [Goto Description]. Lectotype: NHMUK 1919.7.7.3528: sad ♀, skull and alcoholic. Collected by: Dr. Walter F. Innes Bey; collection date: 1885. See Qumsiyeh (1985). Paralectotype: MSNG unknown |1|: ♂. . - Etymology: In honour of M. Walter Innes, curator of the Medical Museum, who collected the type specimens (see Lataste, 1887b: 628).
1891. *Vesperugo innesi:* Noack, Jb. Hamb. Wiss. Anst., 9: 139. (Name Combination).
1902. *Vespertilio innesi:* Anderson and de Winton, Zoology of Egypt: Mammalia, 121. (Name Combination).
1919. *E[ptesicus] innesi:* Thomas, J. Bomb. nat. Hist. Soc., 26: 746.
1932. *Eptesicus innesi:* Flower, Proc. zool. Soc. Lond., 101: 382. (Name Combination).
1942. *Eptesicus [(Eptesicus)] bottae:* Tate, Bull. Am. Mus. Nat. Hist., 80: 275, 277. (Name Combination).
1955. *Eptesicus isabellinus innesi:* Sanborn and Hoogstraal, J. Egypt. Publ. Health Ass., 30 (4): xxx.
1956. *Eptesicus isabellinus bottae:* Harrison, Proc. zool. Soc. Lond., 127: ???. (Name Combination).
1963. *E[ptesicus] bottae:* Harrison, Z. Säugetierk., 28 (1): 109. (Name Combination).
1964. *Eptesicus bottae bottae:* Harrison, Mammals of Arabia, 140. (Name Combination).
1964. *Eptesicus bottae innesi:* Harrison, Mammals of Arabia, 140. (Name Combination).
1964. *Eptesicus bottae:* Harrison, Mammals of Arabia, 140. (Name Combination).
1971. *Eptesicus [(Eptesicus)] bottae innesi:* Hayman and Hill, Mammals of Africa: Chiroptera, 45. (Name Combination).
1990. *Eptesicus (Eptesicus) bottae bottae:* Nader and Kock, Senckenb. biol., 79 (1/3): 2 (for 1989). (Name Combination).
1994. *E[ptesicus (Eptesicus)] b[ottae] bottae:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 120. (Name Combination).
1994. *E[ptesicus (Eptesicus)] b[ottae] innesi:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 120. (Name Combination).
2023. *Cnephaeus bottae:* Cláudio, Novaes, Gardner, Nogueira, Wilson, Maldonado, Oliveira and Moratelli, Zoologia, 40 (e22029): 13, 21. Publication date: 17 July 2023. (Current Combination).

TAXONOMY:
Revised by Nader and Kock (1990a).

Cláudio *et al.* (2023: 11) transferred this species from the genus *Eptesicus* to *Cnephaeus*.

Populations in Turkey and northern Syria (and possibly other areas) are considered by Felten (1971) and Benda *et al.* (2006) to be a separate species: *Cnephaeus anatolicus* Felten 1971.

Based on mtDNA analyses, Artyushin *et al.* (2018: 473) distinguished two clusters in "*E. bottae*": one including "*E. b. ognevi*" and the second including "*E. b. hingstoni*", "*E. b. innesi*" and "*E. b. taftanimontis*", and the differences between them are almost large enough to distinguish them as separate species. The relation of these taxa to "*E. b. bottae*" still needs to be determined.

COMMON NAMES:
Albanian: Serotinë e Botta's. Arabian: Khaffash. Armenian: Ամպպատային մաշկեղ. Azerbaijani: Səhra gönlücəsi. Basque: Botta serotino. Belarusian: Кажан Бота. Bosnian: Botin šišmiš. Breton: Serotin Botta. Bulgarian: Полунощен прилеп на Бот. Castilian (Spain): Murciélago hortelano de Botta, La serotina de Botta. Catalan (Spain): Ratpenat dels graners de Botta.

Croatian: Bottin noćnjak. Czech: Netopýr Bottův, Netopýr Ogněvův. Danish: Bottas sydflagermus. Dutch: Botta's vleermuis. English: Botta's Serotine, Botta's Serotine Bat. Estonian: Kõrbe-nahkhiir. Finnish: Turkinserotiini. French: Sérotine de Botta. Frisian: Botta's lette flearmûs. Galician (Spain): Morcego das hortas de Botta. Georgian: უდაბნოს მეგვიანე. German: Bottas Breitflügelfledermaus, Bottas Fledermaus. Greek: Ασιατική τρανονυχτερίδα. Hebrew: אפלול מצוי, Aflul Matzuy, Aflul Matsui. Hungarian: Botta-késeidenevér. Irish Gaelic: Ialtóg Botta. Italian: Serotino di Botta. Latvian: Botas sikspārnis. Lithuanian: Uolinis šikšnys. Luxembourgish: Botta-Fliedermaus. Macedonian: Ботев лилјак. Maltese: Serotin ta' Botta. Montenegrin: Svijetlotrbušasti slijepi miš. Norwegian: Blekflaggermus. Polish: Mroczek Botty. Portuguese: Morcego-hortelão de Botta. Rhaeto-Romance: Serotin da Botta. Romanian: Liliacul lui Botta. Russian: Кожан пустынный. Serbian: Блискоисточни поноћњак [= Bliskoistočni ponoćnjak]. Scottish Gaelic: Ialtag Botta. Slovak: Večernica Bottova. Slovenian: Svetlotrebušni poznik. Swedish: Blek sydfladdermus. Turkish: Bottae'nin Genişkanatlı Yarasası. Ukrainian: илик (Пергач) пустельний. Welsh: Ystlum adain-lydan Botta.

Conservation status:

Global Justification

The species as described has a relatively wide range. Although generally considered uncommon it is described as locally common in at least part of the range (Egypt). No major threats are known. Hence it is listed as Least Concern (LC ver 3.1 (2001)) (Aulagnier *et al.*, 2008d; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) (Aulagnier *et al.*, 2008d; IUCN, 2009). 2004: LC ver 3.1 (2001) (Benda and Juste, 2004; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

Legal Status

Protected through Eurobats (Bonn Convention) and Bern Convention, and included in Annex IV of EU Habitats and Species Directive in the very small part of the range where these apply.

Major threats:

The species requires ruins which are decreasing in number and can be disturbed by tourists (A. Karatas *pers. comm.,* 2007), however, this is not thought to be a major threat to the species as a whole at present (Aulagnier *et al.*, 2008d; IUCN, 2009). Bilgin *et al.* (2012: 434) predict that climatic change will result in a major range contraction for this species.

Holderied *et al.* (2005: 6) indicated that this species is vulnerable for light pollution.

Conservation actions:

Aulagnier *et al.* (2008d) [in IUCN (2009)] suggest that taxonomic work is required to determine if more than one species is involved here and what the ranges of these are, and what their population status is.

General distribution:

Cnephaeus bottae is a Palaearctic species, occurring from the eastern Mediterranean around margins of Arabian peninsula to Iraq, Iran and southern Caucasus states; also central Asia to India, northwestern China and possibly Mongolia.

Native: Afghanistan; Armenia; Azerbaijan; Egypt (Sinai); Georgia; Greece (East Aegean Is.); India; Iran, Islamic Republic of; Iraq; Israel; Jordan; Kazakhstan; Kyrgyzstan; Lebanon; Oman; Pakistan; Palestinian Territory, Occupied; Saudi Arabia; Syrian Arab Republic; Tajikistan; Turkey; Turkmenistan; United Arab Emirates; Uzbekistan; Yemen.

Presence uncertain: Djibouti; Eritrea; Mongolia; Russian Federation; Somalia; Sudan.

Dental Formula:

The permanent dental formula is as follows: $I^{2}/_{3}$, $C^{1}/_{1}$, $PM^{1}/_{2}$, $M^{3}/_{3}$ = 32.

Detailed morphology:

Baculum

Hill and Harrison (1987).

Sexual dimorphism:

Korine (2021: 3) mentions that a weak sexual dimorphism exists, but does not provide any details.

Echolocation:

Walters *et al.* (2012: suppl.) report the following figures for 26 calls (21 sequences) from bats from Egypt and Israel: duration: 8.35 ± 2.16 ms, F_{max}: 44.18 ± 6.90 kHz, F_{min}: 30.44 ± 1.10 kHz, bandwidth: 13.73 ± 6.25 kHz, F_{peak}: 33.47 ± 1.80 kHz.

In Jordan, the following parameters were reported by Benda *et al.* (2010b: 204) for 146 calls: F_{start} 53.6 ± 9.3 (37.9 - 83.0) kHz, F_{end}: 30.4 ± 1.5 (27.0 - 33.7) kHz, F_{peak}: 34.3 ± 1.8 (29.6 - 39.5) kHz,

Pulse duration: 5.5 ± 1.3 (2.7 - 9.4) ms, and Inter-pulse interval: 123.6 ± 39.7 (52.0 - 241.0) ms.

Hackett *et al.* (2016: 223) reported on 147 calls from Israel: Pulse duration: 6.19 ± 1.51 ms, F_{start}: 42.63 ± 4.05 (38 - 51) kHz, F_{end}: 30.51 ± 1.21 (28.8 - 35.0) kHz, F_{peak}: 32.08 ± 1.29 (29.2 - 37.1) kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 32.08 kHz, F_{start}: 42.63 kHz, F_{end}: 30.51 kHz, Band width: 12.12 kHz, and duration: 6.19 ms.

The loudest *C. bottae* call registered by Holderied *et al.* (2005: 1321) was at 133·dB·peSPL. They also determined that the maximum detection distance for large flying prey or conspecifics was 21 m.

Molecular Biology:

Karyotype

Volleth *et al.* (2001) reported 2*n* = 50, FN = 48, BA = 0, a metacentric X chromosome and a metacentric Y chromosome for a male from Greece.

Roost:

Korine (2021: 7) mentioned that many roosts are in ruins.

Diet:

Hackett *et al.* (2013: 7) classify *Cnephaeus bottae* as a background cluttered space aerial insectivore.

In the Dead Sea area of Israel Hymenoptera, Lepidoptera and Coleoptera form the most important groups of food items, whereas in Syria, Coleoptera were the prime food category, followed by Heteroptera and Auchenorrhyncha, and in Iran Hymenoptera (Formicoidea) (89 % volume) and Coleoptera (Scarabaeidae) were the most important food items, indicating that *C. bottae* is a flexible species feeding opportunistically especially on ants and beetles. (Benda *et al.*, 2012a: 387).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 106 minutes, and a digestibility rate of 76.6 %.

Population:

Structure and Density

Reported to be locally common in Egypt, with colonies of up to 200 females being reported (African Mammal Assessment Workshop, 2004).

Trend

2008: Unknown (Aulagnier *et al.*, 2008d; IUCN, 2009). *Cnephaeus bottae* populations within the Asia Minor and Levant region are unknown population trend, under predictive climate change scenarios (Bilgin *et al.*, 2012: 433).

Activity and Behaviour:

In the Negev desert, Polak *et al.* (2011: 25) found that this species only passed through areas lighted by street lamps (flight speed: 9.25 ± 1.19 m/s), and never foraged there (contrary to *Pipistrellus kuhlii*. The flight speed during foraging in dark areas was 5.7 ± 1.3 m/s.

Reproduction and Ontogeny:

Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

Postnatal Development:

Korine (2021: 3) mentions that age classification based on the ossification of the epiphyses becomes difficult once the young start to fly independently.

Parasites:

DIPTERA

Nycteribiidae

In bats from a non-specified country, Júnior *et al.* (2020: Suppl.) mention the presence of *Phthiridium integrum* (Theodor and Moscona, 1954).

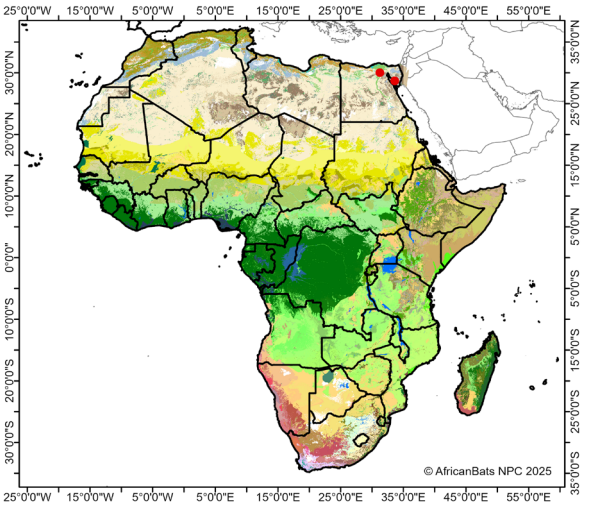

Figure 298. Distribution of *Cnephaeus bottae*.

Distribution based on voucher specimens:

Egypt, Yemen.

Cnephaeus hottentotus (A. Smith, 1833)

*1833. *Vespertilio Hottentota* A. Smith, S. Afr. Quart. J., ser 2, 1 (2): 59. Publication date: November 1833. Type locality: South Africa: Cape province: Uitenhage [ca. 33 45 S 25 25 E]. [Goto Description]. - Comments: Type locality restricted to Uitenhage (from Uitenhage and Albany) by Ellerman *et al.* (1953): see Meester *et al.* (1986: 57).

1840. *Vespertilio megalurus* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome Seconde, 2 (13): 206. Publication date: 1840. Type locality: South Africa: "Interior of South Africa". [Goto Description]. Syntype: RMNH MAM.35893: ad, mounted skin and skull. Collected by: Dr. Hubertus Benedictus Van Horstok. The RMNH catalog mentions two numbers: 35893.a (skull + loose bones) and 35893.b (mounted skin). - Comments: Type specimen: RMNH. (Name Combination).

1849. *Vespertilio minutus* A. Smith, Illustrated Zoology of South African Mammals, pl 51 and text. - Comments: Preoccupied by *Vespertilio minutus* Montagu, 1808 and *Vespertilio minuta* Temminck, 1840. (Name Combination).

1855. *V[espertilio] Smithii* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 747, footnote. Publication date: 28 September 1855. Type locality: South Africa: "South Africa". - Comments: . (Name Combination).

1855. *Vespertilio (Vesperus) megalurus:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 747. (Name Combination).

1855. *Vespertilio smithii* Wagner, Supplementband 5. In: Schreber, J.C.D. von: Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen, 747 [Goto Description]. (Name Combination).

1860. *Cateorus megalurus:* Kolenati, Monographie der Europäischen Chiroptern, 20. (Name Combination).

1878. *Vesperugo (Vesperus) megalurus:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 199. Publication date: 15 June 1878. (Name Combination).

1878. *Vesperugo (Vesperus) smithii:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 198. Publication date: 15 June 1878. - Comments: Dobson (1878) considered it to be a synonym of *Vesperugo (Vesperus) capensis*. (Name Combination).

1887. *Vesperus megalurus:* Jentink, Mus. Hist. nat. Pays-Bas, Leyden, 275. (Name Combination).

1897. *Vesperugo (Eptesicus) megalurus:* Thomas, Proc. zool. Soc. Lond., 1896, IV: 791. (Name Combination).

1901. *Vespertilio (Eptesicus) megalurus:* Sclater, Mammals of South Africa, 123. (Name Combination).

1924. *E[ptesicus] smithi:* Roberts, Ann. Transv. Mus., 10 (2): 60. (Name Combination).

1931. *Eptesicus megalurus:* Hewitt, A guide to the Vertebrate fauna of the Eastern Cape Province, 23. (Name Combination).

1938. *Scotophilus angusticeps* Shortridge and Carter, Ann. S. Afr. Mus., 32 (4): 282. Publication date: July 1938. Type locality: South Africa: Western Cape province: 10 mi (16 km) N Citrusdal: Hex River Estate [33 30 S 19 35 E, 100 m]. [Goto Description]. Holotype: KM 1984: ad ♀. Collected by: Captain Guy Chester Shortridge and Thomas Donald Carter; collection date: 28 December 1937; original number: 1937. Cotype: KM 1985: ad ♀. Collected by: Captain Guy Chester Shortridge and Thomas Donald Carter; collection date: 3 January 1938; original number: 3308. (Name Combination).

1939. *Eptesicus smithii:* G.M. Allen, Bull. Mus. comp. Zool., 83: 87. (Name Combination).

1942. *Eptesicus megalurus pallidior* Shortridge, Ann. S. Afr. Mus., 36: 37. Type locality: South Africa: NW Cape province: Klein Namaqualand, Orange River: Goodhouse [ca. 28 54 S 18 15 E, 300 ft]. [Goto Description]. Holotype: KM 1986: ad ♀. Collected by: Captain Guy Chester Shortridge; collection date: 29 December 1936; original number: 1157. - Comments: Holotype (ad F, orig nr. 1157) possibly in the collection of the NHMUK or KM. (Name Combination).

1946. *E[ptesicus] h[ottentotus] hottentotus:* Roberts, Ann. Transv. Mus., 20 (4): 305. (Name Combination).

1946. *Eptesicus hottentotus bensoni* Roberts, Ann. Transv. Mus., 20 (4): 305. Type locality: Malawi: Ncheu [=Ntcheu] [14 49 S 34 38 E, 1 100 m]. [Goto Description]. Holotype: TM 9167: ad ♂, skin and skull. Collected by: Constantine ("Con") Walter Benson; collection date: 31 October 1939; original number: 94. (Name Combination).

1951. *Eptesicus hottentotus angusticeps:* Roberts, Mammals of South Africa, 551. (Name Combination).

1951. *Eptesicus hottentotus hottentotus:* Roberts, Mammals of South Africa, 86. (Name Combination).

1951. *Eptesicus hottentotus pallidior:* Roberts, Mammals of South Africa, 86. (Name Combination).

1953. *Eptesicus (Eptesicus) hottentotus bensoni:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).

1953. *Eptesicus (Eptesicus) hottentotus hottentotus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).

1953. *Eptesicus (Eptesicus) hottentotus pallidior:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).

1953. *Eptesicus (Eptesicus) hottentotus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).

1954. *Eptesicus hottentotus:* Ellerman, Ann. Univ. Stellenbosch, 30 A (1): 32. (Name Combination).

1969. *Eptesicus serotinus hottentotus:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 214. (Name Combination).

1986. *Eptesicus hottentotus portavernus* Schlitter and Aggundey, Cimbebasia, (A) 8 (20): 172, fig 5. Publication date: 14 February 1986. Type locality: Kenya: Rift Valley province: Naivasha district: 20 km S, 14 km W Naivasha: Hell's Gate Canyon (=Njorowa Gorge) [00 54 S 36 19 E]. [Goto Description]. Holotype: CM 89000: ad ♂, skin and skull. Collected by: Dr. Duane Albert Schlitter; collection date: 30 September 1985; original number: 6906. See Schlitter and Aggundey (1986: 172). (Name Combination).

1986. *Eptesicus hottentotus protavernus:* Schlitter and Aggundey, Cimbebasia, (A) 8 (20): 174. (Lapsus).

1994. *E[ptesicus (Eptesicus)] h[ottentotus] portavernus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 120. (Name Combination).

2003. *Eptesicus (Cnephaeus) hottentotus:* Hoofer and Van Den Bussche, Acta Chiropt., 5 (Suppl): 38. (Name Combination).

? *Cnephaeus hottentotus:* (Current Combination).

TAXONOMY:



Figure 299. *Cnephaeu) hottentotus* (TM 48193) caught at Farm Schaapplaats, Free State, South Africa.

Revised by Schlitter and Aggundey (1986), who described a new subspecies from Kenya - "*Eptesicus hottentotus portavernus*". Besides the nominate form and the newly described subspecies, their work recognised one other subspecies "*E. h. bensoni*" (Roberts, 1946), but not "*E. h. pallidior*" (Shortridge, 1942), which they synonymised with the nominate subspecies (Schlitter and Aggundey, 1986). Simmons (2005: 455) recognised the same subspecies. An analysis of specimens from southern Africa showed support for the synonymization of "*E. h. pallidior*", but also indicated that either the subspecies delineation between "*E. h. hottentotus*" and "*E. h. bensoni*" is also not as distinct, or the distribution of "*E. h. bensoni*", described from Malawi, requires revision (Kearney, 2005). Although the distribution of "*E. h. bensoni*" in Meester *et al.* (1986: 57) included parts of South Africa, as well as Mozambique, Zimbabwe and Malawi, Hayman and Hill (1971) listed only Malawi and Zambia, and the subspecies was not included in the list of mammals from South Africa by Roberts (1951, 1954). Included in the subgenus *Cnephaeus* by Hoofer and Van Den Bussche (2003: 38), which was raised to full genus status by Cláudio *et al.* (2023).

Based on mitochondrial and nuclear DNA analyses, Juste *et al.* (2013: 449) retain two subspecies: *R. h. hottentotus* and *R. h. pallidior*, but they only included material from South Africa.

COMMON NAMES:

Afrikaans: Langstert-dakvlermuis. Chinese: 长尾棕蝠. Czech: netopýr hotentotský. English: Long-tailed Serotine Bat, Hottentot Serotine Bat, Long-tailed Greater Serotine Bat, Long-tailed House Bat, Hottentot bat. French: Sérotine hottentote, Sérotine des maisons à longue queue, Sérotine hottentote. German: Hottentotten-Breitflügelfledermaus, Capische Trugfledermaus. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego caseiro Hottentot.

ETYMOLOGY OF COMMON NAME:

The colloquial name is derived from the fact that the tail of this species is much longer than in its sister taxa (see Smithers, 1983; Skinner and Smithers, 1990: 108; Taylor, 2005).

SIMILAR SPECIES:

Has been confused with *Scotophilus* (Roberts, 1946; 1951: 86; 1954: 86; Kearney and Seamark, 2004), although *E. hottentotus* has bicoloured hair and two upper incisors, while *Scotophilus* has single coloured hair and one upper incisor.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Butler (1978) reported as *Eptesicus* cf. *hottentotus* (Smith) from the early Pleistocene deposits at Olduvai. *E. hottentotus* was found from the upper Pleistocene at Border Cave and possibly the late Holocene at Nkupe, South Africa (Avery, 1991: 6). Further South African Pleistocene (Wonderwerk) and Holocene (Blinkklipkop) findings were reported by Avery and Avery (2011: 19).

CONSERVATION STATUS:

Global Justification

Listed [as *Eptesicus hottentotus*] as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs and Cotterill, 2008a; IUCN, 2009; Monadjem *et al.*, 2017ac).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Eptesicus hottentotus*] (Monadjem *et al.*, 2017ac). 2008: LC ver 3.1 (2001) [assessed as *Eptesicus hottentotus*] (Jacobs and Cotterill, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as *Eptesicus hottentotus*] (Jacobs and Cotterill, 2004a; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Watson *et al.*, 2016). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species (Jacobs and Cotterill, 2008a; IUCN, 2009; Monadjem *et al.*, 2017ac).

CONSERVATION ACTIONS:
Jacobs and Cotterill (2008a) [in IUCN (2009)] and Monadjem *et al.* (2017ac) indicate that *C. hottentotus* has been recorded from several protected areas in South Africa, and presumably is present in protected areas within other parts of the species range. Further studies are needed into the distribution of this species.

GENERAL DISTRIBUTION:
Cnephaeus hottentotus is largely a Southern African species ranging from southern Angola in west, through parts of Namibia, South Africa, southern Lesotho, Botswana, Zimbabwe, Mozambique, Malawi and Zambia, with a single record as far north as southwestern Kenya.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 813,384 km^2. In the RSA, its distribution is best predicted by geology (Babiker Salata, 2012: 50).

Native: Angola (Crawford-Cabral, 1966: 137; 1989; Feiler, 1990; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562; Taylor *et al.*, 2018b: 63); Eswatini (Monadjem *et al.*, 2021: 5): Kenya (Schlitter and Aggundey, 1986; Kearney *et al.*, 2008b); Lesotho (Lynch, 1994: 196; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562); Malawi (Kershaw, 1922b: 182; Roberts, 1946: 305;Happold *et al.*, 1988; Ansell and Dowsett, 1988: 38; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562); Mozambique (Smithers and Lobão Tello, 1976: 60; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562; Monadjem *et al.*, 2010c: 382); Namibia (Griffin, 1999: 30; Rautenbach *et al.*, 1993: 93; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562); South Africa (Shortridge and Carter, 1938: 282; Shortridge, 1942: 38; Roberts, 1951: 86; 1954; Rautenbach *et al.*, 1981b; Rautenbach and Espie, 1982; Herselman and Norton, 1985: 100; Rautenbach *et al.*, 1993: 93; Lynch, 1994; Taylor, 1998; Watson, 1998; Avery, 1991: 6; Kearney and Seamark, 2004; Seamark and Brand, 2005: 8; Seamark and Kearney, 2007: 4; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562); Zambia (Ansell, 1960a: 20; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562); Zimbabwe (Peterson and Nagorsen, 1975; Cotterill, 1996a: 78; Kearney *et al.*, 2008b; Monadjem *et al.*, 2010d: 562).

GEOGRAPHIC VARIATION:
See also the section on "Taxonomy". *C. h. bensoni* is smaller than either *C. h. hottentotus* or *C. h. portavernus* (Schlitter and Aggundey, 1986). *C. h. bensoni* is darker in colour, "tawny olive" (Roberts, 1946), than *C. h. portavernus* (Schlitter and Aggundey, 1986), and *C. h. hottentotus* (Roberts, 1946: 305). Morphometric analysis of cranial size supported synonymising *C. h. pallidior* with the nominate species (Schlitter and Aggundey, 1986; Kearney, 2005), which had been described on the basis of the paler colour, "rufous-buff" (Shortridge, 1942), that is found in specimens from the Northern Cape and Namibia. Although, colour is darker in specimens from Taung in the North West Province of South Africa (Herselman and Norton, 1985: 100), and in specimens from Angola - "gold brownish" (Crawford-Cabral, 1966; 1989: 19). Relative to *C. h. hottentotus*, *C. h. portavernus* has a deeper braincase and shorter palatal length (Schlitter and Aggundey, 1986).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
For a general description of overall size, and pelage and membrane colour see Temminck (1840), Sclater (1901: 126), Shortridge and Carter (1938: 282), Shortridge (1942), Roberts (1946), Smithers (1983), Skinner and Smithers (1990: 108), Taylor (2000), Taylor (2005: 318). For a general description of the ear and tragus see Temminck (1840), Sclater (1901: 126), Smithers (1983), Skinner and Smithers (1990: 108), Taylor (2000), Taylor (2005: 318).

Schoeman and Jacobs (2002: 157) reported the following parameters for 6 specimens from the Algeria Forestry Station (RSA): Fa: 48.9 ± 1.4 mm, Wing area: 173.7 ± 14.1 cm^2, Wing span: 33.0 ± 0.5 cm, Wing loading: 10.3 ± 1.6 N/m^2, and aspect ratio: 6.3 ± 0.6.

DENTAL FORMULA:
See Menu (1985; 1987).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
For a general description of the skull, see Shortridge and Carter (1938: 282), Roberts (1946). For a general description of the teeth, see Sclater (1901: 126).

DETAILED MORPHOLOGY:
Baculum
See Hill and Harrison (1987) and Kearney *et al.* (2002).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value

of 14.0 Pa, aspect ratio 7.2 for a wingspan of 39 cm and a wing area of 210 cm^2 and a body mass of 30 g.

SEXUAL DIMORPHISM:
An analysis of specimens from southern Africa showed no significant difference between the sexes in 12 cranial and dental, and eight external measurements, but females were significantly larger than males by 5.21 and 6.78 percent respectively for forearm and third metatarsal lengths (Kearney, 2005).

ECHOLOCATION:
Based on a single room-flown individual the call was recorded as a short duration (2 - 4 ms), broad-band (20 - 54 kHz) call with a dominant frequency of 28 - 32 kHz, and harmonic components (Taylor, 2000: 89). The call frequency, outside the sensitivity range of moths, is suggested to have evolved in response to moth hearing (Schoeman and Jacobs, 2002). These authors (p. 157) also reported the call type to be a low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 31.8 ± 1.0 kHz.

Taylor *et al.* (2013b: 17) recorded the following parameters for 3 *C. hottentotus* calls from Soutpansberg, South Africa: F_{max}: 60.6 ± 8.23 (54.0 - 69.8) kHz, F_{min}: 30.1 ± 1.74 (28.2 - 31.6) kHz, F_{knee}: 35.2 ± 1.48 (34.2 - 36.9) kHz, F_{char}: 32.2 ± 1.75 (30.4 - 33.8) kHz, duration: 3.1 ± 0.86 (2.6 - 4.1) ms.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg area (RSA): F_{min}: 28 - 32 khz, F_{char}: 30 - 34 kHz, F_{knee}: 34 - 37 kHz, slope: 367 - 773 OPS, duration: 3 - 4 ms.

Three calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 39.66 ± 9.59 kHz, F_{min}: 31.83 ± 2.30 kHz, F_{knee}: 33.54 ± 1.37 kHz, F_{char}: 32.38 ± 1.14 kHz, slope: 33.69 ± 35.48 OPS, duration: 3.64 ± 1.91 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 9 bats: F_{max}: 53.81 ± 10.93 kHz, F_{min}: 30.93 ± 5.14 kHz, F_{knee}: 34.73 ± 2.32 kHz, F_{char}: 31.1 ± 1.83 kHz, slope: 326.44 ± 1214.91 OPS, duration: 4.46 ± 1.75 ms. 15 calls from the Venatia mine recorded by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 4.01 ± 1.01 ms, F_{min}: 30.84 ± 0.70 kHz, F_{max}: 40.77 ± 4.95 kHz, F_{knee}: 33.87 ± 0.86 kHz and F_{char}: 31.23 ± 0.65 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 13 "*Eptesicus hottentotus*" calls from the Kruger Park (RSA): F_{min}: 30.4 ± 1.8 (26.9 33.8) kHz, Duration: 3.3 ± 0.7 (2.2 4.5) ms, F_{max}: 55.9 ± 9.0 (40.1 70.2) kHz, F_{knee}: 36.9 ± 2.2 (32.3 41.1) kHz, F_{char}: 33.5 ± 2.5 (31.5 40.1) kHz.

88 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 28 - 32 kHz, F_{max}: 54 - 70 kHz, F_{char}: 30 - 34 kHz, F_{knee}: 34 - 37 kHz and duration 3 - 4 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 33.50 ± 2.50 kHz, F_{max}: 55.90 ± 9.00 kHz and F_{min}: 30.40 ± 1.80 kHz.

MOLECULAR BIOLOGY:
Karyotype
Results of all analyses, based on specimens from Zimbabwe (Peterson and Nagorsen, 1975), Namibia and Limpopo Province in South Africa (Rautenbach *et al.*, 1993: 93), and the Western Cape Province in South Africa (Kearney *et al.*, 2002: 59), agreed the diploid number is $2n$ = 50, with 24 pairs of acrocentric autosomes, hence a fundamental number of FN = 48. The X chromosome is a medium-sized submetacentric, and the Y a small acrocentric (Peterson and Nagorsen, 1975; Rautenbach *et al.*, 1993: 93; Kearney *et al.*, 2002: 59).

Protein / allozyme
See Morales *et al.* (1991) for results from ten specimens from Namibia.

Genetics
See Hoofer and Van Den Bussche (2003), Stadelmann *et al.* (2004b), Eick *et al.* (2005) and Matthee *et al.* (2006).

HABITAT:
Often associated with mountainous country, in close proximity to water (see references under "Habits"). Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *C. hottentotus* activity was not significantly, nor positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body.

HABITS:
In Angola specimens collected from Capolopopo were "performing sweeping flights over a water tank, apparently catching insects" (Crawford-Cabral, 1989: 19), as was also noted by Roberts, 1951: 87) for individuals observed at Eronga Mountain in Namibia. In Mozambique a single specimen was mistnetted in the Zambezi Valley

northwest of Tete (Smithers and Lobão Tello, 1976: 60). Specimens collected at Goodhouse in the Northern Cape Province of South Africa were shot "whilst 'planing' very slowly in wide circles around a cattle kraal, to which they were attracted by a swarm of flies" (Shortridge, 1942: 38). Shortridge (1942: 38) also observed them to be weak fliers, coming out at late dusk after *Cistugo* and *Sauromys*. In 1985, near Buxton in the North West Province of South Africa, some 11 years after this species had been taken from a roost at the entrance to an old mine tunnel (see below under "Roost"), three females were netted flying out of the tunnel, two at 20h45, and another at 21h40, while a male was caught returning at 23h30 (James, 1986: 219). The first specimen of this bat caught in the northern part of the Kruger National Park in South Africa was mistnetted after sunset in a figtree forest on the banks of the Luvuvhu River (Rautenbach and Espie, 1982: 112). In the Free State Province of South Africa a specimen was netted at Sterkfontein Dam in "well-wooded, broken country with patches of marshy open grassland" (Watson, 1998). A specimen from Ithala Game Reserve in northern KwaZulu-Natal Province of South Africa was netted over a river with well-wooded banks (Rautenbach *et al.*, 1981b: 24). At Rocherpan in the Western Cape Province of South Africa specimens were netted flying low over a marsh (Herselman and Norton, 1985: 100). In the Cederberg region of the Western Cape Province of South Africa specimens were netted, in January and February between 20h45-21h52, at the edges of water bodies (Seamark and Brand, 2005: 8). In Lesotho specimens were netted over grassy banks adjacent to rivers in mountainous terrain, at Malealea the species was caught in October at 20h30 (Lynch, 1994: 197).

ROOST:
In Zimbabwe a specimen was found "clinging to a wall in an open building with a corrugated iron roof" (Smithers and Lobão Tello, 1976: 60), and at Marandellas "hanging on the wall of a squash court" (Smithers and Wilson, 1979: 45). Specimens from Taung in the North West Province of South Africa were taken (between 1976 - 1979) from a hollow in rocks at the entrance to an old mine tunnel inhabited by *Miniopterus schreibersii* (Herselman and Norton, 1985: 100).

Happold and Happold (2023: 133) mention that these bats roost singly or in small sized groups (no groups larger than five have been reported).

DIET:
Insectivorous (Smithers, 1983; Skinner and Smithers, 1990: 108; Taylor, 2005: 318). Schoeman and Jacobs (2002) identified tympanate moths in the diet of individuals from the Western Cape Province of South Africa.

From the Algeria Forestry Station (RSA) Schoeman and Jacobs (2002: 157) reported the following prey groups based on 67 faecal pellets from 6 bats (in volume percent): Coleoptera (88.3 ± 9.0), Diptera (4.5 ± 9.0), Hemiptera (1.5 ± 3.0), and unknown (1 ± 2).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 156 minutes, and a digestibility rate of about 72.7 %.

PREDATORS:
Avery *et al.* (2005: 1054) found this species to be present in pellets from *Tyto alba* (Scopoli, 1769) in South Africa.

Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
Shortridge (1942:38) indicated this bat was not plentiful around Goodhouse in the Northern Cape of South Africa and only observed half a dozen individuals. In other instances specimens have either been found singly or in groups of two to five (Smithers and Wilson, 1979; Herselman and Norton, 1985: 100; Smithers, 1983; Watson, 1998). Monadjem *et al.* (2017ac) report that although the species is considered to be sparsely distributed, it is locally common in part of the ranges, such as Zimbabwe but is thought to be rarer elsewhere (e.g., South Africa).

Trend
2016: Unknown (Monadjem *et al.*, 2017ac).
2008: Unknown (Jacobs and Cotterill, 2008a; IUCN, 2009).

PARASITES:
Ectoparasite - *Pteracarus pusillus* (Fain, 1978: 78).

ACARI
Spinturnicidae
Orlova *et al.* (2020a: 1) reported the first occurrence of *Spinturnix kolenatii* Oudemans, 1910 from a bat in Africa (Namibia). This mite was considered to have a Palearctic distribution, where it exclusively occurs on bats from the genus *Eptesicus*.

Argasidae

Reeves *et al.* (2020b: 663) collected larvae of *Argas transgariepinus* White, 1846 from three Namibian *Cnephaeus hottentotus* bats.

VIRUSES:

Paramyxoviridae

Mortlock *et al.* (2015: 1841) reported that one of two examined South African *C. hottentotus* specimens tested positive for *Paramyxovirus* sequences.

Rhabdoviridae

Lyssavirus - Rabies related viruses

Rabies

Oelofsen and Smith (1993) tested one individual brain, by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), which did not tested positive.

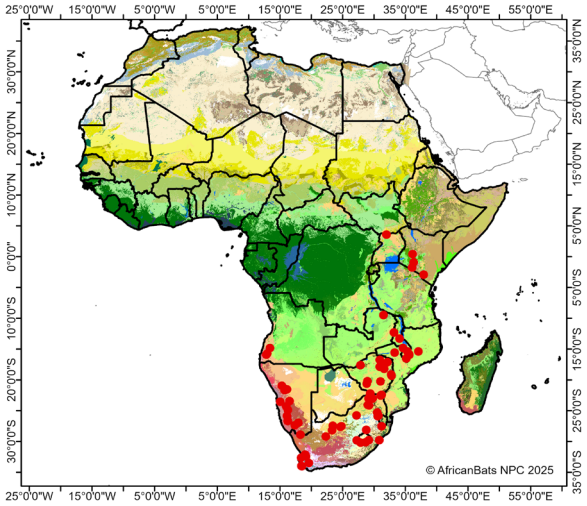

Figure 300. Distribution of *Cnephaeus hottentotus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Kenya, Lesotho, Malawi, Mozambique, Namibia, South Africa, Uganda, Zambia, Zimbabwe.

Cnephaeus isabellinus (Temminck, 1840)

*1840. *Vespertilio isabellinus* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe, 2 (13): 205, pl 52, fig 1, 2. Publication date: 1840. Type locality: Libya: near Tripoli [ca. 32 58 N 13 12 E]. [Goto Description]. Lectotype: RMNH MAM.17648: ad, mounted skin and skull. Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. Paralectotype: RMNH MAM.17649: ad, mounted skin (skull not removed). Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. Paralectotype: RMNH MAM.17650: ad. Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. Paralectotype: RMNH MAM.17651: ad, mounted skin (skull not removed). Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. Paralectotype: RMNH MAM.17652: ad ♀, skin and skull. Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. Paralectotype: RMNH MAM.17653: ad, mounted skin (skull not removed). Collected by: J.F.H. Clifford Cocq van Breugel; collection date: 1829 - 1835. - Comments: Considered a valid subspecies by Horáček *et al.* (2000: 124). Considered a valid species of *serotinus* by Benda *et al.* (2004b: xx), and Mayer *et al.* (2007: Additional file 1) based on mitochondrial DNA analyses. Dalhoumi *et al.* (2017b: 142) indicate that the original specimens were collected by J. F. H. Clifford Cocq van Breugel.

1855. *Vespertilio (Vesperus) isabellinus:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 746. (Name Combination).

1860. *Meteorus isabellinus:* Kolenati, Monographie der Europäischen Chiroptern, 20. (Name Combination).

1880. *Vesperugo (Vesperus) serotinus, Sous-espèce A, Vesperus isabellinus:* Dobson, Bull. Soc. zool. France, 5: 234. (Name Combination).

1885. *Vesperugo serotinus isabellinus:* Lataste, Act. Soc. Linn. Bordeaux, 39: 189. (Name Combination).

1887. *Vesperugo isabellinus:* Lataste, Catalogue critique des Mammifé apélagiques sauvages de Tunisie, 2. Publication date: 1887. (Name Combination).

1904. *Vespertilio Boscai* Cabrera, Mem. Soc. Esp. Hist. Nat., 2: 265, pl 3, figs 5, 6, 8. Type locality: Spain: Alicante, Muchamiel. [Goto Description].

1905. *Vespertilio (Eptesicus) serotinus isabellinus:* Trouessart, Caus. sci. Soc. zool. France, 1 (10): 369. (Name Combination).

1905. *Vespertilio (Eptesicus) serotinus:* Trouessart, Caus. sci. Soc. zool. France, 1 (10): ???. (Name Combination).

1909. *Eptesicus serotinus isabellinus:* Satunin, Mitt. Kauk. Mus., 4: 297. - Comments: However, this is not *isabellinus* Temminck, 1835-1841, but *isabellinus* Blyth, 1851. (Name Combination).

1937. *Eptesicus isabellinus:* Laurent, Mammalia, 1: 153. (Name Combination).

1938. *[Eptesics] serotinus gaboensis:* Frechkop, Exploration du Parc National Albert, 52. (Lapsus).

1939. *Eptesicus serotinus gabonensis:* Allen, Bull. Mus. comp. Zool., 83: 87. (Name Combination).

1939. *Eptesicus serotinus isabellinus:* G.M. Allen, Bull. Mus. comp. Zool., 83: 87. - Comments: First use for *isabellinus* Temminck, 1835-1841. (Name Combination).

1942. *Eptesicus [(Eptesicus)] isabellinus:* Tate, Bull. Am. Mus. Nat. Hist., 80: 275. (Name Combination).

1951. *Eptesicus isabellinus isabellinus:* Ellerman and Morrison-Scott, 156. (Name Combination).

1962. *E[ptesicus] gabonensis:* Basilio, La vida animal en la Guinea Española, 182. (Name Combination).

1971. *Eptesicus (Eptesicus) serotinus isabellinus:* Hayman and Hill, Mammals of Africa: Chiroptera, 44. (Name Combination).

2013. *Eptesicus isabellinus boscai:* Juste, Benda, Garcia-Mudarra and Ibáñez, Zool. Scr., 42 (5): 447. Publication date: 19 May 2013. (Name Combination).

2023. *Cnephaeus isabellinus:* Cláudio, Novaes, Gardner, Nogueira, Wilson, Maldonado, Oliveira and Moratelli, Zoologia, 40 (e22029):: 13, 21. Publication date: 17 July 2023. (Current Combination).

2023. *Eptesicus isabbelinus:* Dalhoumi, El Mokni, Ouni, Beyrem and Aulagnier, Diversity, 15 (1108): Suppl. Publication date: 25 October 2023. (Lapsus).
? *Cnephaeus isabellinus isabellinus:* (Name Combination).
? *Eptesicus (Amblyotus) isabellinus:* (Name Combination).
? *Eptesicus serotinus boscai:* (Name Combination).

TAXONOMY:
Recent genetic studies (Ibañez *et al.*, 2006; Mayer *et al.*, 2007; García-Mudarra *et al.*, 2009) support the specific status of this serotine which occurs sympatrically with *C. serotinus* in the Iberian Peninsula.

Le Berre (1990: 102) considers "*Eptesicus isabellinus*" to be a synonym of "*Eptesicus bottae*" (see also comments under that species).

The study of five nuclear genes and the mitochondrial cytochrome *b* gene led Artyushin *et al.* (2018: 471) to the conclusion that *C. serotinus* and *C. isabellinus* form a monophyletic clade, but with significant genetic differences, which confirm the species status of the later taxon. Ibañez *et al.* (2006: 288) indicate that the genetic differences between the two species correspond to a Late Miocene - Early Pliocene divergence.

The status of *gabonensis* still remains unclear. Although originally described by Trouessart (1897: 108) from Gabon, Hayman and Hill (1971: 44) and Ibáñez and Valverde (1985: 242) suggest it almost certainly originated from Kashmir or Northern India. Kock (1969a: 162) considered it to be senior synonym of "*Eptesicus platyops*", which is supported by Grubb (2004: 92), who discussed this in detail (and who indicates that Gabon might not be rejected as country of origin). Pending further analyses, we retain *gabonensis* in the synonymy of *Cnephaeus isabellinus*.

COMMON NAMES:
Albanian: Serotinë Isabeline. Armenian: Իզաբելլայի մաշկեղ. Azerbaijani:İzabel gönlücə. Basque: Baratze-saguzar isabeldar. Belarusian: Кажан ізабэлавы. Bosnian: Izabelin šišmiš. Breton: Serotin melenwenn. Bulgarian: Изабелинов прилеп. Castilian (Spain): Murciélago hortelano pardo, Murciélago hortelano mediterráneo, Murciélago hortelano meridional. Catalan (Spain): Ratpenat dels graners meridional. Croatian: Izabelin noćnjak. Czech: Netopýr tripolitánský. Danish: Isabellasydflagermus. Dutch: Isabelvleermuis. English: Isabelline Serotine Bat, Meridional serotine. Estonian: Ibeeria nahkhiir. Finnish: Vaaleaetelänlepakko. French: Sérotine isabelle, Vespertilion isabelle, Sérotine isabelline, Sérotine méditerranéen. Frisian: Isabelkleurde lette flearmûs. Galician (Spain): Morcego das hortas meridional. Georgian: ტყის მეგვიანე. German: Isabellfledermaus, Isabell-Breitflügelfledermaus, isabellfarbenen Abendfledermaus. Greek: Ωχρή τρανονυχτερίδα. Hungarian: Izabella-késeidenevér. Irish Gaelic: Ialtóg isibéalach. Italian: Serotino isabellino. Latvian: Izabellas sikspārnis. Lithuanian: Izabelos šikšnys. Luxembourgish: Isabel-Fliedermaus. Macedonian: Изабелов лилјак. Maltese: Serotin tas-Sider Pallidu. Montenegrin: Kraljičin slijepi miš. Norwegian: Isabellaflaggermus. Polish: Mroczek pustynny. Portuguese: Morcego-hortelão-claro. Rhaeto-Romance: Serotin isabellin. Romanian: Liliacul cu aripi late mediteranean. Russian: Кожан изабелловый. Serbian: Магребски поноћњак [= Magrebski ponoćnjak]. Scottish Gaelic: Ialtag isibealach. Slovak: večernica tripolitánska. Slovenian: Kraljičin poznik. Swedish: Isabellfladdermus. Turkish: İzabel Genişkanatlı Yarasası. Ukrainian: Лилик ізабеліновий. Welsh: Ystlum adain-lydan llwydfelyn.

SIMILAR SPECIES:
Santos *et al.* (2014: 158) indicate that *C. isabellinus* and *C. serotinus* have an extensive niche overlap, indicating that they explore very similar conditions. Each species thrives in a specific biogeographical zone, *C. serotinus* in Atlantic climates and *C. isabellinus* in Mediterranean areas, but considering the large niche overlap it is quite possible that competition may occur if prey resources are limited in contact zones.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Gunnell *et al.* (2015a: 13) report on a right distal humerus from the Olduvai Gorge (Tanzania), which they assigned to cf. "*E. isabellinus*".

CONSERVATION STATUS:
Global Justification
The species is locally abundant and widespread. Regional trends are difficult to determine due to the lack of reliable data but it seems that there are no reasons to consider the population to be declining globally (Juste, 2016a).

Assessment History
Global
2016: LC ver 3.1 (2001) [as *Eptesicus isabellinus* (Juste, 2016a). 2008: LC ver 3.1 (2001) [as part of *Eptesicus serotinus*] (Hutson *et al.*, 2008h; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Sherwin *et al.* (2012: 174) report the aerial hawking feeding style and the long-distance dispersal of *E. serotinus* in Europe and NW Africa to be important risk factors related to climatic change.

No specific threats are known for the species although it can accumulate biocides due its feeding habits in agricultural areas (Guillén et al. 1991).

CONSERVATION ACTIONS:
No specific conservation actions known (Hutson *et al.*, 2008h; IUCN, 2009). No specific actions seem to be required to guarantee the species' future. *C. isabellinus* is profiting from most of the man-made constructions that are being used more and more often as roosting places making the species quite common in urban areas (Juste, 2016a).

GENERAL DISTRIBUTION:
Eptesicus isabellinus has been recorded from North Africa and the Iberian Peninsula.

Martinoli and Spada (2023: 70) [referring to Trujillo (1992: 65) as "*Eptesicus serotinus*"] mention this species from Lanzarote (Canary Islands).

Native: Algeria; Libya; Morocco (Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 363 [as "*Eptesicus serotinus (= E. isabellinus)*"]; Dbiba *et al.*, 2025: 7); Portugal; Spain; Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26; 2023: 4).

GEOGRAPHIC VARIATION:
The populations from the Iberian Peninsula, Morocco and western Algeria are assigned to *E. isabellinus boscai* by Juste *et al.* (2013: 443), whereas those from the remaining part of Algeria, Tunisia and western Libya are assigned to "*E. i. isabellinus*". However, they do indicate (p. 450) that the specimens from western Libya seem to form a supported, separate clade.

SEXUAL DIMORPHISM:
In a year-round study in Tunisia, Dalhoumi *et al.* (2016a: 157) found adult females to be significantly heavier than males. Both sexes reach their maximum weight in October (♀♀: 22.68 ± 3.61 g; ♂♂: 21.45 ± 3.34 g) and their minimum weight in January-February (♀♀: 16.75 ± 0.35 g; ♂♂: 14.69 ± 1.13 g) (see also Martinoli and Spada, 2023: 72).

ECHOLOCATION:
Benda *et al.* (2010a: 163) report for 23 Moroccan specimens a start frequency of 35.1 ± 1.0 (33.7 - 36.3) kHz, a maximum energy frequency of 26.9 ± 0.7 (25.8 - 28.3) kHz, an end frequency of 23.3 ± 0.8 (22.4 - 24.2), with a duration of 9.7 ± 2.8 (5.6 - 16.3) ms, and an inter-pulse interval of 244.2 ± 66.7 (128.5 - 362.7) ms.

Also from Morocco, Disca *et al.* (2014: 226) indicate that the type of call is FM-QFC, with the following parameters: F_{start}: 42.3 ± 13.0 kHz, F_{end}: 25.3 ± 1.5 kHz, F_{peak}: 27.4 ± 2.2 kHz, bandwidth: 17.0 ± 11.6 kHz, duration: 11.5 ± 3.0 ms.

In Tunisia, Dalhoumi *et al.* (2016b: 867; 2017b: 143) reported FM/QCF calls with a short constant frequency at 18.5 - 27.1 kHz and maximum energy at 21.7 - 30.3 kHz (25.3 ± 2.0 kHz). Dalhoumi *et al.* (2023: 5) reported F_{start}: 38.74 ± 8.21 (25.8 - 61.8) kHz, F_{end}: 24.28 ± 1.01 (21.8 - 26.4) kHz, F_{max}: 25.76 ± 1.03 (23.3 - 27.9) kHz, duration: 12.44 ± 2.63 (7.2 - 18.5) ms and Interpulse interval: 241.01 ± 74.08 (104.5 - 483.2) ms.

Ait-Abdesselam *et al.* (2025: 40) reported an F_{max} value of 25.97 ± 1.50 kHz for Algerian bats.

MOLECULAR BIOLOGY:
Karyotype
Baker *et al.* (1974) reported 2n = 50, aFN = 48, X = submetacentric for specimens from Tunisia.

Genetics
See Ibañez *et al.* (2006), Mayer *et al.* (2007), García-Mudarra *et al.* (2009), Juste *et al.* (2009).

Extralimitally, in the Iberian contact area between *C. isabellinus* and *C. serotinus*, Centeno-Cuadros *et al.* (2019: "1") examined nuclear markers and found a male-mediated ongoing asymmetric hybridization from *C. isabellinus* to *C. serotinus* (28 % hybrids in *C. serotinus* and 5 % in *C. isabellinus*).

HABITAT:
In the Iberian Peninsula, Lisón *et al.* (2014: 59) found that *E. isabellinus* is primarily found near water courses, scrublands, and zones with high primary productivity. Non-irrigated croplands are avoided, and no preferences were found for human settlements or irrigated croplands. The preference for water bodies was also confirmed in Tunisia by Dalhoumi *et al.* (2017b: 149).

HABITS:
In Spain, Lisón and Calvo (2014: 99) found that the activity of this species increases with high

temperatures, showing the highest activity in June.

ROOST:
Benda *et al.* (2014c: 46) reported solitary males to roost in the ruined Roman town of Leptis Magna (Libya), and additional specimens were found in fissures in ceilings and walls of other ruins. Kelm *et al.* (2015: 27) indicate that this species' roosts are mostly found in anthropogenic structures. Dalhoumi *et al.* (2017b: 142) also mentions rock crevices, tree holes and bridges.

DIET:
Benda *et al.* (2014c: 51) examined four sets of faecal pellets and three digestive tracts from Libya *E. isabellinus* and found primarily ants (Hymenoptera: Formicoidea) and beetles (Coleoptera: mostly Scarabaeidae and Cerambycidae, but also Carabidae, Curculionidae, Staphylinidae, and Tenebrionidae). A set of five pellets from one animal was dominated by moths (Lepidoptera).

Edwards *et al.* (2022: 8) [referring to Kelm *et al.* (2015)] indicate that it takes about 2 hours for the food to pass through the digestive system.

PREDATORS:
Martinoli and Spada (2020: 4) mention that "*Eptesicus isabellinus*" is a frequent prey for the barn owl (*Tyto alba* (Scopoli, 1769), tawny owl (*Strix aluco* Linnaeus, 1758), long-eared owl (*Asio otus* (Linnaeus, 1758)), and the Eurasian eagle-owl (*Bubo bubo* (Linnaeus, 1758)). Diurnal predators include peregrine falcon (*Falco peregrinus* Tunstall, 1771), the common kestrel (*Falco tinnunculus* Linnaeus, 1758) and the Eurasian sparrowhawk (*Accipiter nisus* (Linnaeus, 1758)). Additionally; the horseshoe whip snake (*Hemorrhois hippocrepis* (Linnaeus, 1758)) was found to be an occasional predator.

POPULATION:
Structure and Density
Cnephaeus isabellinus is the most common bat species in northwest Algeria and Libya (Hutson *et al.*, 2008h; IUCN, 2009). While Juste (2016a) reports that there are no estimates of the population figures for the species. Nevertheless, it is reported to be very abundant locally and in some areas of Southern Spain is considered one of the commonest species with density values up to 7.5 individuals per km^2 (Ibáñez 2007). Lifespan is not well known but annual survival rate of adults was found to vary across colonies with an average value around 0.70 (Papadatou *et al.*, 2011). This species is the main host of a differentiated strand of rabies virus in Iberia (Vázquez-Morón *et al.*, 2011).

Trend
2016: Unknown (Juste, 2016a). 2008: Unknown [as part of *C. serotinus* (Hutson *et al.*, 2008h; IUCN, 2009)].

LIFESPAN:
In southern Spain, Papadatou *et al.* (2010: 925) followed six colonies over a period varying between 8 and 26 years and found a mean annual survival probability of 0.71. The mean longevity of the species is 5 to 10 years.

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

Baker *et al.* (1974: 701) mentions four lactating females collected on 5 June 1973. In Tunisia, Dalhoumi *et al.* (2017b: 141) captured pregnant females from April to June (one even in August) and lactating females from May to June. All of the females captured by Dalhoumi *et al.* (2015: 265) in May were pregnant, whereas other bats were found to be pregnant in May and June, but they also captured one pregnant female in August. Two juveniles were captured in June and October.

Benda *et al.* (2014c: 48) refer to a record of two juvenile females made by Hanák and Elgadi (1984) in the spring of 1978 from Janzur (Libya), and to a non-volant juvenile they observed at Sabratha on 28 May 2002.

PARASITES:
Benda *et al.* (2014c: 52) reported the following parasites from Libya: Argasidae: *Argas vespertilionis* (Latreille, 1802), Ischnopsyllidae: *Ischnopsyllus intermedius* (Rothschild, 1898).

From Algeria, Bendjeddou *et al.* (2013: 325) reported the Nycteribiid *Phthiridium biarticulatum* Hermann, 1804 from "*E. serotinus*": Bendjeddou *et al.* (2017: 15) added the following species: Siphonaptera:*Nycteridopsylla longiceps* Rothschild, 1908, *Ischnopsyllus intermedius* (Rothschild, 1898); Heteroptera: *Cimex pipistrelli* Jenyns, 1839, *Cacodmus vicinus* Horváth, 1934; Arachnida: *Argas transgariepinus* White, 1846. Bendjoudi *et al.* (2019: 71) and Khelfaoui *et al.* (2018: 68) furthermore found *Ixodes ricinus* (Linnaeus, 1758), *Steatonyssus occidentalis* (Ewing, 1933), *Ischnopsyllus octactenus* (Kolenati, 1856)

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Carios vespertilionis* Latreille, 1802, *Secretargas*

transgariepinus (White, 1846); Cicimidae: *Cacodmus vicinus* Horváth, 1934, *Cimex pipistrelli* Jenyns, 1839; Ischnopsyllidae: *Ischnopsyllus hispanicus* (Rothschild, 1898), *Nycteridopsylla longiceps* Rothschild, 1908; Ixodidae: *Ixodes ricinus* (Linnaeus, 1758); and Macronyssidae: *Steatonyssus occidentalis* (Ewing, 1933).

Sándor *et al.* (2021a: 4) reported the presence of the Argasid ticks *Secretargas transgariepinus* (White, 1846) and *Carios vespertilionis* Latreille, 1802. A larval specimen of *Secretargas transgariepinus* was also reported from Libya by Ševčík *et al.* (2024: 3), However, the tick was retrieved from a jar containing ticks from four "*Eptesicus isabellinus*", one *Myotis punicus* and four *Pipistrellus kuhlli*. Sándor *et al.* (2025: Suppl.) also mentioned the presence of the Ixodid tick Rhipicephalus sanguineus (Latreille, 1806) on bats from Algeria.

Martinoli and Spada (2020: 5) mentioned the following parasites: Acarina: *Spinturnix kolenatii* Oudemans, 1910, *Spinturnix psi* (Kolenati, 1856), *Spinturnix plecotinus* (Koch, 1839), *Steatonyssus occidentalis* (Ewing, 1933), *Macronyssus cyclaspi* (Oudemans, 1906), *Argas vespertilionis* (Latreille, 1796) - Diptera: *Basilia nattereri* (Kolenati, 1857) - Siphonaptera: *Ischnopsyllus intermedius* (Rothschild, 1898), *Nycteridopsylla pentactena* (Kolenati, 1856).

VIRUSES:
Coronaviridae - Coronaviruses
Betacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from Spain.

Papillomaviridae – Papillomaviruses
García-Pérez *et al.* (2014: 100) pointed out that there is no strict species specificity in papillomaviruses as they found DNA from EserPV2 and EserPV3 in pharyngeal swaps of both *Cnephaeus serotinus* and *C. isabellinus*.

Rhabdoviridae
"Various European bat lyssaviruses" were reported from various European countries by Kohl and Kurth (2014: 3114).

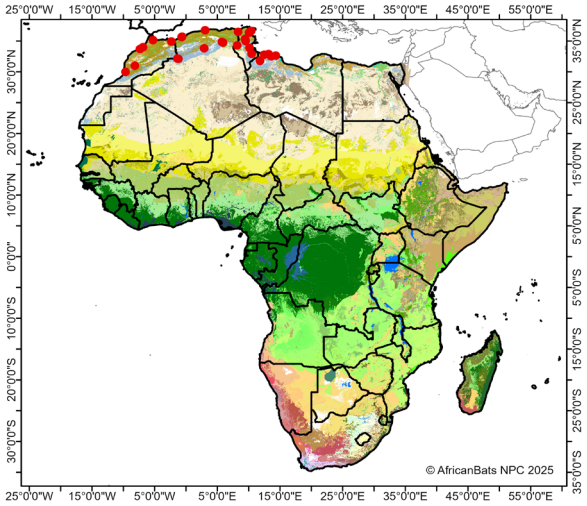

Figure 301. Distribution of *Cnephaeus isabellinus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Libya, Morocco, Tunisia.

Cnephaeus platyops (Thomas, 1901)

*1901. *Vespertilio platyops* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 31. Publication date: 1 July 1901. Type locality: Nigeria: Western region: Lagos [06 27 N 03 23 E]. [Goto Description]. Holotype: NHMUK 1888.5.17.3: ad ♀, skull and alcoholic. Presented/Donated by: George Edward Dobson. - Etymology: From the Greek "*platyops*" for broad-faced or flat-faced.
1939. *Eptesicus platyops:* G.M. Allen, Bull. Mus. comp. Zool., 83: 86. (Name Combination).
1969. *Eptesicus serotinus platyops:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 214. (Name Combination).
1980. *Eptesicus (Eptesicus) platyops:* Corbet and Hill, A world list of mammalian species, 69. (Name Combination).
1994. *E[ptesicus (Eptesicus)] s[erotinus] platyops:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 120. (Name Combination).
? *Cnephaeus platyops:* (Current Combination).

TAXONOMY:
Considered a subspecies of *C. serotinus* by Ibáñez and Valverde (1985) and Koopman (1994: 120), but no comparison with *C. bottae* was made.

COMMON NAMES:
Czech: netopýr nigerijský. English: Lagos Serotine Bat, Flat-faced Serotine Bat, Lagos Serotine. French: Sérotine à grands yeux, Sérotine de Lagos. German: Lagos-Breitflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements,

threats and conservation status (Schlitter, 2008a; IUCN, 2009; Schlitter, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) as *Eptesicus platyops* (Schlitter, 2019b). 2008: DD ver 3.1 (2001) (Schlitter, 2008a; IUCN, 2009). 2004: DD ver 3.1 (2001) (IUCN, 2004; Schlitter, 2004e). 1996: VU (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Schlitter, 2008a; IUCN, 2009; Schlitter, 2019b).

CONSERVATION ACTIONS:
Schlitter (2008a) [in IUCN (2009)] and Schlitter (2019b) reports that it is not known if the species is present in any protected areas and additional surveys are needed to try to locate and study a population of this species.

GENERAL DISTRIBUTION:
Cnephaeus platyops is a poorly known West African species known only from a few specimens. It is known from the type locality at Lagos in Nigeria, from specimens from the island of Bioko (Equatorial Guinea) (although these specimens may not have originated on Bioko) and from an unspecified locality in Senegal (Schlitter, 2008a). Senegal specimens were collected around 1900 (Happold, 1987).

Native: Nigeria (Happold, 1987).

Presence uncertain: Equatorial Guinea [= Bioko]; Senegal (Happold, 1987).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 94.6 minutes, and a digestibility rate of about 77.8 %.

POPULATION:
Structure and Density
There is no good information on the population abundance or size of this bat (Schlitter, 2008a; IUCN, 2009; Schlitter, 2019b).

Trend
2018: Unknown (Schlitter, 2019b). 2008: Unknown (Schlitter, 2008a; IUCN, 2009).

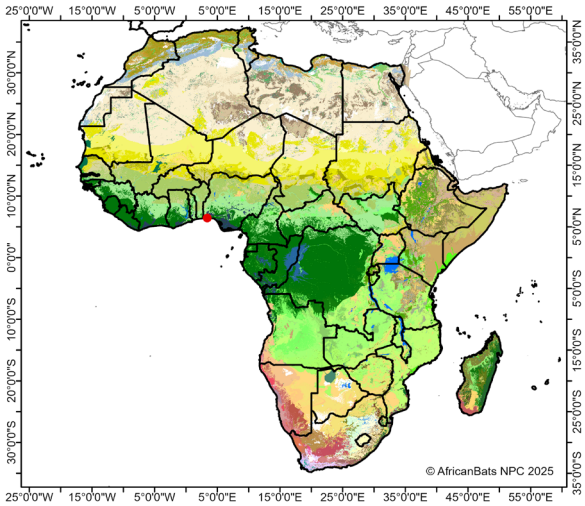

Figure 302. Distribution of *Cnephaeus platyops*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Nigeria, Senegal.

Subgenus *Cnephaeus (Rhinopterus)* Miller, 1906

*1906. *Rhinopterus* Miller, Proc. Biol. Soc. Wash., 19: 85. Publication date: 4 June 1906 [Goto Description]. - Comments: Type species: *Glauconycteris floweri* de Winton, 1901. The date mentioned on the publication is 4 June 1906, although in many cases 23 July 1906 is found as publication date.

Cnephaeus (Rhinopterus) floweri (de Winton, 1901)

*1901. *Glauconycteris Floweri* de Winton, Ann. Mag. nat. Hist., ser 7, 7 (37): 46. Publication date: 1 January 1901. Type locality: Sudan: 12 mi (18 km) S from Khartoum, on White Nile: Wad Marium [ca. 15 25 N 32 25 E]. [Goto Description]. Holotype: NHMUK 1903.2.7.14: ad ♂, skin and skull. Collected by: Mrs. Anderson and H.F. Witherby; collection date: 12 May 1900; original number: 35. - Comments: de Winton (1901b: 45) mentions Mr. H.F. Witherby as collector and the late Dr. John Anderson as acquirer.
1908. *S[cabrifer] floweri:* G.M. Allen, Bull. Mus. comp. Zool., 52 (3): 46. (Name Combination).
1915. *Rhinopterus lowei* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 559. Publication date: 1 June 1915. Type locality: Sudan: Blue Nile province: Sennaar, 20 mi (30 km) above [ca. 15 35 N 33 38 E, 450 m]. [Goto Description]. Holotype: NHMUK 1915.3.6.70: ad ♂, skull and alcoholic. Collected by: Willoughby P. Lowe; collection date: 13 December 1913.
1918. *Scabrifer floweri:* Wettstein, Denkschr. k. Akad. Wiss. Wien, Math.-Naturw. Kl., 94: 651. (Name Combination).

1939. *Rhinopterus floweri:* G.M. Allen, Bull. Mus. comp. Zool., 83: 97. (Name Combination).
1969. *Eptesicus (Rhinopterus) floweri:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 166. (Name Combination).
1971. *Eptesicus (Rhinopterus) lowei:* Hayman and Hill, Mammals of Africa: Chiroptera, 45. (Name Combination).
1974. *Eptesicus floweri:* Seal and Makey, ISIS Mammalian Taxonomic Director, ???. (Name Combination).
? *Cnephaeus (Rhinopterus) floweri:* (Current Combination).
? *Eptesicus (Rhinopterus) floweri lowei:* (Name Combination).

TAXONOMY:
Includes *lowei*; see Bræstrup (1935b: 92); but also see Hayman and Hill (1971).

COMMON NAMES:
Czech: netopýr Flowerův. English: Horn-skinned Pipistrelle Bat, Flower's Pipistrelle Bat, Horn-skinned Bat, Sudan Horn-skinned Bat, Lesser Sudan Horn-skinned Bat, Sudan Serotine, Horn-skinned Serotine. French: Sérotine de Flower, Sérotine du Soudan. German: Chagrin Fledermaus, Warzen-Breitflügelfledermaus.

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a broad range of non-threatened habitats, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017am).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Eptesicus floweri*] (Monadjem *et al.*, 2017am). 2008: LC ver 3.1 (2001) [assessed as *Eptesicus floweri*] (Jacobs *et al.*, 2008ah; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) [assessed as *Eptesicus floweri*] (Jacobs *et al.*, 2004at; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species (Jacobs *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017am). However, Siddig (2014: 548) mentions that the conflicts between Sudan and South Sudan, in combination with droughts form an important threat.

CONSERVATION ACTIONS:
Jacobs *et al.* (2008ah) [in IUCN (2009)] and Monadjem *et al.* (2017am) report that there appear to be no direct conservation measures in place, and it is not known if the species is present within any protected areas. Further studies are needed into the distribution and natural history of this poorly known species.

GENERAL DISTRIBUTION:
Cnephaeus (Rhinopterus) floweri has been recorded from Mali (Timbuktu) and Sudan (all records within a 200-mile radius of Ed Dueim) and Mahmûdé Lake, Wilaya Hodh Ech Chargui in Mauritania.

The identification of the two specimens from Mauritania (EBD 26179M and EBD 26180M) was confirmed by Padial and Ibáñez (2005: 240).

Native: Mali (Koopman, 1975); Mauritania (Padial and Ibáñez, 2005: 240); Sudan (Bræstrup, 1935b; Koopman, 1975).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 303. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1903.2.7.14, holotype of *Glauconycteris floweri* de Winton, 1901.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 89 minutes, and a digestibility rate of about 78.4 %.

POPULATION:
Structure and Density
It is known from very few specimens (Jacobs *et al.*, 2008ah; IUCN, 2009; Monadjem *et al.*, 2017am).

Trend
2016: Stable (Monadjem *et al.*, 2017am). 2008: Stable (Jacobs *et al.*, 2008ah; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Mauritania, Sudan.

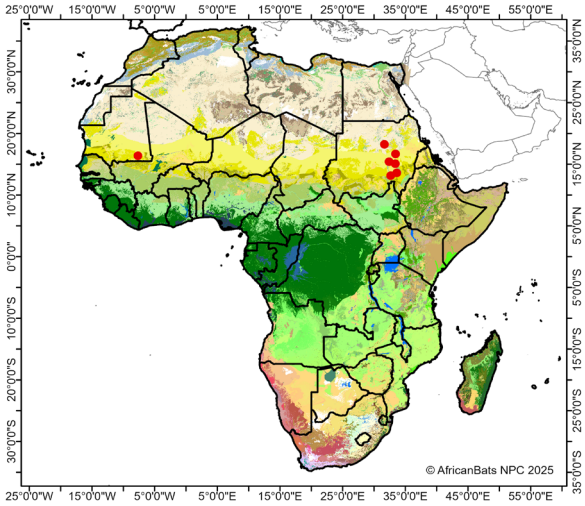

Figure 304. Distribution of *Cnephaeus (Rhinopterus) floweri*.

Genus ***Glauconycteris*** Dobson, 1875

1867. *Chalinolobus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 1866: 680. - Comments: in part. Type species: *Vespertilio tuberculatus* Forster, 1844 [= *Chalinolobus tuberculatus* (Forster, 1844: 62)], by monotypy (see Jackson and Groves, 2015: 271). - Phonetics: kal-in-oh-loh′-bus.

*1875. *Glauconycteris* Dobson, Proc. zool. Soc. Lond., 1875, III: 383. Publication date: October 1875. - Comments: Type species: *Kerivoula poensis* Gray, 1842. - Etymology: From the Greek "*γλαυκός*", meaning gray and "*γλαυκός*", meaning bat, referring to the fur, which is light gray or cream-colored at the tips (see Palmer, 1904: 295). Rambaldini (2010: 252) indicates that the Greek "glaucos" means bluish gray. Lanza *et al.* (2015: 349) indicate that the first part of the name is a feminine Latin adjective *glàuca*, meaning "glaucous, blue-green".

2013. *Niumbaha* Reeder, Helgen, Vodzak, Lunde and Ejotre. - ZooBank: EDF16BEE-0749-41BC-AE19-BAE130BE58F8.

2014. *Glauconycteries:* Rahoum, SJS, 6 (1): 45. Publication date: February 2014. (Lapsus).

2014. *Glauconyctris:* Rahoum, SJS, 6 (1): 45. Publication date: February 2014. (Lapsus).

2014. *Scotophyllus:* Rahoum, SJS, 6 (1): 45. Publication date: February 2014. (Lapsus).

2021. *Glauconysteris:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 5. Publication date: 14 May 2021. (Lapsus).

TAXONOMY:
Bronner *et al.* (2003) state that although occasionally treated as a subgenus of *Chalinolobus* (Koopman, 1971; Swanepoel *et al.*, 1980; Koopman, 1982; Meester *et al.*, 1986; Koopman, 1993a; Taylor, 1998: 49; Wilson and Cole, 2000), *Glauconycteris* has often been considered as a distinct genus (Allen, 1939a; Roberts, 1951; Ellerman *et al.*, 1953; Hayman and Hill, 1971; Corbet and Hill, 1980, 1992). Despite some superficial cranial resemblance, the marked difference in baculum morphology (Hill and Harrison, 1987) and karyotypic properties (Rautenbach *et al.*, 1993). Ansell and Dowsett (1988), Volleth and Heller (1994) and Eger and Schlitter (2001: 1) support the recognition of these taxa as discrete genera (N. Simmons in litt.). *Glauconycteris* is thus represented in the southern African subregion by a single species, *G. variegata* (butterfly bat), while *Chalinolobus* is extralimital (Australia).

Hassanin *et al.* (2017: 1) analysed the *Cytb* and RAG2 data of the various members of this genus and distinguished three lineage in the small sized species: the "*poensis*" (*G. poensis, G. alboguttata, G. argentata* and *G. egeria*); the "*beatrix*" group (*G. beatrix* and *G. curryae*); and the "*humeralis*" group (*G. humeralis* and *G. atra*).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Glauconycteris*: ***alboguttata*** J. A. Allen, 1917; ***argentata*** (Dobson, 1875); ***atra*** Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, 2017; ***beatrix*** Thomas, 1901; ***curryae*** Eger and Schlitter, 2001; ***egeria*** Thomas, 1913; ***gleni*** Peterson and Smith, 1973; ***humeralis*** J. A. Allen, 1917; ***kenyacola*** Peterson, 1982; ***machadoi*** Hayman, 1963; ***poensis*** (Gray, 1842); ***superba*** Hayman, 1939; ***variegata*** (Tomes, 1861).

COMMON NAMES:
Czech: motýlí netopýři. English: Butterfly Bats, Lobe-lipped Bats, Silvered Bats, Blue-grey Bats, Dobson's Bats, Glauconycterids. French: Glauconyctères, Murins à bajoues. German: Schmetterlingsfledermäuse. Italian: Glauconittèridi. Glauconictèridi.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Gabon, Guinea, Kenya, Liberia, South Africa, South Sudan, Tanzania.

Glauconycteris alboguttata J.A. Allen, 1917

*1917. *Glauconycteris alboguttatus* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 449, text-fig 7 B. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Medje [02 25 N 27 18 E, 800 m]. [Goto Description]. Holotype: AMNH 49317: ad ♀, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 14 March 1914; original number: 2351. - Etymology: From the Latin "*alboguttata*" meaning white spotted.
2021. *Glauconysteris albogutata:* Atagana, Bakwo Fils and Kekeunou, Trop. Cons. Sci., 14: 5. Publication date: 14 May 2021. (Lapsus).
? *Chalinolobus alboguttatus:* (Name Combination).
? *Glauconycteris alboguttata:* (Current Combination, Current Spelling).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr pruhovaný. English: Allen's Butterfly Bat, Striped Butterfly Bat, White-spotted Butterfly Bat, Allen's Striped Bat. French: Glauconyctère à gorge blanche, Murin à bajoues d'Allen, Barbastelle d'Allen. German: Gestreifte Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution (that is likely to be even wider than is currently known), extensive available habitat, presumed large overall population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017cn).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cn). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008c; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004e; IUCN, 2004). 1996: VU [assessed as *Chalinolobus alboguttatus*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known (Jacobs *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017cn).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008c) [in IUCN (2009)] and Monadjem *et al.* (2017cn) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the species distribution, natural history and threats.

GENERAL DISTRIBUTION:
Glauconycteris alboguttata is distributed in Central Africa where it has been recorded from Cameroon and the Democratic Republic of the Congo. The range is poorly known, and it may be distributed more widely (Jacobs *et al.*, 2008c).

Native: Cameroon; Congo (Bates *et al.*, 2013: 323 - 1st record); Congo (The Democratic Republic of the).

HABITAT:
This species is associated with lowland tropical moist forest (Jacobs *et al.*, 2008c).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 81 minutes, and the digestibility rate about 79.5 %.

POPULATION:
Structure and Density
It is generally considered to be rare, however, there have been few recent surveys within the species range (Jacobs *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017cn).

Trend
2016: Unknown (Monadjem *et al.*, 2017cn). 2008: Unknown (Jacobs *et al.*, 2008c; IUCN, 2009).

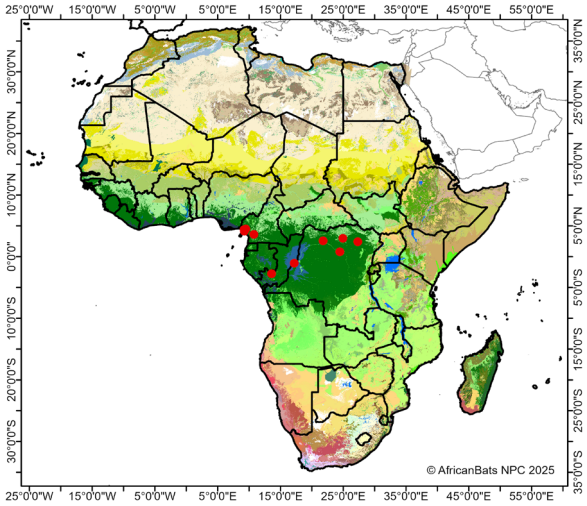

Figure 305. Distribution of *Glauconycteris alboguttata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo, Congo (Democratic Republic of the).

Glauconycteris argentata (Dobson, 1875)

*1875. *Chalinolobus argentatus* Dobson, Proc. zool. Soc. Lond., 1875, III: 385. Publication date: October 1875. Type locality: Cameroon: Western province: Mount Cameroon [04 13 N 09 11 E]. [Goto Description]. Holotype: NHMUK 1871.7.10.5: ad ♀, alcoholic (skull not removed). Purchased (see Dobson (1878: 254). - Etymology: From the feminine Latin adjective *argentàta*, meaning "silvery", referring to the "beautiful dark silvery gray" (Dobson, 1875c: 386) of the terminal third of the dorsal hairs (see Lanza *et al.*, 2015: 351).

1889. *Chalinolobus congicus* Noack, Zool. Jb. Syst., 4: 223, pl 2, fig 1; pl 5, fig 66 - 68. Publication date: 28 February 1889. Type locality: Congo (Democratic Republic of the): Bas Congo province: near mouth of Congo River, Banana Creek: Netonna [05 58 S 12 27 E]. [Goto Description]. Lectotype: SMF 2516: ad ♂, skull only. Collected by: P. Hesse. Mertens (1925: 22) considers this specimen to be a lectotype rather than "the" type. Paralectotype: SMF 11850: Collected by: P. Hesse. Paralectotype: SMF 11851: Collected by: P. Hesse. Paralectotype: SMF 11852: Collected by: P. Hesse. Paralectotype: SMF 11853: Collected by: P. Hesse. Paralectotype: SMF 11854: Collected by: P. Hesse. Paralectotype: SMF 11855: Collected by: P. Hesse. Paralectotype: SMF 2517: Collected by: P. Hesse. Paralectotype: SMF 2518: Collected by: P. Hesse. Paralectotype: SMF 2519: Collected by: P. Hesse. Paralectotype: SMF 2520: Collected by: P. Hesse. Paralectotype: SMF 2521: Collected by: P. Hesse. Paralectotype: SMF 2522: Collected by: P. Hesse. - Comments: Noack (1889: 22) refers to 8 specimens in alcohol 4 ♂♂ and 4 ♀♀, collected in April - May, by P. Hesse).

? *Glauconycteris argentata:* (Current Combination).

? *Glauconycteris argentatus:* (Name Combination, Alternate Spelling).

TAXONOMY:
See Simmons (2005).

Monadjem *et al.* (2016y: 368) collected a *Glauconycteris* specimen in the Mount Nimba area, which looked very similar to this species in measurements and colouration but differed from it by the colouration of its wings (not pale). They also indicated that as *G. argentata* has not been found west of Cameroon, their specimen might represent an undescribed species. Tentatively, they assigned their specimen to *G.* cf. *argentata*.

COMMON NAMES:
Chinese: 银蝶蝠. Czech: netopýr stříbrný. English: Common Butterfly Bat, Silvery Butterfly Bat, Silvered Butterfly Bat, Silvered Bat. French: Glauconyctère argentée, Murin à bajoues argenté, Barbastelle argentée. German: Silberne Schmetterlingsfledermaus. Italian: Glauconitterìde argentàta, Glauconicterìde argentàta. Tshokwe (Angola): Kafukufuku-mutoma.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008d; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008d; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004g; IUCN, 2004). 1996: LR/lc [assessed as part of *Chalinolobus argentatus*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Glauconycteris argentata is threatened in the western and eastern parts of its range by deforestation resulting from logging activities, and the conversion of land to agricultural use (Jacobs *et al.*, 2008d; IUCN, 2009).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008d) [in IUCN (2009)] report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further studies are needed into the distribution, natural history and threats to this little recorded species.

GENERAL DISTRIBUTION:
Glauconycteris argentata is widespread in Central and East Africa. It ranges from Cameroon and Equatorial Guinea (Rio Muni), into the Democratic Republic of the Congo, Rwanda, Burundi, Uganda, Kenya, Tanzania and possibly northern Malawi, with the southernmost record from northwestern Angola. The range is not well-known, and the species is expected to be distributed more widely than is currently known.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 562); Burundi (Hayman *et al.*, 1966); Cameroon; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 562); Equatorial Guinea (Jones, 1971); Gabon (1st record: Peereboom *et al.*, 2012 3); Kenya (Aggundey and Schlitter, 1984); Malawi (Ansell and Dowsett, 1988: 39; Monadjem *et al.*, 2010d: 562); Rwanda (Baeten *et al.*, 1984); Tanzania (Stanley and Goodman, 2011: 43).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
Peereboom *et al.* (2012: 4) report the following values: F_{min}: 28.42 - 34.45 (31.59 ± 1.48) kHz; F_{max}: 77.95 - 101.60 (89.16 ± 7.11) kHz, F_{peak}: 40.26 - 47.14 (43.96 ± 1.8) kHz, duration: 2.0 - 3.0 (2.4 ± 0.31) ms; first harm: 81.82 - 104.60 (94.04 ± 8.55), and interpulse interval: 24 - 128 (55 ± 34) ms.

From Kenya, López-Baucells *et al.* (2017: 24) reported some different values: F_{min}: 16.32 - 40.62 (35.20 ± 3.11) kHz, F_{max}: 41.37 - 75.09 (56.45 ± 9.40) kHz, F_{peak}: 36.19 - 44.77 (40.38 ± 1.68) kHz, duration: 0.7 - 8.52 (4.03 ± 1.86) ms, slope: -48.51 - -0.69 (-5.28 ± 6.19) kHz/ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 41 calls of 2 bats: F_{peak}: 42.5 ± 0.5 (42.2 - 42.9) kHz, F_{min}: 40.6 ± 0.1 (40.5 - 40.6) kHz, F_{max}: 75.1 ± 4.3 (64.8 - 78.2) kHz, duration: 1.7 ± 0.1 (1.6 - 1.8) ms.

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Recorded from lowland tropical moist forest and moist savanna habitats.

ROOST:
At Uzungwa Scarp Forest Reserve, Tanzania, Trentin and Rovero (2011: 51) reported a group of 10 females and their young to roost underneath the leaves of palm trees.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 85 minutes, and the digestibility rate about 78.9 %.

POPULATION:
Structure and Density
This is a rarely recorded, poorly known species (Jacobs *et al.*, 2008d; IUCN, 2009).

Trend
2008: Unknown (Jacobs *et al.*, 2008d; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Trentin and Rovero (2011: 51) observed about 10 adult females with young in December 2005 at Uzungwa Scarp Forest Reserve, Tanzania.

VIRUSES:
Phenuiviridae
Phlebovirus
de Jong *et al.* (2011: 11), Luis *et al.* (2013: Suppl.), and Willoughby *et al.* (2017: Suppl.) report the occurrence of Rift Valley fever virus.

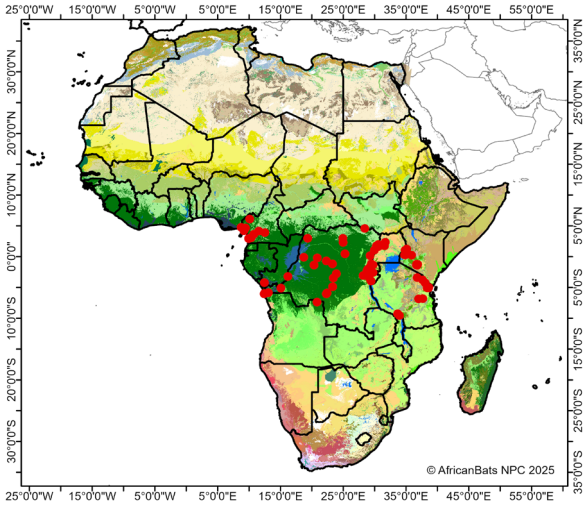

Figure 306. Distribution of *Glauconycteris argentata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Burundi, Cameroon, Congo, Congo (Democratic Republic of the), Kenya, Rwanda, South Sudan, Tanzania, Uganda.

Glauconycteris atra Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, 2017

*2017. *Glauconycteris atra* Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, J. Syst. Evol. Res., 56 (1): 6, fig 2 (for 2018). Publication date: 22 August 2017. Type locality: Congo (Democratic Republic of the): Tshopo province: Yaengo [00 20 56 N 24 28 55 E, 400 m]. Holotype: MNHN ZM-2016-2792: ad ♀, skull and alcoholic. Collected by: Alexandre Hassanin, Guy-Crispin Gembu Tungaluna, Prescott Musaba Akawa, Raphaël Colombo, Tamás Görföl and Vuong Tam Tu; collection date: 5 December 2013; original number: K13-215. - Etymology: Atra refers to the colour of the pelage, which is dark and gloomy (blackish brown) (see Hassanin *et al.*, 2017: 6). (Current Combination).

COMMON NAMES:
English: Blackish Butterfly Bat. French: Glauconyctère sombre. German: Dunkle Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Known only from three localities in the riparian zone on the left bank of the Congo River (DRC).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

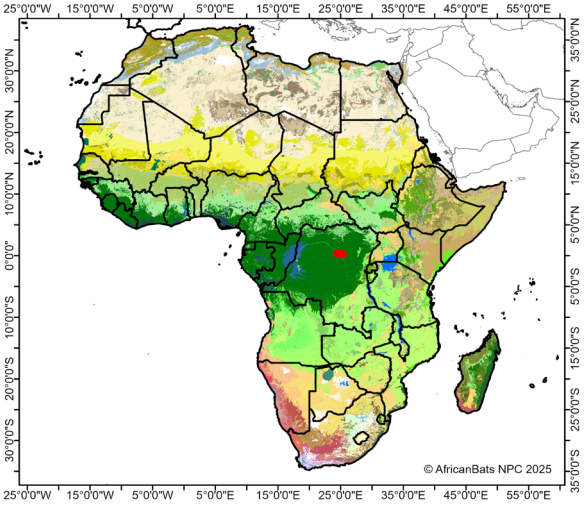

Figure 307. Distribution of *Glauconycteris atra*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the).

Glauconycteris beatrix Thomas, 1901

*1901. *Glauconycteris beatrix* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (45): 256. Publication date: 1 September 1901 [Goto Description]. Holotype: NHMUK 1898.5.4.19: ♀. Collected by: George Latimer Bates Esq. Collection

date: January 1898. - Comments: Equatoria Guinea: Rio Muni, Benito River, 15 mi. (24 km) from mouth. (Grubb *et al.* (1998: 89) mention "Benito River, French Congo, fifteen miles from mouth [Mbini River, in Equatorial Guinea]". (Current Combination).

1998. *Glauconycteris beatrix beatrix:* Grubb, Jones, Davies, Edberg, Starin and Hill, Mammals of Ghana, Sierra Leone and The Gambia, 89. (Name Combination).

? *Chalinolobus beatrix:* (Name Combination).

TAXONOMY:
Koopman (1993a: 199) included *humeralis*; see Koopman (1971: 7, 8), but see Simmons (2005).

COMMON NAMES:
Castilian (Spain): Murciélago Mariposa. Czech: netopýr rovníkový. English: Beatrix Bufferfly Bat, Beatrix's Bat. French: Glauconyctère de Béatrix, Murin à bajoues de Béatrice, Barbastelle de Béatrix. German: Kleine Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1, 2001) in view of its wide distribution, presumed large population (especially in Central Africa), and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017cp).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cp). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008e; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004f; IUCN, 2004). 1996: LR/nt [assessed as *Chalinolobus beatrix*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is threatened by general habitat loss, often resulting from logging activities and the conversion of land to agricultural use (Jacobs *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017cp).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008e) [in IUCN (2009)] and Monadjem *et al.* (2017cp) suggest that this species has been recorded from a number of protected areas and further studies are needed into the distribution, natural history and threats to this little-known bat.

GENERAL DISTRIBUTION:
Glauconycteris beatrix is distributed in West and Central Africa. It ranges from Côte d'Ivoire in the west, through Ghana and Nigeria to Cameroon and Equatorial Guinea (Rio Muni and Bioko), with scattered records from Gabon, Central African Republic, Angola and the Democratic Republic of the Congo.

Native: Angola (Eger and Schlitter, 2001; Monadjem *et al.*, 2010d: 562); Cameroon; Central African Republic (Heller *et al.*, 1994; Lunde *et al.*, 2001: 537); Congo (Bates *et al.*, 2013: 324 - 1st authenticated record); Congo (The Democratic Republic of the) (Monadjem *et al.*, 2010d: 562); Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Guinea-Bissau (Rainho and Ranco, 2001: 69); Nigeria (Happold, 1987).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Sanborn (1953: 166) reports a male specimen, collected in Gabon, which looks very similar to the description of *G. beatrix*, but has a small tuft of white hairs on each shoulder, but he also indicates that this character is sometimes variable, as was already mentioned by Hayman and Jones (1950: 762).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
In their study on the reversibility of the mandibular symphyseal fusion, Scott *et al.* (2012: 2943) mention that in this species the symphysis is unfused with smooth surfaces.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Heller *et al.* (1994: 6).

MOLECULAR BIOLOGY:
Karyotype
Volleth and Heller (2008) reported 2*n* = 22, FN = 40, only bi-armed chromosomes and an autosome-X translocation for a female from the Democratic Republic of Congo. Porter *et al.* (2010) report for Gabon 2*n* = 22, with all chromosomes being distinctly biarmed, with ten pairs are metacentric or slightly submetacentric and one pair (the smallest) is subtelocentric. 2 *n* = 22 was also reported by Volleth and Eick (2012: 167), who also mention a segment number of 24.

Sotero-Caio *et al.* (2017: 3) indicate that the pericentromeric regions of the chromosomes show an increased amount of heterochromatin.

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
This species is generally associated with lowland tropical moist forest (Happold, 1987).

ROOST:
There appears to be little information available on the roosting habits of this species, but presumably it can be found within hollow trees and dense vegetation (Jacobs *et al.*, 2008e).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 76 minutes, and the digestibility rate about 80.1 %.

POPULATION:
Structure and Density
This appears to be a rare, or at least a rarely recorded, species (Jacobs *et al.*, 2008e; IUCN, 2009; Monadjem *et al.*, 2017cp).

Trend
2016: Unknown (Monadjem *et al.*, 2017cp).
2008: Unknown (Jacobs *et al.*, 2008e; IUCN, 2009).

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
One faecal sample, collected in Febuary 2008 in Ghana, tested negative for coronavirus (CoV) RNA (Pfefferle *et al.*, 2009).

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen they examined from Ghana did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

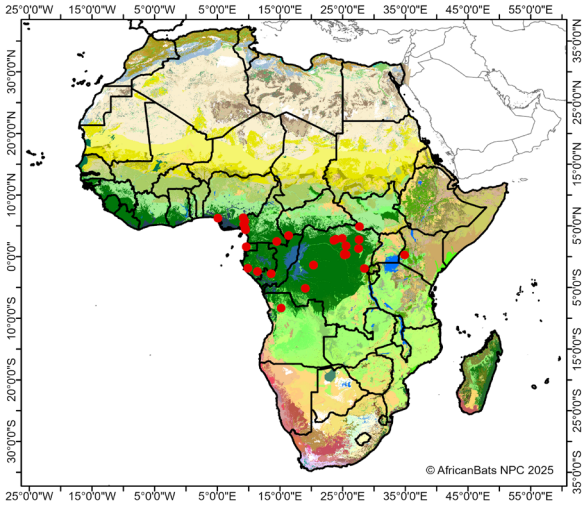

Figure 308. Distribution of *Glauconycteris beatrix*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Equatorial Guinea, Gabon, Kenya, Nigeria, South Sudan, Uganda.

Glauconycteris cf. beatrix Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, 2017

2017. *G[lauconycteris] cf. beatrix:* Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, J. Syst. Evol. Res., 56 (1): 7 (for 2018). Publication date: 22 August 2017.
*2017. *Glauconycteris cf. beatrix:* Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, J. Zool. Syst. Evol. Res., 56 (1): Suppl (for 2018). Publication date: 22 August.
? *Glauconycteris beatrix:* (Name Combination).

TAXONOMY:
In their study on the multilocus phylogeny of *Glauconycteris* specimens from the DRC, Hassanin *et al.* (2017: 7) found a number of specimens in the collection of the ROM that were identified as *G. beatrix* but scored very different in their analyses as compared to other specimens assigned to this species. Their scores were much more like those of *G. curryae*, which seemed to be related to the length of the tail and the skull profile. Their analyses of the mitochondrial tree (*CO1, Cytb* and *12S* genes), however, showed these specimens not to be directly related to either *beatrix* or *curryae*, but closer to *humeralis*. Further investigation is necessary to elucidate this problem.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana.

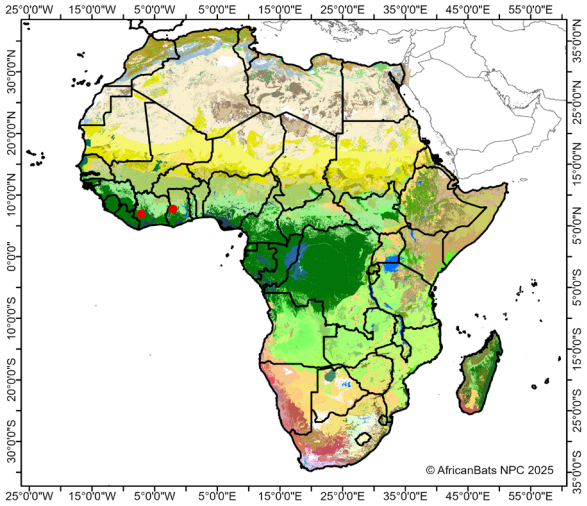

Figure 309. Distribution of *Glauconycteris* cf. *beatrix*.

Glauconycteris cf. humeralis Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, 2017

2017. *G[lauconycteris] cf. humeralis:* Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, J. Syst. Evol. Res., 56 (1): 6 (for 2018). Publication date: 22 August 2017.
*2017. *Glauconycteris cf. humeralis:* Hassanin, Colombo, Gembu, Merle, Tu, Görföl, Musaba Akawa, Csorba, Kearney, Monadjem and Ing, J. Zool. Syst. Evol. Res., 56 (1): Suppl (for 2018). Publication date: 22 August 2017.

TAXONOMY:
For their study on the multilocus phylogeny of *Glauconycteris* specimens from the DRC, Hassanin *et al.* (2017: 6) used data collected from two specimens from the Central African Republic, which were originally identified as *G. humeralis*. Their analyses indicated that these specimens were quite different from the other *humeralis* included and suggested that they might represent a new species. Unfortunately, however, these two animals were released after the biopsy was taken. Therefore, Hassanin *et al.* (2017: 16) did not describe this species as new.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Tanshi *et al.* (2022a: 317) mention this species from Nigeria.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

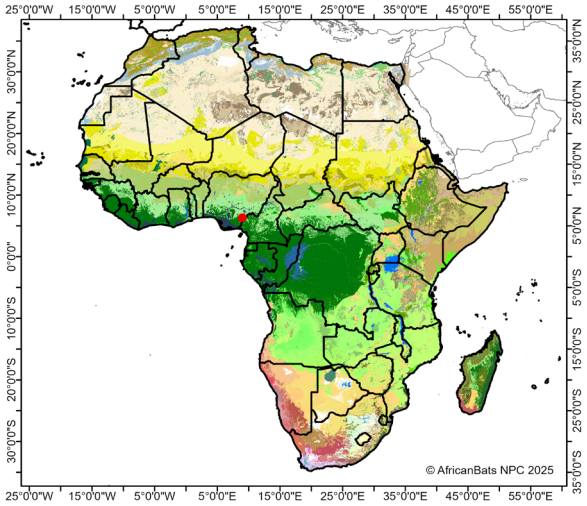

Figure 310. Distribution of *Glauconycteris* cf. *humeralis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Nigeria.

Glauconycteris curryae Eger and Schlitter, 2001

2001. *Glauconycteris curryae:* Eger, Acta Chiropt., 3 (2): 248. (Current Combination, Emendation, Current Spelling).
*2001. *Glauconycteris curryi* Eger and Schlitter, Acta Chiropt., 3 (1): 2, figs 1 - 4. Type locality: Cameroon: Bipindi, 10 km W [03 05 N 10 25 E, ca. 300 m]. [Goto Description]. Holotype: ROM 56243: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, Robert M. Glen and Philip Imbayi; collection date: 19 February 1970. Note: netted over a pool in a vast stand of bamboo, by a river (see Eger and Schlitter (2001: 2). - Etymology: Named in honour of Noreen Curry, in recognition of her interest in bats and her support of Royal Ontario Museum field research in Africa and bat education at the ROM (see Eger and Schlitter, 2001).
? *Chalinolobus curryi:*

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr konžský. English: Curry's Butterfly Bat, Curry's Bat. French: Glauconyctère de Curry. German: Currys Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) since it has only recently been described, and there is still very little information on its extent of occurrence, status, threats and ecological requirements (Schlitter, 2008b; IUCN, 2009; Schlitter, 2019c).

Assessment History
Global
2018: DD ver 3.1 (2001) (Schlitter, 2019c). 2008: DD ver 3.1 (2001) (Schlitter, 2008b; IUCN, 2009). 2004: DD ver 3.1 (2001) (Schlitter, 2004f; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Schlitter, 2008b; IUCN, 2009; Schlitter, 2019c).

CONSERVATION ACTIONS:
Schlitter (2008b) [in IUCN (2009)] and Schlitter (2019c) suggests that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:
Glauconycteris curryae is a Central African species, known only from southern Cameroon, Gabon and a single locality in the Democratic Republic of the Congo (Yalosemba North of the River).

Native: Cameroon; Congo (The Democratic Republic of the), Gabon.

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2023a: 8) mention this species has the largest amount of constitutive heterochromatin (cH) (> 40% of the total autosome length) of all the species they examined, and a karyotype composed of only 22 chromosomes.

HABITAT:
This species has been recorded from lowland tropical moist forest and swamp forest (Schlitter, 2008b).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 79 minutes, and the digestibility rate about 79.7 %.

POPULATION:
Structure and Density
Population size unknown (Schlitter, 2008b; IUCN, 2009). The area where this species has been recorded is often
inaccessible and it is difficult to catch this species (Schlitter, 2019c).

Trend
2018: Unknown (Schlitter, 2019c). 2008: Unknown (Schlitter, 2008b; IUCN, 2009).

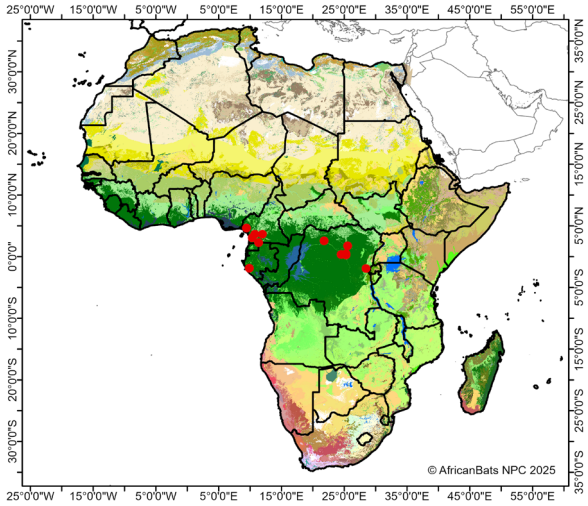

Figure 311. Distribution of *Glauconycteris curryae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Gabon.

Glauconycteris egeria Thomas, 1913

*1913. *Glauconycteris egeria* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (61): 144. Publication date: 1 January 1913. Type locality: Cameroon: Western province: Bibundi [04 15 N 08 58 E]. [Goto Description]. Holotype: NHMUK 1912.12.13.3: ♂. Original number: 22. Presented/Donated by: Prof. E. Lampe (Wiesbaden Museum). (Current Combination).
2015. *Chalinolo busegeria:* Carr et al., Ecosystem profile, 18. Publication date: 31 December 2015. (Lapsus).
? *Chalinolobus egeria:* (Name Combination).
? *Chalinolobus egerius:* (Name Combination).
? *G[lauconycteris] cf egeria:* (Name Combination).
? *Glauconycteris poensis:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr bibundinský. English: Bibundi Bufferfly Bat, Bibundi Bat. French: Glauconyctère de Bibundi, Murin à bajoues de Bibundi, Barbastelle du Bibundi. German: Bibundi Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Jacobs *et al.*, 2008f; IUCN, 2009; Jacobs *et al.*, 2019b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019b). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008f; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004n; IUCN, 2004). 1996: LR/lc [concern assessed as *Chalinolobus egeria*] (Baillie and Groombridge, 1996: 137).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs *et al.*, 2008f; IUCN, 2009; Jacobs *et al.*, 2019b).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008f) [in IUCN (2009)] and Jacobs *et al.* (2019b) report that it has been recorded from the Dzanga-Sangha Special Dense Forest Reserve in the Central African Republic (Lunde *et al.*, 2001), and may be present in additional protected areas. Further field surveys are needed to better determine the distribution, natural history and possible threats to this little-known bat.

GENERAL DISTRIBUTION:
Currently only been recorded from three localities. The type locality is Bibundi in the Western Province of Cameroon (Thomas, 1913b); three individuals (as *G.* cf. *egeria*) were collected from Dzanga-Sangha Special Dense Forest Reserve in the Central African Republic (Lunde *et al.*, 2001); the species indicated as being present in western Uganda by Koopman (1993a: 199), although further details are needed of the collection site in this country (Jacobs *et al.*, 2008f; IUCN, 2009).

Native: Cameroon (Thomas, 1913b); Central African Republic (Lunde *et al.*, 2001); Nigeria (Tanshi *et al.*, 2022a: 317).

Presence uncertain: Uganda (Koopman, 1993a; Simmons, 2005: 487).

ECHOLOCATION:
From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 24 calls of 2 bats: F_{peak}: 26.3 ± 2.5 (21.5 - 37.0) kHz, F_{min}: 22.0 ± 2.1 (19.9 - 26.1) kHz, F_{max}: 53.8 ± 2.6 (47.3 - 56.2) kHz, duration: 2.6 ± 0.6 (1.6 - 3.3) ms.

HABITAT:
Lunde *et al.* (2001) recorded three specimens (allocated to *G.* cf. *egeria*) collected in dense secondary tropical lowland forest and along a forest road. Bakwo Fils *et al.* (2021b: 6) reported one specimen collected in undisturbed Afromontane forest in Cameroon.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 81 minutes, and the digestibility rate about 79.5 %.

POPULATION:
Structure and Density
This species is known from very few specimens (Jacobs *et al.*, 2008f; IUCN, 2009; Jacobs *et al.*, 2019b).

Tend
2018: Unknown (Jacobs *et al.*, 2019b). 2008: Unknown (Jacobs *et al.*, 2008f; IUCN, 2009).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Central African Republic, Nigeria, Uganda.

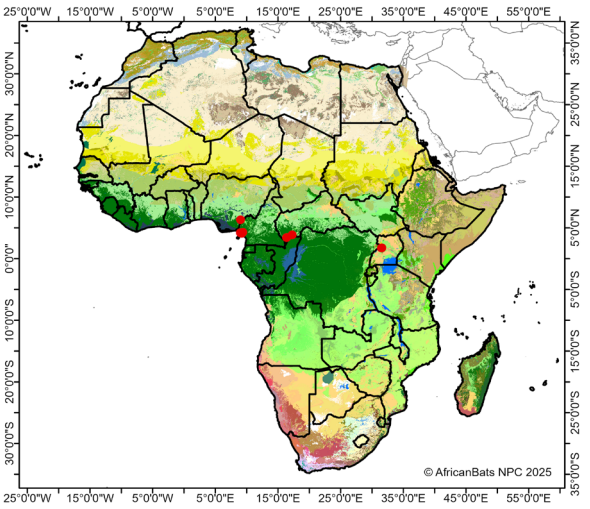

Figure 312. Distribution of *Glauconycteris egeria*.

Glauconycteris gleni Peterson and Smith, 1973

*1973. *Glauconycteris gleni* Peterson and Smith, Life Sci. Occ. Pap., R. Ont. Mus., 22: 3, figs 1 - 4. Publication date: 17 August 1973. Type locality: Cameroon: near Lomie [ca. 03 10 N 13 37 E]. [Goto Description]. Holotype: ROM 57125: ad ♀, skin and skull. Collected by: Robert M. Glen and Vincent N. Ngam; collection date: 16 June 1970. - Etymology: In honour of Mr. Robert Glenn, Nairobi, Kenya, who collected the holotype, assisted in the collection of the Uganda series of the new species, and who has been a field companion extraordinaire. (see Peterson and Smith, 1973: 1). (Current Combination).
? *Chalinolobus gleni:* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr Glenův. English: Glen's Butterfly Bat, Glen's Wattled Bat. French: Glauconyctère de Glen, Murin à bajoues de Glen, Barbastelle de Glen. German: Glens Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Jacobs *et al.*, 2008g; IUCN, 2009; Jacobs *et al.*, 2019a).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019a). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008g; IUCN, 2009). 2004: VU D1 ver 3.1 (2001) (Jacobs *et al.*, 2004m; IUCN, 2004). 1996: LR/nt [assessed as *Chalinolobus gleni*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is presumably threatened in parts of its range by logging and the conversion of forest habitat to agricultural use (Jacobs *et al.*, 2008g; IUCN, 2009; Jacobs *et al.*, 2019a).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008g) [in IUCN (2009)] and Jacobs *et al.* (2019a) report that there appear to be no direct conservation measures in place for this species. It is not known if the species is present within any protected areas. Additional studies are needed into the distribution, abundance, general ecology and potential threats to this species.

GENERAL DISTRIBUTION:
Glauconycteris gleni is a poorly known species and has only been recorded from the three localities in Africa. The type locality 'near Lomie' in Cameroon, from a single site in western Uganda and Tanzania (1st record: Stanley and Foley, 2008: 119).

Native: Cameroon, Tanzania (Stanley and Foley, 2008: 119); Uganda.

HABITAT:
This poorly known bat is associated with lowland tropical moist forest.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 92 minutes, and the digestibility rate about 78.1 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008g; IUCN, 2009; Jacobs *et al.*, 2019a).

Trend
2018: Unknown (Jacobs *et al.*, 2019a). 2008: Unknown (Jacobs *et al.*, 2008g; IUCN, 2009).

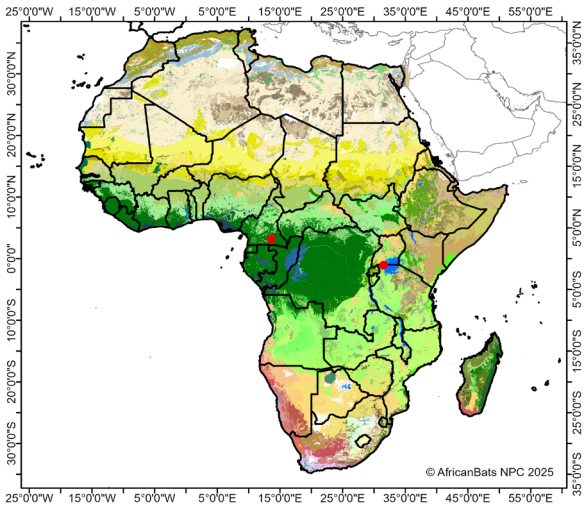

Figure 313. Distribution of *Glauconycteris gleni*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Tanzania.

Glauconycteris humeralis J.A. Allen, 1917

*1917. *Glauconycteris humeralis* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 448, text-fig 7 A. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Medje [02 25 N 27 18 E, 800 m]. [Goto Description]. Holotype: AMNH 49013: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 7 September 1910; original number: 956. (Current Combination).
? *Chalinolobus humeralis:* (Name Combination).
? *Glauconycteris beatrix humeralis:* (Name Combination).
? *Glauconycteris beatrix:* (Name Combination).
? *Glauconycteris cf. humeralis R13-98*

TAXONOMY:
Included in *beatrix* by Koopman (1993a: 199), considered a subspecies of *beatrix* by Eger and Schlitter (2001), but considered a valid species by Simmons (2005).

COMMON NAMES:
Chinese: 花蝶蝠. Czech: netopýr medžeský. English: Allen's Spotted Bat. French: Glauconyctère tachetée. German: Gefleckte Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Schlitter, 2008c; IUCN, 2009; Schlitter, 2019d).

Assessment History
Global
2018: DD ver 3.1 (2001) (Schlitter, 2019d). 2008: DD ver 3.1 (2001) (Schlitter, 2008c; IUCN, 2009).

2004: DD ver 3.1 (2001) (Schlitter, 2004k; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known. It may be threatened within parts of its range by deforestation resulting from logging and mining activities, and the conversion of forest to farmland (Schlitter, 2008c; IUCN, 2009; Schlitter, 2019d).

CONSERVATION ACTIONS:
Schlitter (2008c) [in IUCN (2009)] and Schlitter (2019d) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the distribution, natural history and threats to this poorly known forest species.

GENERAL DISTRIBUTION:
Native: Congo (The Democratic Republic of the) (Stephan *et al.*, 1987: 71; Heller *et al.*, 1994: 6; Eger and Schlitter, 2001: 7); Tanzania (Stanley and Foley, 2008: 119); Uganda.

Presence uncertain: Kenya (Aggundey and Schlitter, 1984).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 65 minutes, and the digestibility rate about 81.9 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Schlitter, 2008c; IUCN, 2009; Schlitter, 2019d).

Trend
2018: Unknown (Schlitter, 2019d). 2008: Unknown (Schlitter, 2008c; IUCN, 2009).

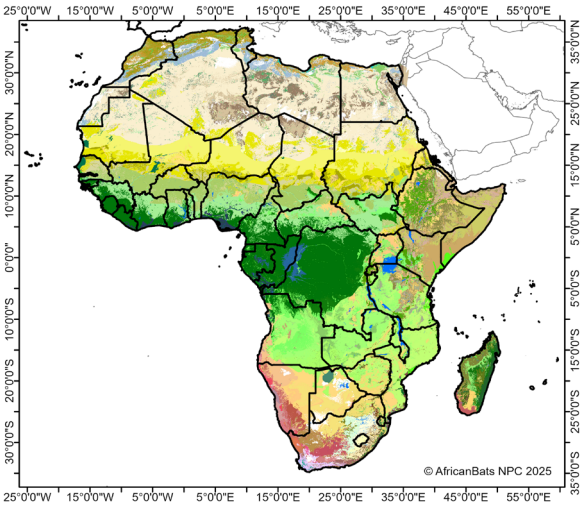

Figure 314. Distribution of *Glauconycteris humeralis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Congo (Democratic Republic of the), Kenya, Tanzania, Uganda.

Glauconycteris kenyacola Peterson, 1982

*1982. *Glauconycteris kenyacola* Peterson, Can. J. Zool., 60: 2521, figs 1 - 4. Type locality: Kenya: Coast province: on Galole road: Garsen, 8.5 km N [02 12 S 40 05 E]. [Goto Description]. Holotype: ROM 71305: ad ♀, skin and skull. Collected by: Judith L. Eger and Robert M. Glen; collection date: 30 December 1970. - Etymology: From the geographical scientific Latin substantive *Kènya* and the Latin suffix -còla (-còla) "denoting one who inhabits", i.e. the species is an inhabitant of Kenya (see Peterson, 1982: 2522; Lanza *et al.*, 2015: 355. (Current Combination).
? *Chalinolobus kenyacola:* (Name Combination).
? *Chalinolobus kenyacolus (?):* (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Chinese: 肯尼亚蝶蝠. Czech: netopýr keňský. English: Kenyan Butterfly Bat, Kenyan Wattled Bat, Kenya Barbastelle. French: Glauconyctère du Kenya, Murin à bajoues du Kenya, Barbastelle du Kenya. German: Kenya-Schmetterlingsfledermaus. Italian: Glauconitterìde keniòta, Glauconicterìde keniòta.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Jacobs *et al.*, 2008h; IUCN, 2009; Jacobs *et al.*, 2019f).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019f). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008h; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004l; IUCN, 2004). 1996: DD [assessed as *Chalinolobus kenyacola*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are unclear. If it is associated with coastal forest habitats, it is likely to be threatened by extraction of wood and conversion of land to agricultural use (Jacobs *et al.*, 2008h; IUCN, 2009; Jacobs *et al.*, 2019f).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008h) [in IUCN (2009)] and Jacobs *et al.* (2019f) report that it is not known if this species is present in any protected area. There is a need for additional field surveys to better understand the distribution, natural history and possible threats to this little-known species.

GENERAL DISTRIBUTION:
Glauconycteris kenyacola has only been recorded from the type locality of 'Galole Road, 8.5 km north of Garsen, Coast Province, Kenya' (Peterson, 1982).

Native: Kenya (Peterson, 1982; Aggundey and Schlitter, 1984).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 74 minutes, and the digestibility rate about 80.4 %.

POPULATION:
Structure and Density
This species is known only from the type collection (Jacobs *et al.*, 2008h; IUCN, 2009; Jacobs *et al.*, 2019f).

Trend
2018: Unknown (Jacobs *et al.*, 2019f). 2008: Unknown (Jacobs *et al.*, 2008h; IUCN, 2009).

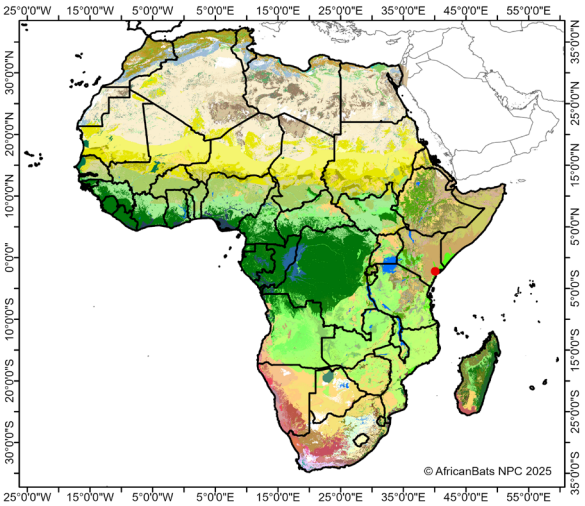

Figure 315. Distribution of *Glauconycteris kenyacola*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Glauconycteris machadoi Hayman, 1963

*1963. *Glauconycteris machadoi* Hayman, Publ. Cult. Comp. Diamantes Angola, Lisboa, 66: 107. Type locality: Angola: Lac Calundo [11 48 S 20 52 E]. [Goto Description]. Holotype: NHMUK 1962.2074. - Etymology: In honour of Dr. A. de Barros Machado, whose researches into the zoology of the Lunda District of Angola have proved so fruitful in many directions (see Hayman, 1963: 107)... (Current Combination).
? *Chalinolobus machadoi:* (Name Combination).

TAXONOMY:
Included in *variegata* as a melanistic population by Koopman (1993a: 200), but considered a valid species by Simmons (2005).

COMMON NAMES:
Czech: netopýr Machadův. English: Machado's Butterfly Bat. French: Glauconyctère de Machado. German: Machados Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Schlitter, 2008d; IUCN, 2009; Schlitter, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) (Schlitter, 2019a). 2008: DD ver 3.1 (2001) (Schlitter, 2008d; IUCN, 2009). 2004: DD ver 3.1 (2001) (Schlitter, 2004d; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Schlitter, 2008d; IUCN, 2009; Schlitter, 2019a).

CONSERVATION ACTIONS:
Schlitter (2008d) [in IUCN (2009)] and Schlitter (2019a) reports that this species does not appear to be present in a protected area. Further taxonomic studies are needed for this species, as is field research into the distribution, natural history and possible threats to this little-known species.

GENERAL DISTRIBUTION:
Glauconycteris machadoi has only been recorded from the type locality of 'Lac Calundo'. in eastern Angola (see Rambaldini, 2010: 252).

Native: Angola (Hayman, 1963).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 79 minutes, and the digestibility rate about 79.7 %.

POPULATION:
Structure and Density
It is known only from the holotype (Schlitter, 2008d; IUCN, 2009; Schlitter, 2019a).

Trend
2018: Unknown (Schlitter, 2019a). 2008: Unknown (Schlitter, 2008d; IUCN, 2009).

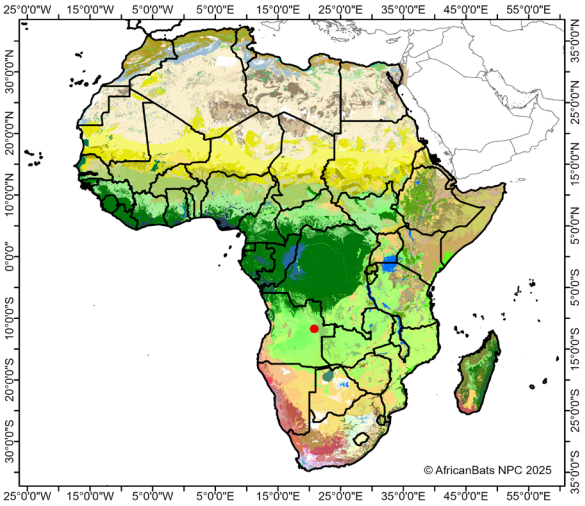

Figure 316. Distribution of *Glauconycteris machadoi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola.

Glauconycteris poensis (J. E. Gray, 1842)

*1842. *Kerivoula poensis* J. E. Gray, Ann. Mag. nat. Hist., [ser 1], 10 (65): 258. Publication date: 1 December 1842. Type locality: Nigeria: Lower Niger River: Abo [=Aboh] [05 33 N 06 32 E]. Holotype: NHMUK 1842.11.4.33. - Comments: Type locality originally "Fernando Po", but in reality Abo, Lower Niger: see Allen and Thomson, Exp. Niger, 2: 479, 1848 in Allen, 1939a: 88, Grubb *et al.*, 1998: 89). Dobson (1878: 256) mentions an ad skull, as type presented by T. Thompson, Esq. R.N., originating from Fernando Po.
1868. *Vesperus (Hesperoptenus) kraussii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 638. Publication date: 1868. Type locality: Nigeria: S Nigeria: Yoruba. - Comments: Type specimen: SMNH ???, ad ♀ (see Dobson, 1878: 255). (Name Combination).
? *Chalinolobus poensis:* (Name Combination).
? *Glauconycteris poensis:* (Name Combination, Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr abonský. English: Abo Butterfly Bat, Abo Bat. French: Glauconyctère d'Abo, Murin à bajoues d'Abo, Barbastelle d'Abo. German: Abo-Schmetterlingsfledermaus, Westafrikanische Nachtfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017cq).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cq). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008l; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004k; IUCN, 2004). 1996: LR/nt [assessed as *Chalinolobus poensis*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
It is presumably threatened in parts of its range by habitat loss resulting from logging and similar activities (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017cq).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008l) [in IUCN (2009)] and Monadjem *et al.* (2017cq) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected area. Further field surveys are needed to better determine the distribution of this species, and to gather additional information on the natural history of this little-known bat.

GENERAL DISTRIBUTION:
Glauconycteris poensis is largely distributed in West and Central Africa, with a possible record from northeastern Tanzania. It ranges from Senegal in the west, through much of West Africa to Cameroon, Equatorial Guinea (the island of Bioko) and the Democratic Republic of the Congo in Central Africa.

Native: Benin (Capo-Chichi *et al.*, 2004: 162); Cameroon; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966); Côte d'Ivoire; Equatorial Guinea (Bioko); Ghana (Jeffrey, 1975; Decher and Fahr, 2007: 20); Guinea (Fahr *et al.*, 2006a: 74); Guinea-Bissau (Rainho and Ranco, 2001: 68); Liberia (Koopman, 1989b; Koopman *et al.*, 1995; Monadjem and Fahr, 2007: 50); Nigeria (Happold, 1987); Senegal; Sierra Leone; Tanzania (Stanley and Foley, 2008: 119); Togo.

Presence uncertain: Kenya.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Hayman and Jones (1950) mention a large variation in shoulder spots and flank stripes in individuals from Sierra Leone, sometimes being asymmetrical (a spot on one shoulder only). During their study of *Glauconycteris*, Hassanin *et al.* (2017: 16) never found asymmetrical spots in *G. poensis*, and they therefore caution the statement by Hayman and Jones (1950) and indicate that the specimens from Sierra Leone should be re-examined to confirm their identification.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Heller *et al.* (1994: 6).

ECHOLOCATION:
In Benin, the bat's call was categorized as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype by Roemer *et al.* (2021: Suppl.).

MOLECULAR BIOLOGY:
Karyotype
Porter *et al.* (2010) report for Gabon $2n = 22$, with all chromosomes being distinctly biarmed, with ten pairs are metacentric or slightly submetacentric and one pair (the smallest) is subtelocentric. The lack of chromosomal heteromorphism in the male suggests a neo-XY sex determining system in this species.

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Associated with lowland tropical moist forest (Happold, 1987).

In the Mount Nimba area, Monadjem *et al.* (2016y: 368) found this species widely present in forested habitats, in degraded secondary forests as well as on the edge of a small village, at altitudes between 450 and 880 m.

ROOST:
Roost in holes in trees, on the fronds of coconut palms, and presumably in similar vegetation (Rosevear, 1965; Jeffrey, 1975; Happold, 1987).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 73 minutes, and the digestibility rate about 80.6 %.

POPULATION:
Structure and Density
Colonies are formed of small groups of animals, up to eight individuals. While the species is generally rare, it is considered to be one of the more common forest species of the genus *Glauconycteris* (Jacobs *et al.*, 2008l; IUCN, 2009; Monadjem *et al.*, 2017cq).

Trend
2016: Unknown (Monadjem *et al.*, 2017cq).
2008: Unknown (Jacobs *et al.*, 2008l; IUCN, 2009).

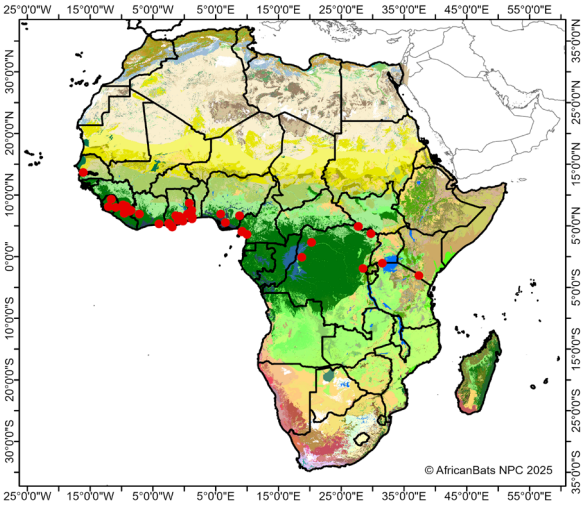

Figure 317. Distribution of *Glauconycteris poensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Cameroon, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone, South Sudan, Tanzania, Togo.

Glauconycteris superba Hayman, 1939

*1939. *Glauconycteris superba* Hayman, Ann. Mag. nat. Hist., ser 11, 3 (14): 219, figs 1 - 2. Publication date: 1 February 1939. Type locality: Congo (Democratic Republic of the): Oriental province: Ituri District: about 30 mi (45 km) ENE of Medje: Pawa [02 32 N 27 40 E]. [Goto Description]. Holotype: RMCA 14765: ad ♂, skull and alcoholic. Collected by: Dr. Albert Dubois. Hayman (1939: 220) mentions that this specimen is probably a male as the sexual organs were cut away by Dr. Dubois when preparing the specimen. (Current Combination).

1947. *Glauconycteris superba sheila* Hayman, Ann. Mag. nat. Hist., ser 11, 13 (103): 503 (for 1946). Publication date: 7 August 1947. Type locality: Ghana: Central province: Oda district: Oda [05 55 N 00 56 W]. [Goto Description]. Holotype: NHMUK 1947.10: ad ♀, skull and alcoholic. Collected by: George Soper Cansdale; collection date: 6 December 1946; original number: 807. - Etymology: In honour of Mrs. Cansale, wife of the collector (see Hayman, 1947c: 550).

2013. *Niumbaha superba:* Reeder, Helgen, Vodzak, Lunde and Ejotre. (Name Combination).

? *Chalinolobus superbus:* (Name Combination).

TAXONOMY:
See Simmons (2005).

Reeder *et al.* (2013: 93) proposed to place *superba* into a separate, new genus: *Niumbaha* Reeder, Helgen, Vodzak, Lunde and Ejotre, 2013 as they found most external features to be different from *Glauconycteris sensu stricto*. However, as this view is not yet confirmed, we tentatively retain this species in the genus *Glauconycteris*.

Using *Cytb* and RAG2 data, Hassanin *et al.* (2017: 1) found that *superba* is a sister-group of *G. variegata*, which seems to confirm that *Niumbaha* should probably be considered a synonym of *Glauconycteris*.

COMMON NAMES:
Czech: netopýr iturijský. English: Superb Butterfly Bat, Pied Butterfly Bat, Pied Bat, Badger bat, Panda Bat. French: Glauconyctère pie, Murin à bajoues pie, Barbastelle bariolée. German: Schwarz-Weiße Schmetterlingsfledermaus, Große Schmetterlingsfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017af).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017af). 2008: LC ver 3.1 (2001) (Fahr *et al.*, 2008; IUCN, 2009). 2004: VU B2ab(iii) ver 3.1 (2001) (Fahr *et al.*, 2004; IUCN, 2004). 1996: VU [assessed as *Chalinolobus superbus*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
As it has only been recorded from closed forest, it may be threatened by deforestation due to general logging and conversion of land to agricultural use (Fahr *et al.*, 2008; IUCN, 2009; Monadjem *et al.*, 2017af).

CONSERVATION ACTIONS:
Fahr *et al.* (2008) [in IUCN (2009)] and Monadjem *et al.* (2017af) report that there appear to be no direct conservation measures in place for this species. It may be protected within the Ituri Forest, although this needs to be confirmed. There is a need for further directed field surveys to better determine the distribution, natural history and possible threats to this species.

GENERAL DISTRIBUTION:
Recorded from Côte d'Ivoire (locality not given) (Peterson and Smith, 1973); from Oda in Oda Province, Ghana (Hayman, 1947c; Grubb *et al.*, 1998); and from the Ituri Forest in northeastern Congo (Hayman, 1939; Hayman *et al.*, 1966). It has previously been reported to occur in Uganda, however, this is now considered to be in error. It may be present in Sierra Leone, however, it has yet to have been recorded in this country (Grubb *et al.*, 1998).

In 2013, two new records were reported: one from the Democratic Republic of the Congo (Gembu Tungaluna *et al.*, 2013), and one from South Sudan (Reeder *et al.*, 2013).

Native: Congo (The Democratic Republic of the) (Hayman, 1939; Hayman *et al.*, 1966; Gembu Tungaluna *et al.*, 2013); Côte d'Ivoire (Peterson and Smith, 1973); Ghana (Hayman, 1947c; Grubb *et al.*, 1998), South Sudan (Reeder *et al.*, 2013).

Presence uncertain: Sierra Leone (Grubb *et al.*, 1998).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Based on a series of 10 specimens, Ing *et al.* (2016: 479) found that both males and females have the same coloration pattern: three white markings on the head; a large white ruff on the throat, which is disconnected from two large white lateral stripes; and two white spots on the shoulders. One specimen had three shoulderspots. They also have four white stripes on the back. Around the sexual organs, the white colour is not pure, but yellowish, possibly the result of polution by bodily fluids.

Based on the Fa (47.5 mm) and Tibia (21.3 mm), Ing *et al.* (2016: 482) suspect that the holotype of *G. superba* is rather a female than "probably a male" as indicated by Hayman (1939).

SEXUAL DIMORPHISM:
On a series consisting of four ♀♀ and six♂♂, Ing *et al.* (2016: 479) found the females to be 5 % larger (Fa, Tib and 5th finger) and 10 % heavier than males.

ECHOLOCATION:
Ing *et al.* (2016: 481) found that the bats emitted sounds alternating between two distinct frequencies: **A**: range: 20.5 - 57.0 kHz, F_{min}: 22.9 ± 1.4 (20.5 - 25.1) kHz, F_{max}: 36.8 ± 6.6 (29.1 - 57.0) kHz, F_{peak}: 25.7 ± 2.2 (22.4 - 30.9) kHz, bandwidth: 13.8 ± 6.3 (5.9 - 32.6) kHz, duration: 5.6 ± 1.9 (3.1 - 9.6) ms; and **B**: range: 27.3 - 73.3 kHz, F_{min}: 29.8 ± 1.3 (27.3 - 31.3) kHz, F_{max}: 57.0 - 13.5 (38.8 - 73.3) kHz, F_{peak}: 33.0 ± 3.0 (28.8 - 38.2) kHz, bandwidth: 27.1 ± 13.2 (9.1 - 43.3) kHz, duration: 6.4 ± 1.8 (4.0 - 10.1) ms. The B type of call is produced when the wing beat becomes constant.

HABITAT:
This species is associated with 'heavy' or closed lowland tropical moist forest (Rosevear, 1965; Hayman and Hill, 1971).

Based on wing measurements, however, Ing *et al.* (2016: 482) found that *G. superba* has long wings, which are adapted for high-speed flight. The high wing loading values, furthermore, indicate low manoeuvrability. These are features which are generally found in bats flying in uncluttered or open space, i.e., above the canopy.

HABITS:
After being released, the bats flew at speeds of about 1 to 9 m/s (average 4 - 6 m/s) (Ing *et al.*, 2016: 482).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 81 minutes, and the digestibility rate about 79.5 %.

POPULATION:
Structure and Density
It is currently known only from three specimens. It is very rare, or at least rarely collected (Hayman and Hill, 1971; Grubb *et al.*, 1998).

Trend
2008: Unknown (Fahr *et al.*, 2008; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Two of the four females that were captured on Mbiye island (DRC) by Ing *et al.* (2016: 479) in December 2013 were lactating.

VIRUSES:
Circoviridae
Bat associated circovirus 12
This virus was reported by Vidovszky *et al.* (2023: Suppl.) from bats from the DRC.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, South Sudan.

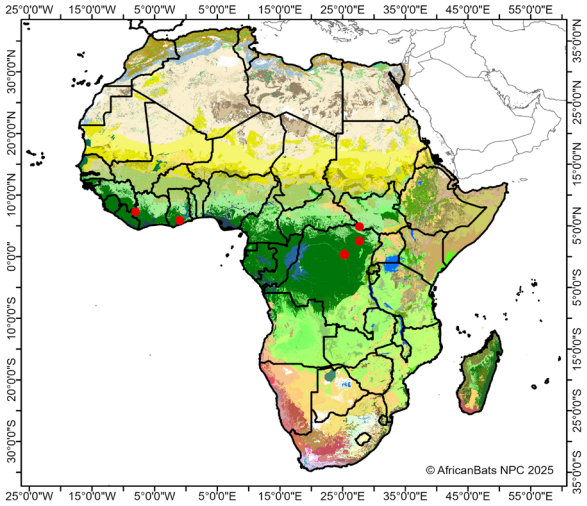

Figure 318. Distribution of *Glauconycteris superba*.

Glauconycteris variegata (Tomes, 1861)

*1861. *Scotophilus variegatus* Tomes, Proc. zool. Soc. Lond., 1861, I: 31, 36. Publication date: May 1861. Type locality: Namibia: Ovamboland: about 32 km west of Ondongwa: Otjoro [=Otjihoro] [ca. 17 54 S 15 38 E]. [Goto Description]. Syntype: NHMUK 1907.1.1.437: skin and skull. Collected by: 1 Anderson; collection date: 1 December 1859. See Tomes (1861b: 39). Syntype: NHMUK 1907.1.1.438: skin and skull. Collection date: 1 December 1859. See Tomes (1861b: 39). Syntype: ZMB 3033: ♂, skin and skull. Collected by: Andersson; collection date: 1 December 1859. See Turni and Kock (2008). - Comments: For details about the type locality, see Shortridge (1934), Meester *et al.* (1986: 54). - Etymology: From the feminine scientific Latin adjective *variegàta*, meaning "variegated", referring to the dark reticular pattern on the wings (see Lanza *et al.*, 2015: 356).

1905. *Glauconycteris papilio* Thomas, Ann. Mag. nat. Hist., ser 7, 15 (85): 77. Publication date: 1 January 1905. Type locality: Uganda: Entebbe [00 04 N 32 28 E, 3 800 ft]. [Goto Description]. Holotype: NHMUK 1899.8.4.14: ♀, skin and skull. Collected by: Sir F.J. Jackson Esq. Collection date: 10 April 1895. Presented/Donated by: Sir F.J. Jackson Esq. Thomas (1905a: 77), who also mentions specimens from "Gambaga, Gold Coast (Giffard), and Tette, Zambesi (Boyd Alexander)".

1915. *Glauconycteris phalæna* Thomas, Ann. Mag. nat. Hist., 8, 15 (90): 560. Publication date: 1 June 1915. Type locality: South Sudan: White Nile province: Malakal district: Fashoda, near [09 53 00 N 32 07 00 E, 271 m]. [Goto Description]. Holotype: NHMUK 1915.3.6.67: ad ♀. Collected by: Willoughby P. Lowe; collection date: 27 January 1914; original number: 71. - Etymology: From the Greek for moth (see Jaeger, 1972).

1926. *Glauconycteris variegatus:* Thomas, Ann. Mag. nat. Hist., ser 9, 17 (103): 609. Publication date: 1 May 1926. (Name Combination, Alternate Spelling).

1996. *Glauconycteris variegate:* Yalden, Largen, Kock and Hillman, Trop. Zool., 9: 142. (Lapsus).

2014. *Scotophyllus v[ariegata] variegata:* Rahoum, SJS, 6 (1): 45. Publication date: February 2014. - Comments: Rahoum (2014: 45) refers to Hill and Morris (1971) for the name "*Scotophyllus v. variegata*", but that publication doesn't contain that name, but the correct *Glauconycteris variegata variegata*. (Lapsus).

? *Chalinolobus (Glauconycteris) variegata:* (Name Combination, Alternate Spelling).

? *Chalinolobus (Glauconycteris) variegatus:* (Name Combination).

? *Chalinolobus variegatus:* (Name Combination).

? *Glauconycteris variegata papilio:* (Name Combination).

? *Glauconycteris variegata variegata:* (Name Combination).

? *Glauconycteris variegata:* (Current Combination).

TAXONOMY:
Koopman (1971: 6; Koopman, 1993a: 200) included *machadoi*, and believed it to be a melanistic mutant population, but see Simmons (2005).

COMMON NAMES:
Afrikaans: Vlindervlermuis. Chinese: 彩蝶蝠. Czech: netopýr motýlí. English: Variegated Butterfly Bat, Butterfly Bat, Leaf-winged bat. French: Glauconyctère papillon, Murin à bajoues papillon, Chauve-souris réticulée, Chauve-souris papillon. German: Genetzte Schmetterlingsfledermaus. Italian: Glauconitterìde variegàta, Glauconicterìde variegàta. Malawian: Liputiputi, Ndemiya, Namsimsi, Namzeze. Portuguese: Morcego borboleta.

ETYMOLOGY OF COMMON NAME:
The colloquial name may be derived from the dark reticulated pattern on the wings, which has led to their being called leaf-winged bats Taylor, 2005). Although it is said that they resemble a large butterfly in flight, they are by no means butterfly-like in this respect (Taylor, 2005).



Figure 319. *Glauconycteris variegata* (ECJS-??/2010), caught at Rocktail Bay, Northern KwaZulu Natal, South Africa.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Rambaldini (2010: 255) refers to Avery (1991), who mentioned finding fossil remains in very late Holocene layers at Border Cave, KwaZulu Natal.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008j; IUCN, 2009; Rambaldini, 2010: 256; Monadjem *et al.*, 2017cr).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cr). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008j; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004j; IUCN, 2004). 1996: LR/lc [assessed as *Chalinolobus variegatus*] (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) [assessed as (Schoeman *et al.*, 2016c).2004: NT ver 3.1 (2001) [assessed as *G. variegatus*] (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
In view of the species wide range and availability of extensive suitable habitat, there are no major threats to this species. This species is threatened in parts of its range by habitat loss resulting from logging activities and the conversion of land to agricultural use (Jacobs *et al.*, 2008j; IUCN, 2009; Monadjem *et al.*, 2017cr).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008j) [in IUCN (2009)] and Monadjem *et al.* (2017cr) report that there appear to be no direct conservation measures in place. In view of the species wide distribution it is presumably present in some protected areas.

GENERAL DISTRIBUTION:
Glauconycteris variegata is widely, but patchily, recorded throughout much of sub-Saharan Africa. It ranges from Senegal and The Gambia in West Africa, through West and Central Africa to Ethiopia and Somalia in the east, from here it ranges south through East Africa and southern Africa, being recorded as far south as northeastern South Africa.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 976,983 km^2.

Rambaldini (2010: 254-255) confirms that there are no records from the central regions of The Democratic Republic of the Congo, northern Congo Republic, northeastern Gabon, Equatorial Guinea, and the southern parts of Cameroon, Nigeria and Benin. Furthermore, it seems missing from the coastal areas of southwestern Ghana, Côte d'Ivoire, Liberia and Sierra Leone.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 562); Benin (Capo-Chichi *et al.*, 2004: 162); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 562); Burkina Faso (Kangoyé *et al.*, 2012: 6025; 2015a: 618); Cameroon; Chad; Congo; Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 562); Ethiopia (Yalden *et al.*, 1996; Lavrenchenko *et al.*, 2004b: 137); Gabon; Gambia; Ghana; Kenya; Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988; Happold and Happold, 1997b: 821; Monadjem *et al.*, 2010d: 562); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 562; Monadjem *et al.*, 2010c: 383); Namibia (Cotterill, 2004a: 262; Monadjem *et al.*, 2010d: 562); Nigeria (Happold, 1987); Rwanda; Senegal; Somalia; South Africa (Monadjem *et al.*, 2010d: 562); Sudan (Koopman, 1975); Swaziland; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62); Zambia (Ansell, 1957; Ansell, 1969; Ansell, 1973; Ansell, 1974; Monadjem *et al.*, 2010d: 562); Zimbabwe (Monadjem *et al.*, 2010d: 563).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 8.6 Pa, aspect ratio 6.2 for a wingspan of 30 cm and a wing area of 148 cm^2 and a body mass of 13 g.

SEXUAL DIMORPHISM:
Rambaldini (2010: 253) indicates that females are slightly larger than males in body dimensions, but not in weight.

ECHOLOCATION:
Rambaldini (2010: 255) mentions that the echolocation vocalizations are high-intensity, frequency-modulated calls typically starting from 70 kHz and ending at 30 kHz, and are sometimes including a 2nd harmonic, and rarely a 3rd one.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 37.5 kHz and duration: 5.3 ms.

For Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 8 calls: Inpterpulse interval: 89.9 ± 36.1 (48.2 - 148.0) ms; F_{max}: 37.6 ± 2.7 (34.6 - 42.6) kHz; Start slope: -17.7 ± 7.3 (-12.1 - -5.9) kHz/ms; End slope: -6.4 ± 4.6 (-0.1 - -4.7) kHz/ms; Ledge duration: 0.6 ± 0.1 (0.4 - 0.8) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 18, FN = 32, BA = 16, a medium sized subtelocentric X chromosome, and a small metacentric Y chromosome, for specimens from South Africa.

Genetics
See Hoofer and Van Den Bussche (2003).

HABITAT:
Glauconycteris variegata is an inhabitant ot savannah, woodland, or open country–bushveldt habitats (see Rambaldini, 2010: 255).

ROOST:
Thatched roofs of abandoned huts and among dense vegetation (Allen *et al.*, 1917; Ansell and Dowsett, 1988; Taylor, 1998).

Happold and Happold (2023: 136) mention that these bats were found roosting singly, in pairs or in groups of three to 12 individuals.

DIET:
Glauconycteris variegata eats airborne prey, primarily soft-bodied insects such as moths (see Kingdon, 1974; Fenton *et al.*, 1977a).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 94 minutes, and the digestibility rate about 77.9 %.

POPULATION:
Structure and Density
Colonies of this species are small, and there are believed to be less than 10,000 individuals in total (Jacobs *et al.*, 2008j; IUCN, 2009; Monadjem *et al.*, 2017cr).

Trend
2016: Unknown (Monadjem *et al.*, 2017cr). 2008: Unknown (Jacobs *et al.*, 2008j; IUCN, 2009, Rambaldini, 2010: 256).

REPRODUCTION AND ONTOGENY:
Anciaux de Faveaux (1970) in Rambaldini (2010: 255) indicates that this species is monoestrus, but that the seasonal reproductive cycle can change across its range. Kingdon (1974) reported sexually active males from southern Uganda in July and October, whereas Monard (1935) did not find any sexually active adults in July in Angola. Lang and Chapin (1917b) reported pregnant females from the Democratic Republic of the Congo in March. From Zimbabwe, Smithers and Wilson (1979) reported pregnant females in August.

Bernard and Cumming (1997) [in Krutzsch (2000: 116)] suggested that *H. caffer* poses some kind of a problem as it is clearly monoestrous in some parts of its range but possibly bimodally or continuously polyoestrous in other parts.

PARASITES:
BACTERIA
Dietrich *et al.* (2016b: 3) found one out of three bats tested positive for *Rickettsia* in Rocktail Bay (RSA). Also from the RSA, Dietrich *et al.* (2018a: 4) reported the presence of *Leptospira kirschneri*.

PROTOZOA
Kassahun *et al.* (2015: 168) examined eight Ethiopian *G. variegata* specimens and found one of them (from Bedele) to be infected by *Leishmania* parasites (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 5). Baleela *et al.* (2020: 360) reported *Leishmania donovani* from these bats in Sudan.

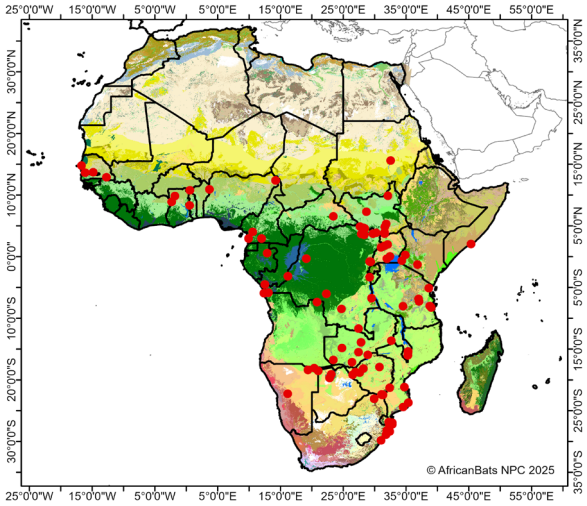

Figure 320. Distribution of *Glauconycteris variegata*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Benin, Botswana, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Kenya, Malawi, Mozambique, Namibia, Nigeria, Senegal, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

TRIBE Pipistrellini Tate, 1942

1942. *Pipistrellini* Tate, Bull. Am. Mus. Nat. Hist., 80 (7): 221, 231. Publication date: 27 November 1942. - Comments: Type genus: *Pipistrellus* Kaup, 1829. Introduced as tribe, and originally including the genera *Pipistrellus* Kaup, 1829 and *Glischropus* Dobson, 1875 (see Jackson and Groves, 2015: 274).

Genus ***Nyctalus*** Bowdich, 1825

*1825. *Nyctalus* Bowdich, Excur. Madeira and Porto Santo, 36, and footnote. Publication date: 1825. - Comments: Type species: *Nyctalus verrucosus* Bowdich, 1825 (=*Vespertilio leisleri* Kuhl, 1817). - Etymology: From the Greek "*νυκταλός*" (="*νυσταλός*"), meaning drowsy, referring to its crepuscular habits (see Palmer, 1904: 464). From the Greek "*nyctos*" meaning night and "*ala*" meaning wing (see Kapteyn, 1995: 115). (Current Combination).

1829. *Pterygistes* Kaup, Skizzierte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 90. Publication date: 1829. - Comments: Type species: *Vespertilio noctula* Schreber, 1774. - Etymology: From the Greek "*πτερυγίζω*", meaning to flutter, referring to the manner of flight (see Palmer, 1904: 596).

1839. *Vesperugo* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 312. Publication date: 1839. - Comments: In part (see Allen, 1939a: 92; Pavlinov *et al.*, 1995: 104). Included 13 species now referred to *Eptesicus, Pipistrellus, Neoromicia, Hypsugo*.

1842. *Noctulinia* J. E. Gray, Ann. Mag. nat. Hist., [ser 1], 10 (65): 258. Publication date: 1 December 1842. - Comments: Mentioned as "in part" by Allen (1939a: 92). Contained two species (*Noctulinia proterus* Kuhl, 1818 =*Nyctalus noctula* Schreber, 1774, and *N. fulvus* Grey, 1843 =*Scotophilus kuhlii* Leach, 1821; see Allen (1939a: 92), one a synonym of *Vespertilio noctula* Schreber, 1774 (see Corbet and Hill, 1992: 143). - Etymology: From the Latin of, or belonging to night (from "*noctus*" = "*nox*", meaning night), referring to the animal's crepuscular habits (see Palmer, 1904: 461).

1856. *Panugo* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Type species: *Vespertilio noctula* Schreber, 1774 and *Vespertilio leisleri* Kuhl, 1817.

1872. *Noctulina* Macalister, Ann. Mag. nat. Hist., ser 4, 9 (53): 402. Publication date: 1 May 1872.

1914. *Noctulinia* Cabrera, Fauna Ibérica, 123. - Comments: (also mentioned by Allen (1939a: 92), Corbet (1978: 54), and Simmons (2005))?.

2002. *Nyctalis:* Sheshurak and Kedrov, Plecotus et al., pars spec: 62. (Lapsus).

2019. *Nyactulus:* Fagre and Kading, Viruses, 11 (3): 215 (p 4). Publication date: 3 March 2019. (Lapsus).

TAXONOMY:
Species referred by Koopman (1994) in the *Stenopterus* group are placed into *Pipistrellus* by Corbet and Hill (1992) and Hoofer and Van Den Bussche (2003: 38). Whereas Simmons (2005) placed it as a subgenus of *Hypsugo*.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Nyctalus*: *aviator* Thomas, 1911 - Japan, Korea, E and C China; ***azoreum*** (Thomas, 1901); *furvus* Imaizumi and Yoshiyuki, 1968 - Japan, Korea; ***lasiopterus*** (Schreber, 1780); ***leisleri*** (Kuhl, 1817); *montanus* (Barrett-Hamilton, 1906) - Afghanistan, Pakistan, N India, Nepal (?), N Myanmar; *noctula* (Schreber, 1774); *plancyi* (Gerbe, 1880) - N China, Philippines.

COMMON NAMES:
Czech: lesní netopýři (lesní létači). English: Noctules, Noctule Bats. French: Noctules, Chauves-souris à nez large. German: Abendsegler. Ukrainian: Вечірниця (= Vechirnytsya).

GENERAL DISTRIBUTION:
Species of the genus *Nyctalus* are distributed across the entire Palaerctic region, and enter only marginally into the Indomalay region (Koopman, 1994; Simmons, 2005)

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa".

Nyctalus azoreum (Thomas, 1901)

*1901. *Pterygistes azoreum* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 33. Publication date: 1 July 1901. Type locality: Azores (Portugal): St. Michael. [Goto Description]. Holotype: NHMUK 1865.10.2.1: ♂. Collected by: Frederick DuCane Godman Esq. Presented/Donated by: Frederick DuCane Godman Esq. - Etymology: The name refers to the Island group where the species occurs.
? *Nyctalus azoreum:* (Name Combination, Current Combination).
? *Nyctalus leisleri azoreum:* (Name Combination).

TAXONOMY:
Listed as a subspecies of *N. leisleri* by Corbet (1978) and Koopman (1994: 118). But recognised as a species by Palmeirim (1991), Koopman (1993a: 216), Horáček *et al.* (2000: 133), Salgueiro *et al.* (2004: 3357), Simmons (2005: 471), Salgueiro *et al.* (2006: 169) and Salgueiro *et al.* (2007: 1163; 2010: 26).

COMMON NAMES:
Albanian: Noktulë e Azoreve. Armenian: Ազորյան իրիկնաչղջիկ. Azerbaijani: Azor axşam yarasası. Basque: Gau-saguzar azoretar. Belarusian: Вячэрніца азорская. Bosnian: Azorski noćni šišmiš. Breton: Nozigell an Azorez. Bulgarian: Азорски вечерник. Castilian (Spain): Nóctulo de Azores. Catalan (Spain): Nòctul de les Azores. Croatian: Azorski večernjak. Czech: Netopýr azorský. Danish: Azorflagermus. Dutch: Azoren rosse vleermuis, Azorenvleermuis. English: Azorean Noctule Bat, Azores noctule. Estonian: Assoori videvlane. Finnish: Azorienisolepakko. French: Noctule des Açores. Frisian: Azoaren reade flearmûs. Galician (Spain): Nóctulo das Azores. Georgian: აზორული მელამურა. German: Azoren-Abendsegler. Greek: Νυκτοβάτης των Αζόρων. Hungarian: Azori-szigeteki koraidenevér. Irish Gaelic: Ialtóg Asórach. Italian: Nottola delle Azzorre. Latvian: Azoru vakarsikspārnis. Lithuanian: Azorinis nakviša. Luxembourgish: Azoren-Bëschfliedermaus. Macedonian: Азорски вечерник. Maltese: Noktula ta' l-Azores. Montenegrin: Azorski noćnik. Norwegian: Asorflaggermus. Polish: Borowiec azorski. Portuguese: Morcego dos Açores. Rhaeto-Romance: Sgolanotg da las Azoras. Romanian: Liliacul de amurg din Azore. Russian: Вечерница азорская. Serbian: Азорски ноћник [= Azorski noćnik]. Scottish Gaelic: Ialtag Asorach. Slovak: Raniak azorský. Slovenian: Azorski mračnik. Swedish: Azorfladdermus. Turkish: Azorlar Akşamcı Yarasası. Ukrainian: Вечірниця азорська. Welsh: Ystlum mawr yr Asores.

SIMILAR SPECIES:
Salgueiro *et al.* (2010: 26) provide a summary of the differences between *N. azoreum* and its closest relative *N. leisleri*. *N. azoreum* is darker and considerably smaller. It is also present in a broader ecological niche, occupying a variety of roosts like buildings, coastal cliffs and trees, whereas *leisleri* is primarily a tree dweller. Finally, it has an echolocation call with a higher peak frequency than its continental counterpart, and it is often active during the day.

CONSERVATION STATUS:
Global Justification
Piraccini (2016d) report that this species' population has been estimated at 2,000-5,000 individuals and the most abundant subpopulation numbers less than 1,000 individuals. For these reasons this species meets the criteria for being assessed as Vulnerable (VU C2a(i)). This species is endemic to the Azores, where it has a small population and range. It is suspected to be declining as a result of disturbance and destruction of colonies, loss and degradation of natural and semi-natural habitats and pesticide use. There is no direct information on dispersal between islands, but genetic research suggests that dispersal is restricted, and so the population is precautionarily regarded as being severely fragmented; further research would be required to confirm this. For these reasons, it may be approaching the Endangered category, which is suggested by Conenna *et al.* (2017: Suppl.).

Assessment History
Global
2016: VU C2a(i) ver 3.1 (2001) (Piraccini, 2016d).
1994: VU A2c, B1+2c ver 2.3 (1994).

MAJOR THREATS:
Human persecution, and the destruction of roost sites, are likely to be the main threats (A. Rainho *pers. comm.* 2006 in Piraccini (2016d)). Habitat loss and degradation, use of pesticides and the spread of exotic plant species may also have a detrimental effect on the species. It is suspected that the extreme scarcity of the species on Santa Maria is attributable to habitat loss and degradation. This species is particularly vulnerable to persecution because it flies during the day, making colonies obvious and easy to find (A. Rainho *pers. comm.* 2006 in Piraccini (2016d)).

Sherwin *et al.* (2012: 174) identified the small distribution range, the species' aerial hawking feeding style and its long-distance dispersal to be the major risk factors linked with climatic change.

CONSERVATION ACTIONS:
There is no specific national legislation. It is protected under Bern Convention and included in Annex IV of EU Habitats and Species Directive. There are proposals for protection and monitoring of roosts, public awareness (with special reference to roosts), reduction of adverse agricultural practices, preservation and restoration of natural habitat, use of lights that attract insects (e.g., mercury), and further studies of the species' biology (Rainho *et al.*, 2002). A bat monitoring program, based on annual acoustic surveys, is currently under development (A. Rainho *pers. comm.* in Piraccini (2016d)).

GENERAL DISTRIBUTION:
Nyctalus azoreum is endemic to the archipelago of the Azores, where it is present on seven of the nine islands (Rainho, 2017: 161).

Native: Azores (Palmeirim, 1991; Koopman, 1993a: 216; Speakman and Webb, 1993; Horáček *et al.*, 2000: 133; Salgueiro *et al.*, 2004: 3357; Simmons, 2005: 471; Salgueiro *et al.*, 2006: 169; Salgueiro *et al.*, 2007: 1163).

BIOGEOGRAPHY:
Molecular data suggest that *N. azoreum* originated from a European population of *N. leisleri*, and that the colonisation of the Azores occurred at the end of the Pleistocene (Salgueiro *et al.*, 2006). Salgueiro *et al.* (2006) suggest the minimum divergence time of insular (Azores) and continental lineages is comprised between 0 and 55,000 years BP. This corresponds roughly to a late Pleistocene/Holocene divergence, which is consistent with previous estimates based on demographic parameters (12,000 and 25,000 years BP) calculated by Salgueiro *et al.* (2004). As humans only colonized the Azores less than 600 years ago, molecular estimates of divergence times suggest that the first bats which arrived on the archipelago were unlikely to be brought by man (Salgueiro *et al.*, 2006).

ECHOLOCATION:
Rainho (2021: 2) mentions this species has an average peak frequency of 32.1 kHz, whereas Dechmann and Ruczynski (2023: 420) indicate a main frequency between 27.3 and 32.9 kHz and duration of 16.8 ms.

MOLECULAR BIOLOGY:
Genetics
Moussy *et al.* (2012: 188), referring to Salgueiro *et al.* (2004; 2007), indicate that *N. azoreum* is one of the species that shows significant genetic differentiation and/or haplotype segregation between islands or groups of islands but not within them.

Boston *et al.* (2015) examined the mitochondrial DNA of *N. azoreum* and *N. leisleri* and found that two separate lineages were present and that *N. azoreum* forms one lineage with *N. leisleri* from Britain and Ireland, whereas the second lineage consists of continental European *N. leisleri*.

HABITS:
Speakman and Webb (1993: 28) refer to Moore (1975) to point out that *N. azoreum* is one of those exceptional bats, which fly during the day. However, this behaviour was found to be spatially restricted (Mikula *et al.*, 2024: 161). Irwin and Speakman (2003: 185) furthermore found that *N. azoreum* clusters when emerging from their roosts. This was quite unexpected as no flying predators are present on the Azores which could capture bats while leaving the roosts.

DIET:
Dechmann and Ruczynski (2023: 420) indicate that these bats can often be seen foraging during the afternoon, which would allow them to take advantage of the insect abundance peak in the early evening.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 133 minutes, and the digestibility rate about 74.3 %.

POPULATION:
Structure and Density
Based on a survey, conducted in September-October 1988, Speakman and Webb (1993: 27) estimated the population of *N. azoreum* to consists of between 1,750 (from daytime activity) and 23,650 (from night-time activity) animals. The latter figure would lead to a population

density of 1 bat per 10 ha. Surveys in 2002, 2003 and 2004 found the Azorean Bat (*Nyctalus azoreum*) quite abundant on San Miguel, Faial, Terceira and San Jorge, but rare on Graciosa and extremely rare on Santa Maria. It is absent from Flores and Corvo. There is no quantitative information on population trend, but it is suspected that the species may be declining as a result of habitat degradation, destruction of or exclusion from roosts (both in trees and buildings), and human persecution. Local environmental groups report that numerous colonies have disappeared (A. Rainho *pers. comm.* 2006 in Piraccini (2016d)). The total population is estimated at 2,000-5,000 individuals, and there are fewer than 1,000 individuals on San Miguel, where the species is most abundant (Cabral *et al.*, 2005; J.M. Palmeirim, A. Rainho and L. Rodrigues *pers. comm.* 2006 in Piraccini (2016d)).

Trend
2016: Decreasing (Piraccini, 2016d).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter). Maternity colonies are found between April and September/October (Dechmann and Ruczynski (2023: 428), and juveniles are born in June/July.

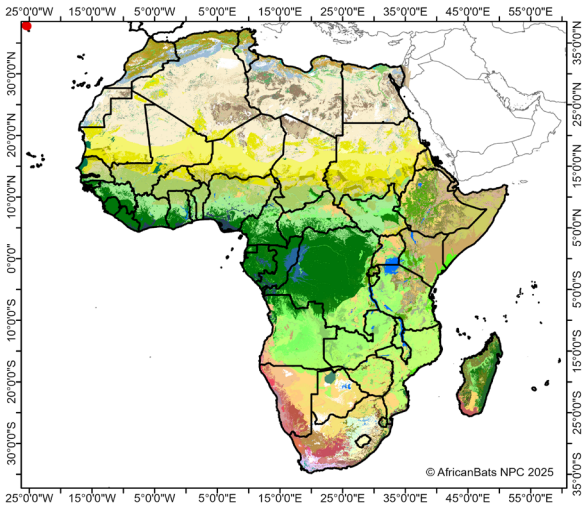

Figure 321. Distribution of *Nyctalus azoreum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Azores (Portugal).

Nyctalus lasiopterus (Schreber, 1780)

*1780. *Vespertilio lasiopterus* Schreber, in: Zimmerman, Geographische Geschichte der Mensch und Vierfussige Thiere, 2: 412. Type locality: Italy: Northern Italy. - Comments: The type locality indication as "Northern Italy" is uncertain. Horáček *et al.* (2000: 132) mention "? Pisa". - Etymology: From the Greek "*lasios*", meaning hairy and "*pteros*", meaning wing (see Kapteyn, 1995: 154).
1827. *Vespertilio ferrugineus* Brehm, Ornis, 3: 26. Type locality: Germany: Thuringia: Renthendorf.
1868. *V[espertilio noctula] var. sicula* Mina-Palumbo, Cat. Mammif. della Sicilia, 13. Type locality: Italy: Sycily: Le Madonie. - Comments: For restriction to "Le Madonie" see Miller (1913: 80). - Etymology: From the Latin "*siculus*" for Sicily (see Kozhurina, 2002: 18).
1869. *Vesperugo noctula var. maxima* Fatio, Faune des Vertébrés de la Suisse, 1: 57. Type locality: Switzerland: Uri: Amsteg. [Goto Description].
2002. *Nyctalus lasiopetrus:* Monsalve, Almenar, Alcocer and Monsorio, Sedeck, 4: 24. (Lapsus).
? *Nyctalus lasiopterus:* (Name Combination, Current Combination).

TAXONOMY:
Reviewed by Corbet (1978: 55 - 56). See Simmons (2005: 471)

COMMON NAMES:
Albanian: Noktulë gjigante. Armenian: Հսկա իրիկնաչղջիկ. Azerbaijani: Nəhəng axşam yarasası. Basque: Gau-saguzar handi. Belarusian: Вячэрніца гіганцкая. Bosnian: Veliki noćni šišmiš. Breton: Nozigell vras. Bulgarian: Голям вечерник. Castilian (Spain): Nóctulo gigante, Nóctulo grande. Catalan (Spain): Nòctul gegant, Rat penat nóctul gran. Croatian: Veliki večernjak. Czech: Netopýr obrovský. Danish: Stor brunflagermus. Dutch: Grote rosse vleermuis. English: Giant Noctule Bat, Giant noctule, Greater noctule, Greater Noctule Bat. Estonian: Hiidvidevlane. Finnish: Rusoisolepakko. French: Grande noctule, Noctule géante. Frisian: Grutte reade flearmûs. Galician (Spain): Nóctulo xigante. Georgian: გიგანტური მელამურა. German: Riesenabendsegler, Riesen Abendsegler, Großabendsegler. Greek: Μεγάλος νυκτοβάτης. Hungarian: Óriás koraidenevér, Nycteris pterygisti i megali. Irish Gaelic: Ollialtóg nochtúil. Italian: Nottola gigante. Latvian: Lielais vakarsiksparnis. Lithuanian: Didysis nakviša. Luxembourgish: Riseg Bëschfliedermaus. Macedonian: Голем вечерник. Maltese: Noktula Kbir. Montenegrin: Veliki noćnik. Norwegian: Riseflaggermus. Polish: Borowiec olbrzymi. Portuguese: Morcego-arboricola-gigante. Rhaeto-Romance: Sgolanotg gigant. Romanian: Liliacul mare de amurg. Russian: Вечерница гигантская, Гигантская вечерница [= Gigantskaya

vechernicha]. Serbian: Велики ноћник [= Veliki noćnik]. Scottish Gaelic: Mòr-ialtag oidhcheach. Slovak: Raniak obrovský. Slovenian: Veliki mračnik. Swedish: Pälsvingad brunfladdermus. Turkish: Büyük Akşamcı Yarasa. Ukrainian: Вечірниця гігантська [= Vechirnytsya veletens'ka]. Welsh: Ystlum mwyaf.

CONSERVATION STATUS:
Global Justification
Deforestation, particularly the loss of old trees, is a problem in many parts of the range and is likely to be causing a population decline. The range is fragmented and the colonies tend to be mainly small (Hutson *et al.*, 2008a; IUCN, 2009). Dozens of individuals have been found dead at wind farms from Spain (C. Ibáñez, S. Sánchez and J.T. Alcalde *pers. comm* in Alcaldé *et al.* (2016)). A critical decline is suspected in Ukraine and European Russia (Vlaschenko *et al.*, 2010; 2016). Although there are no precise figures on population decline it seems reasonable to list this species as Vulnerable given what is currently known about the threats, the population numbers and the range. It qualifies as VU under criteria A4c and C2a(i) (Alcaldé *et al.*, 2016).

Assessment History
Global
2016: VU A4c; C2a(i) ver 3.1 (2001) (Alcaldé *et al.*, 2016). 2008: NT ver 3.1 (2001) (Hutson *et al.*, 2008a; IUCN, 2009). 1996: LR/nt ver 2.3 (1994).

Regional
None known.

MAJOR THREATS:
Little is known about potential threats, but loss of mature woodland and loss of or disturbance to roost sites (in old trees and buildings) may have a negative impact on the species. In Cádiz (Southern Spain) it is estimated that a hundred Giant Noctules are killed each year by wind turbines (Ibáñez and Sánchez-Navarro, submitted), and more individuals have been found in other regions such as Soria and Navarra (Alcalde pers. comm. 2015). Some individuals were found dead at wind farms in Spain (J.T. Alcalde *pers. comm.,* 2006 in Hutson *et al.* (2008a) in IUCN (2009)), and all pups were found dead in 2005 at one of the two known colonies in Spain (located in a city park). The cause of these deaths was not known (J.T. Alcalde *pers. comm.,* 2006 [in Hutson *et al.* (2008a) in IUCN (2009)]). One colony disappeared in Spain due to the cutting of old trees in a city park (Juste, 2007), and the same seems to have happened in a Ukrainian forest (Vlaschenko *et al.*, 2010). Little is known about potential threats, but loss of mature woodland and loss of or disturbance to roost sites (old trees) have a negative impact on the species (Bakwo Fils and Kaleme, 2016b).

Small distribution range, cave/tree roosting, and the aerial hawking feeding style were considered to be risk factors linked with climatic change by Sherwin *et al.* (2012: 174). Piccioli Cappelli *et al.* (2021: 10) identified this species (together with *Rhinolophus mehelyi* as running the highest risk of extinction due to climate change in Europe and North-west Africa.

CONSERVATION ACTIONS:
Hutson *et al.* (2008a) [in IUCN (2009)] report that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention, in parts of its range where these apply. It is included in Annex IV of EU Habitats and Species Directive. No specific conservation actions are known. It occurs in a number of national parks and protected areas within its range (K. Tsytsulina *pers. comm*., 2005)). However, in Spain the two known colonies are outside protected areas (Juste, 2007). It seems that it has declined in Ukraine and European Russia (Vlaschenko *et al.*, 2010; 2016). More information is needed on population size and trends, ecology, and potential threats (Juste, 2007).

GENERAL DISTRIBUTION:
Nyctalus lasiopterus has a very scattered distribution through central and southern Europe (Iberia to the Balkans, Urals) and north Africa (Morocco [only three records in northwest Morocco, the first of which was reported as *N. noctula* by Laurent (1937d), but see Palmeirim (1982: 402)], Libya [five records in Cyrenaica], and possibly Algeria [one record identified as *Nyctalus noctula* by Loche (1867), but the specimen is lost]). There are an increasing number of records from Turkey (Karataş *et al.*, 2007). Outside the Mediterranean region the range extends eastwards through Asia Minor to the Caucasus, northern Iran, Kazakhstan and the Urals in Russia. Of the Mediterranean islands, recorded on Sicily. Until 1999, it had been recorded in 120-130 localities in Europe (Benzal, 1999). It occurs up to 1,900 m in Switzerland

Native: Azerbaijan; Belarus; Bulgaria; Cyprus (Benda *et al.*, 2007: 71); Croatia; Czech Republic; France; Georgia; Germany; Gibraltar; Greece; Hungary; Iran, Islamic Republic of; Italy (Sicilia); Kazakhstan; Libyan Arab Jamahiriya; Macedonia, the former Yugoslav Republic of; Moldova; Monaco; Morocco (El Ibrahimi and Rguibi Idrissi, 2015: 363; Dbiba *et al.*, 2025: 7); Poland; Portugal; Romania; Russian Federation;

Slovakia; Slovenia; Spain; Switzerland; Turkey; Turkmenistan; Ukraine.

Presence uncertain: Algeria; Andorra; Bosnia and Herzegovina; Uzbekistan.

GEOGRAPHIC VARIATION:
Benda *et al.* (2014c: 91) found that the Libyan representatives of the species are on average smaller in the forearm and skull sizes than specimens from other parts of the distribution area. Also, their rostra are relatively long and narrow.

FUNCTIONAL MORPHOLOGY:
Naďo *et al.* (2019: 592) point out that these bats echolocation calls (low frequency and high intensity) are perfectly suited to detect large and fast airborne prey (e.g., birds) at great distances. Furthermore, the swift wing beats allow them to fly fast and change their flight altitude very rapidly; e.g., to high altitudes (124 to 367 m above the ground) where there is little competition and potential food might be abundant.

ECHOLOCATION:
Walters *et al.* (2012: suppl.) report the following figures for 26 calls (22 sequences) from French bats: duration: 22.87 ± 2.92 ms, F_{max}: 17.00 ± 4.68 kHz, F_{min}: 13.28 ± 1.55 kHz, bandwidth: 3.72 ± 3.24 kHz, F_{peak}: 14.29 ± 1.66 kHz.

MOLECULAR BIOLOGY:
Karyotype
Arslan and Zima (2014: 12) reported 2*n* = 42, FNa = 50, FN = 54, a medium-sized metacentric X, and a small acrocentric Y. The autosomal complement contains four large metacentric, one small submetacentric and 15 acrocentric autosomal pairs.

HABITS:
Naďo *et al.* (2019: 588) indicate that *Nyctalus lasiopterus* have very large foraging areas (to over 1,000 km^2 and can travel distances to over 100 km per night.

ROOST:
The only specimen found in a roost in Libya by Benda *et al.* (2014c: 87) was in a fist-sized hole in an overhang, some 6 m above the ground. This represented the first non-tree roost site found for this species.

In Slovakia, Naďo *et al.* (2019: 589) found these bats to roost only in old aspen trees (*Populus tremula*), which were often suffering from hardwood rot. The inhabited cavities were between 4 and 17 m above the ground.

DIET:
In Russia, Smirnov and Vekhnik (2013: 207) found that the diet of *N. lasiopterus* included the following orders of insects: Orthoptera, Coleoptera, Lepidoptera, Diptera, Homoptera, and Neuroptera. They also found an amount of feathers: Out of 14 faecal pellets, the feathers made up 80 - 90 % of the total faecal volume in six pellets, 50 - 60 % in three pellets, 20 - 40 % in four pellets, and less than 10 % in one pellet.

Andreas (2010: 266) referred to three hypotheses concerning the occurrence of feathers in the bat's faeces: "The first possibility was that *N. lasiopterus* is not able to distinguish between flying feathers and its usual preys and eats a lot of this indigestible material. The second possibility was that *N. lasiopterus* regularly feeds on birds and consumes prey that can represent some 30 % of its body weight on the wing. The third possibility can be a predation in tree hollows.", of which Popa-Lisseanu *et al.* (2007: 1) proved the second to be correct, especially during the migration season of the small passerine birds. Benda *et al.* (2012a: 455) furthermore indicate that carnivory is probably a local and/or seasonal phenomenon.

Digestive tracts from five bats collected in Cyrenaica, Libya, contained moths, carabid beetles, heteropterans, neuropterans, and cockroaches (Benda *et al.*, 2014c: 93). 30 faecal pellets from Cyprus contained mainly Hymenoptera, Auchenorrhyncha and Scarabaeid beetles, and also some moths and heteropterans Andreas (2010: 266).

The wide range of food taxa led Ibáñez and Juste (2023: 450) to suggest that *Nyctalus lasiopterus* is a generalist/opportunistic predator.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 204 minutes, and the digestibility rate about 70.2 %.

POPULATION:
Structure and Density
The patchy distribution and low population density in most of range suggest a relatively small global population. Breeding colonies are typically small (up to 35 females), and few are known. Only two larger-sized (50 - 100 females) breeding colonies are known in the world. It is rare throughout the range in the Russian Federation (K. Tsytsulina *pers. comm.,* in Hutson *et al.*, 2008a) [in IUCN, 2009)]). There is a strong population in northern Hungary (Hutson *et al.*, 2008a; IUCN, 2009). The species is difficult to

survey, and difficult to capture with mist nets as it hunts 10-20 m above the ground (K. Tsytsulina *in litt.* 2005 in Alcaldé *et al.* (2016)) or even higher. Although the global population trend is unknown, a decline is suspected in Ukraine and Russia, and in Spain (stronghold of the species), mortality caused by wind farms could noticeably reduce the population (Bakwo Fils and Kaleme, 2016b).

Trend
2016: Decreasing (Vlaschenko *et al.*, 2010).
2008: Decreasing (Hutson *et al.*, 2008a; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Tuttle and Stevenson (1982: 123) indicate that females are sexually mature at about four months, and males at about 16 months.

From Japan, Maeda (1972: 270) reported that in captivity, young were born between 26 June and 13 July. Six of the nine captive females had two young each (= polytocy, see Garbino *et al.*, 2021: Suppl.), while the others had one. The dissection of 10 free-living females indicated that seven had twin embryos (one in each uterine horn). Of the fifteen young born in the laboratory, 10 were females, but of eight embryos from free-living females, five were males. This resulted in an overall sex ratio (♂/♀) of 0.77.

POSTNATAL DEVELOPMENT:
Maeda (1972: 272 - 276) reported that twin young were born either naked or with very few hairs on their backs, whereas single young had scattered, thin hairs. The body hair starts to grow from the dorsal side of the rump to the head and to the ventral sides and reaches the same length as in the adults at about 40 days, but its colour is still darker. For singletons, the eyes opened after four to seven days, but in twins this happened only after seven to 11 days. In some animals there were four days between the opening of one of the eyes and the second. The body size of the single young was larger than for twins, and single young grew up to become larger adults. At birth, the young's hind foot already measured 83 % of the adult size, and their thumbs were 77 % of the adult size, whereas the forearm length was only 36 %, and the fingers were even smaller (23, 24 and 27 % respectively for fingers 3, 4 and 5). At 40 to 45 days, the forearm reaches almost adult size. For the fifth finger, this takes 45 to 50 days and for the third and fourth fingers, this is 50 to 55 days. The hind feet and thumbs were almost fully grown after 20 to 28 days. The body weight increases to about 22 to 30 grams at about 30 days after birth and then decreases until the young starts to feed itself. The young started to fly between 40 and 45 days of age.

PARASITES:
In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Carios vespertilionis* Latreille, 1802; and Spinturnicidae: *Spinturnix acuminata acuminata* (C.L. Koch, 1836).

ARACHNIDA
Argasidae
Sándor *et al.* (2021a: 4) reported the presence of *Carios vespertilionis* Latreille, 1802.

VIRUSES:
Coronaviridae
Alphacoronavirus
Kohl and Kurth (2014: 3112) report this virus from bats in Spain.

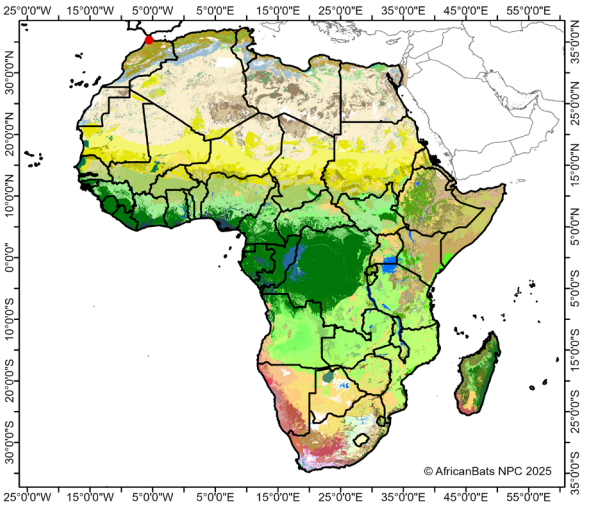

Figure 322. Distribution of *Nyctalus lasiopterus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Morocco.

Nyctalus leisleri (Kuhl, 1817)

*1817. *Vespertilio Leisleri* Kuhl, Die Deutschen Fledermäuse, Hanau, 14, 46. Type locality: Germany: Hessen: Hanau [50 07 N 08 56 E]. Syntype: ZMB 471: skin and skull. See Turni and Kock (2008). Syntype: ZMB 472: skull only. See Turni and Kock (2008). - Comments: Koopman (1992) mentions 1817 as year of publication. Corbet and Hill (1992: 144), however, mention "1819: 46". Baagøe (2001: 90) mentions 1818. - Etymology: In honour of Philipp Achilles Leisler (1772 - 1813) (see Kozhurina, 2002: 16).

1819. *Vespertilio dasykarpos* Kuhl, Die Deutschen Fledermäuse, Hanau, 49. - Comments: Alternative for *leisleri*: see Ellerman and Morrison-Scott (1951: 159).

1825. *Nyctalus verrucosus* Bowdich, Excur. Madeira and Porto Santo, 36, and footnote. Publication date: 1825. Type locality: Madeira (Portugal): "Madeira" [32 44 N 15 58 W]. [Goto Description].
1839. *Vespertilio pachygnathus* Michahelles, in: Wagner, Schreber's Säugeth, Suppl 1: pl 55b. Type locality: Croatia: Dalmatia.
1906. *Pterygistes madeiræ* Barrett-Hamilton, Ann. Mag. nat. Hist., ser 7, 17 (97): 98. Publication date: 1 January 1906. Type locality: Madeira (Portugal): "Madeira" [32 44 N 15 58 W]. [Goto Description]. Holotype: NHMUK 1907.1.1.392: ♀, skull and alcoholic. - Comments: Type specimen procured by Mason, nr 1 Tomes collection (see Barrett-Hamilton, 1906: 99).
? *Nyctalus leisleri:* (Name Combination, Current Combination).

TAXONOMY:
Includes *verrucosus*, see Corbet (1978: 55), who also included *azoreum*; but see Palmeirim (1991) and Salgueiro *et al.* (2006). Based on mitochondrial DNA, Boston *et al.* (2007: 120) indicate that Irish populations belong to the same lineage as *azoreum* and differ from *leisleri* in the rest of Europe, but this is not confirmed by Boston *et al.* (2008).

Simmons (2005: 472) recognises *verrucosus* Bowditch, 1825 as a valid subspecies.

COMMON NAMES:
Albanian: Noktulë e Leisler-it. Armenian: Փոքր իրիկնաչղջիկ. Azerbaijani: Kicik axşam yarasası. Basque: Leisler gau-saguzar. Belarusian: Вячэрніца малая. Bosnian: Mali noćni šišmiš, Mali Lajslerov šišmiš. Breton: Nozigell Leisler. Bulgarian: Лайслеров (малък) вечерник. Castilian (Spain): Murciélago nocturno, Noctulo de Leisler, Nóctulo menor, Nóctulo pequeño. Catalan (Spain): Rat penat nóctul petit, Nòctul petit. Croatian: Mali večernjak. Czech: Netopýr stromový, Nedopír chlupatopěstný, Netopýr chlupatopestrý, Netopýr Leislerův, Letouň lesní. Danish: Leislers flagermus, Leisler's flagermus. Dutch: Bosvleermuis. English: Leisler's Bat, Lesser Noctule Bat, Lesser noctule, Leisler's noctule, Hairy-armed bat. Estonian: Väikevidevlane. Finnish: Metsälepakko. French: Noctule de Leisler, Petite Noctule, le vespertilion de Leisler. Frisian: Boskflearmûs. Galician (Spain): Nóctulo pequeno, Morcego de Leisler. Georgian: მცირე მეღამურა. German: Kleinabendsegler, Kleine Abendsegler, Kleiner Abendsegler, Kleine Waldfledermaus, Leislersche Fledermaus. Greek: Μικρονυκτοβάτης. Hungarian: Szőröskarú koraidenevér, Szőröskarú denevér, Nycteris pterygisti i mikra. Irish Gaelic: Ialtóg Leisler. Italian: Nottola di Leisler. Latvian: Mazais vakarsikspārnis. Lithuanian: Mažasis nakviša. Luxembourgish: Kleng Bëschfliedermaus. Macedonian: Шумски вечерник [= Shumski Vechernik]. Maltese: Noktula Żgħir. Montenegrin: Šumski noćnik. Norwegian: Vetteflaggermus. Polish: Borowiaczek. Portuguese: Morcego-arboricola-pequeno. Rhaeto-Romance: Sgolanotg pitschen. Romanian: Liliacul mic de amurg. Russian: Вечерница малая, Малая вечерница [= Mapaya vechernicha]. Serbian: Мали ноћник [= Mali noćnik]. Scottish Gaelic: Ialtag Leisler. Slovak: Netopier stromový, Raniak malý. Slovenian: Gozdni mračnik. Swedish: Mindre brunfladdermus, Leislers fladdermus. Turkish: Küçük Ağaç Yarasası. Ukrainian: Вечірниця мала [= Vechirnytsya mala]. Welsh: Ystlum Leisler.

CONSERVATION STATUS:
Global Justification
The species is widespread and abundant, and there is no evidence of current significant population decline. Consequently, it is assessed as Least Concern LC ver 3.1 (2001) (Hutson *et al.*, 2008l; IUCN, 2009; Juste and Paunović, 2016c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Juste and Paunović, 2016c). 2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008l; IUCN, 2009). 1996: LR/nt ver 2.3 (1994).

Regional
None known.

MAJOR THREATS:
Threats include disturbance to and destruction of roosts in trees and buildings, and loss or degradation of foraging habitat. However, these are not thought to be major threats at present (Hutson *et al.*, 2008l; IUCN, 2009; Juste and Paunović, 2016c).

The major risk factors related to climatic change were identified by Sherwin *et al.* (2012: 174) as being cave/tree roosting and aerial hawking.

CONSERVATION ACTIONS:
Juste and Paunović (2016c) supports Hutson *et al.* (2008l) [in IUCN (2009)] who reported that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention, in parts of its range where these apply. It is included in Annex IV of EU Habitats and Species Directive, and there is some habitat protection through Natura 2000. It occurs in protected areas

throughout its range. No specific conservation actions known.

GENERAL DISTRIBUTION:
Nyctalus leisleri is largely a western Palaearctic species (Europe and north-west Africa), with scattered records in the western parts of the eastern Palaearctic (Pakistan, Afghanistan, the Himalayas). It is widely distributed in Europe from southern Scotland and Ireland more or less along southern edge of the Baltic Sea south and parts of Mediterranean coast to western Russia. It is present on Madeira and the Canary Islands (on Tenerife and La Palma only) but absent from southwestern Italy and Sicily, eastern Spain, most of Fennoscandia and northern Russia. In North Africa it is recorded from Mediterranean montane Morocco and Algeria and there is one record from Cyrenaica (Libya). It occurs from sea level to 2,400 m.

Native: Afghanistan; Albania; Algeria (Hanák and Gaisler, 1983: 585; Gaisler, 1984: 89); Andorra; Armenia; Austria; Azerbaijan; Belarus; Belgium; Bosnia and Herzegovina; Bulgaria; China; Croatia; Cyprus (Benda *et al.*, 2007: 71); Czech Republic; France (Corse); Georgia; Germany; Gibraltar; Greece; Hungary; India; Iran, Islamic Republic of; Ireland; Italy; Kazakhstan; Latvia; Libyan Arab Jamahiriya (Hanák and Gaisler, 1983: 585); Liechtenstein; Lithuania; Luxembourg; Macedonia, the former Yugoslav Republic of; Moldova; Montenegro; Morocco (Benda *et al.*, 2004d; 2010a: 158; El Ibrahimi and Rguibi Idrissi, 2015: 363; Dbiba *et al.*, 2025: 7); Netherlands; Pakistan; Poland; Portugal (Madeira); Romania; Russian Federation; Serbia; Slovakia; Slovenia; Spain (Canary Is.); Sweden; Switzerland; Turkey; Ukraine; United Kingdom.

BIOGEOGRAPHY:
Molecular data suggest that *N. leisleri* from the Canary Islands probably came from North Africa (Morocco) population (Salgueiro *et al.* (2006).

DENTAL FORMULA:
Matthews (1950: 12) describes the milk dentition, consisting of two trilobed incisors, one canine with one large central lobe and two very small lateral lobes, and two trilobed premolars in the upper cheek. The lower cheek contains two trilobed incisors and one bilobed one, a well-developed, trilobed canine, and two trilobed premolars (but the posterior lobe of the second one is very much reduced).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 19.3 Pa, aspect ratio 7.9 and tip shape index of 1.19 for a wingspan of 26 cm and a wing area of 86 cm^2 and a body mass of 17 g.

ECHOLOCATION:
For 6 Greek specimens, Papadatou *et al.* (2008b: 132) report a start frequency of 47.5 ± 3.67 kHz, a terminating frequency of 27.0 ± 1.10 kHz, a peak frequency of 31.7 ± 0.87 kHz, and a bandwidth of 12.3 ± 2.96 kHz. The duration of the call is 4.2 ± 1.30 ms, and the interpulse interval is 153.4 ± 62.36 ms.
Walters *et al.* (2012: suppl.) present the following numbers for 76 calls from bats from France, Greece, Switzerland and the UK: duration: 9.39 ± 3.86 ms, F_{max}: 42.20 ± 14.77 kHz, F_{min}: 25.75 ± 2.75 kHz, bandwidth: 16.45 ± 12.45 kHz, F_{peak}: 28.61 ± 5.27 kHz.

Benda *et al.* (2012a: 183) present two series of data for specimens from Iran: **1**: F_{start}, 47.4 ± 4.2 (41.7 - 56.2) kHz, F_{end}: 30.3 ± 0.8 (28.7 - 31.3) kHz, F_{peak}: 34.0 ± 1.1 (31.2 - 35.2) kHz, duration: 3.8 ± 1.1 (2.6 - 6.8) ms, and interpulse interval: 112.8 ± 63.2 (48.2 - 262.9) ms; **2** (hand released): F_{start}: 43.3 ± 2.7 (40.4 - 46.7) kHz, F_{end}: 26.3 ± 0.8 (24.8 - 26.8) kHz, F_{peak}: 28.4 ± 0.4 (28.0 - 28.9) kHz, duration: 6.1 ± 0.3 (5.7 - 6.5) ms, and interpulse interval: 106.2 ± 2.0 (104.9 - 109.3) ms.

Luo *et al.* (2019a: Supp.) reported the following data: F_{peak}: 30.7 kHz, F_{start}: 55 kHz, F_{end}: 27.7 kHz, Band width: 27.3 kHz, and duration: 5.3 ms.

MOLECULAR BIOLOGY:
Karyotype
Arslan and Zima (2014: 12) reported 2*n* = 44 + Bs, FNa = 50, FN = 54, a medium-sized metacentric X, and a dot-like acrocentric Y. The autosomal component consists of three large metacentric, one small submetacentric and 17 acrocentric autosomal pairs. They also indicate that this set can also include 1 to 3 dot-like supernumerary chromosomes (Bs). In one Turkish male, Arslan and Zima (2014: 12) furthermore found a dot-like supernumerary chromosome, leading to 2*n* = 45.

Genetics
Molecular analyses performed by Boston *et al.* (2015: 1) revealed that two distinct mitochondrial DNA lineages are present: an eastern lineage of *N. leisleri* distributed throughout continental Europe and a western lineage, including *N. leisleri* from Ireland and Britain, but also *N. azoreum* from the Azores.

HABITAT:
In Switzerland, Szentkuti *et al.* (2013: 110) found that foraging *N. leisleri* selected deciduous

woodlands over other habitat types (pasture, confirous forest and settlements). They also reported that the bat's nightly mean (± SE) distance travelled was 1,969 ± 1,754 m, and that the maximum distance between the most distant location and the previous roost was on average (4,678 ± 1,082; 1,080 - 13,614 m).

On Madeira, Ferreira *et al.* (2022a: 1) found that *Nyctalus leisleri verrucosus* was negatively influenced by Laurisilva (primary forest) cover and that its activities were negatively affected by increasing altitude.

On the Canary islands, Agirre-Mendi (2005: 233) reported this species to occur from sea level to up to 2,100 m, where it lives in woodlands covered with *Pinus canariensis*, subtropical rain forests (laurisilva), but also in man-made rural areas and high-mountain zones.

ROOST:
In southern Switzerland, Spada *et al.* (2008: 81) found that *N. leisleri* prefers to roost in live chestnut trees (*Castanea sativa*), with large diameter and in absence of vegetation near the entrance.

On the Canary Islands, Trujillo and Barone (1991: 102) reported these bats to roost in an abandoned building and a single bat in a bat box in a *Pinus canariensis* forest.

DIET:
Gonçalves *et al.* (2024: 4) found that - on Madeira - the majority of the preys consisted of Lepidoptera (50.5 %), followed by Coleoptera (17.5 %), Diptera (13.6 %), Hemiptera (7.8 %), and Neuroptera (5.3 %). Within the Lepidoptera most of the prey taxa belonged to the Noctuidae (18 %), followed by Cerambycidae (16.5 %), Blastobasidae (8.7 %), Limoniidae (8.3 %), and Geometridae (8.3 %). At species level, *Arhopalus ferus* (Mulsant, 1839) (Cerambicidae - 15.0 %) was most frequently counted, followed by *Gymnoscelis rufifasciata* (Haworth, 1809) (Geometridae - 5.8%), and *Agonopterix scopariella* (Heinemann, 1870) (Depressariidae - 5.3%). Of the 44 taxa consumed by this species, 29.5 % are considered agricultural pests and 15.9 % possible agricultural pests. They also found that male bats have a much broader dietary niche than females.

Kaňuch *et al.* (2005: 253) identified seven orders of insects in 154 faecal pellets examined from Slovakian bats. These belonged to the Aphididae (Homoptera), Heteroptera, Chrysopidae (Neuroptera), Coleoptera, Ichneumonidae and Formicidae (Hymenoptera), Lepidoptera, Nematocera and Brachycera (Diptera). The most important group (in both frequency [100 %] and volume [55.7 %]) were Lepidoptera.
Benda *et al.* (2012a: 460 - 461) indicate that European studies showed that this species' diet is relatively variable depending on the foraging habitat. In forests, Lepidoptera and nematoceran Diptera are most often present, whereas in the landscapes with a larger proportion of pastures the dung flies (Scatophagidae) and scarabaeid beetles were more significantly represented. Other groups that were present include Trichoptera, Neuroptera, and Hymenoptera. In more arid habitats in the Middle East, Hymenoptera (Formicoidea), Trichoptera, and Coleoptera (namely Carabidae and Curculionidae) are the main groups present in the diet.

On the Canary Islands, it was found to feed on Lepidoptera (Noctuidae) (Agirre-Mendi, 2005: 234).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 102 minutes, and the digestibility rate about 77.0 %.

POPULATION:
Structure and Density
It is widespread although patchily distributed in Europe. Common in parts of range (e.g., Ireland), scarce in other parts (Stebbings and Griffith, 1986). Local extinctions have been reported for the central part of Russian Federation (K. Tsytsulina *pers. comm.* 2005), although the species remains common in other parts of Russia and the Caucasus (S. Kruskop *pers. comm.,* 2005). In North Africa it is limited by the distribution of suitable habitat, but is particularly abundant in Djurdjura, NE Algeria (Hutson *et al.*, 2008l; IUCN, 2009; Juste and Paunović, 2016c).

Trend
2016: Unknown (Juste and Paunović, 2016c).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) report a maximum longevity of 16 years.

ACTIVITY AND BEHAVIOUR:
On the Canary Islands, *Nyctalus leisleri* remains active during the winter on lower and middle altitudes (Agirre-Mendi, 2005: 234).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

On the Canary Islands, Trujillo and Barone (1991: 102) mentioned two nursing females in May-June.

MATING:
On the Canary Islands, mating occurs in September-October (Agirre-Mendi, 2005: 234).

PARASITES:
The Nematode *Molinostrongylus vespertilionis* Morosov and Spassky, 1961 was reported by Genov *et al.* (1992) from Hungary, Moldova and Ukraine.

Estrada-Peña and Sanchez (1988: 305) described *Steatonyssus (Steatonyssus) balcellsi* from a *N. leisleri* specimen from Frontera, Canary Islands.

In Slovakia, Kaňuch *et al.* (2005: 252) reported the presence of the following ectoparasites: mites: *Steatonyssus spinosus* (family Dermanyssidae), *Macronyssus flavus* (Macronyssidae), *Spinturnix helvetiae* (Spinturnicidae); fleas: *Ischnopsyllus intermedius, I. variabilis* (Ischnopsyllidae); and flies: *Nycteribia latreillii, N. (Acrocholidia) vexata* (Nycteribiidae).

They found that 100 out of 177 (56.5 %) of the examined bats carried at least one parasite, but only 15.3 % of these had two different species of parasites. Only *S. spinosus* and *S. helvetiae* were found abundantly (resp. 31.3 and 55.4 %), all other species occurred on less than 5 % of the bats.

Sándor *et al.* (2021a: 4) reported the presence of the argasid tick *Carios vespertilionis* Latreille, 1802.

VIRUSES:
Coronaviridae
Alphacoronavirus
This virus was reported from bats from Germany by Kohl and Kurth (2014: 3112).

Betacoronavirus
The virus was reported by Kohl and Kurth (2014: 3112) from Bulgaria and Germany.

Orthomyxoviridae
Despite sampling and testing of 64 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

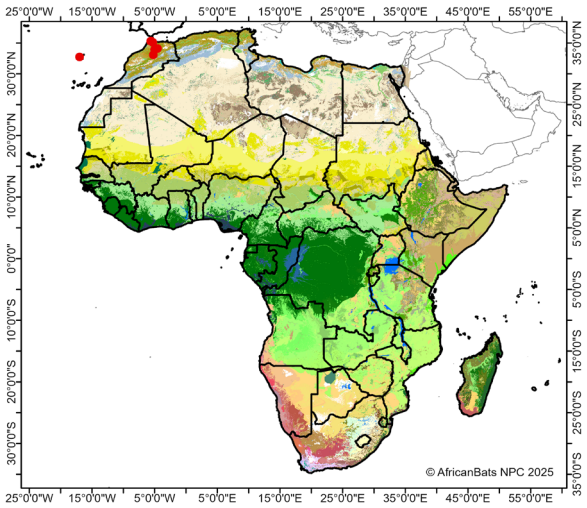

Figure 323. Distribution of *Nyctalus leisleri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Azores (Portugal), Madeira (Portugal), Morocco.

Genus ***Pipistrellus*** Kaup, 1829

*1829. *Pipistrellus* Kaup, Skizzierte Entwicklungs-Geschichte Natürliche Systematik der Europäische Thierwelt, 1: 98. Publication date: 1829. - Comments: Type species: *Vespertilio pipistrellus* Schreber, 1774, by monotypy. Not *Pipistrellus* Gistel, 1848 (Insecta, Diptera, Hybotidae) (see Jackson and Groves, 2015: 274). - Etymology: From the italian "*pipistrello*" meaning bat (see Fujita and Kunz, 1984: 4; Flannery, 1995a: 393). From the Latin "*pipio* meaning squeaking and "*strellus*", which is an attiona indicating a "small animal" (see Kapteyn, 1995: 83). - Phonetics: pip'-is-trell'-us. - ZooBank: D3BD2230-B730-40BA-95D0-E95484EF21C7. (Current Combination).

1837. *Pipistrella* Bonaparte, Iconografia Fauna italiana. - Comments: Icon. fauna Ital.

1838. *Romicia* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 495. Publication date: 1 February 1838. - Comments: Type species: *Romicia calcarata* Gray, 1838 (=*Vespertilio kuhlii* Kuhl, 1817), by monotypy.

1839. *Vesperugo* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 312. Publication date: 1839. - Comments: In part (see Allen, 1939a: 92; Pavlinov *et al.*, 1995: 104). Included 13 species now referred to *Eptesicus, Pipistrellus, Neoromicia, Hypsugo*.

1840. *Romicius* Blyth, Cuvier's Animal Kingdom, 75. Publication date: 1840. - Comments: Variant of *Romicia* (see Allen, 1939a: 93; Meester *et al.*, 1986: 50), or invalid emendation (see Jackson and Groves, 2015: 274). (Emendation).

1856. *Nannugo* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Included *Vespertilio nathusii* Keyserling and Blasius, *V. kuhlii* Kuhl and *V. pipistrellus* Schreber (see Ellerman and Morrison-Scott, 1951: 152; Corbet and Hill, 1992: 133). - Etymology: From the Greek "*νάννος*", meaning dwarf and the suffix -ugo (in analogy with *Hypsugo* and *Vesperugo*) (see Palmer, 1904: 447).

1868. *Alobus* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 707 (for 1867). Publication date: 1868 [Goto Description]. - Comments: Type species: *Vespertilio temminckii* Cretzschmar, 1826 (=*Pipistrellus rueppellii*

Fischer, 1829), by monotypy. Not of Le Conte, 1856 (Insecta, Coleoptera, Scarabaeidae) (see Jackson and Groves, 2015: 274).

1899. *Euvesperugo* Acloque, Faune de France, Mammifères, 35. - Comments: In part: Included six species, one of which was *Vespertilio pipistrellus* Schreber, 1774 (see Ellerman and Morrison-Scott, 1951: 162; Meester *et al.*, 1986: 50). Cabrera (1914: 123) also included it in part into *Nyctalus*.

1926. *Eptesicops* Roberts, Ann. Transv. Mus., 11: 245. Publication date: 14 September 1926. - Comments: Type species: *Scotophilus rusticus* Tomes, 1861, by original designation (see Jackson and Groves, 2015: 275).

1946. *Vansonia* Roberts, Ann. Transv. Mus., 20 (4): 304 [Goto Description]. - Comments: Type species: *Pipistrellus vernayi* Roberts, 1932 (=*Vespertilio rüppellii* Fischer, 1829), by original designation. Not *Vansonia* Schein, 1956 (Insecta, Coleoptera, Scarabaeidae) (see Jackson and Groves, 2015: 275). - Etymology: The name *Vansonia* refers to George van Son, entomologist of the Transvaal Museum (see Lanza *et al.*, 2015: 382). .

1951. *Pipiestrellus:* Watson, Uganda J., 15 (1): xx. (Lapsus).

1987. *Attalepharca* Menu, Palaeovert., 17 (3): 78, 126. Publication date: 15 November 1987 [Goto Description]. - Comments: No type species designated, therefore not available (see Corbet and Hill, 1992: 133).

1987. *Nycterikaupius* Menu, Palaeovert., 17 (3): 108, pl 4, fig 1. Publication date: 15 November 1987 [Goto Description]. - Comments: In part. The species assigned to this genus by Menu (1987: 109) are currently (sensu Monadjem *et al.*, 2020a: 1140) included in the genera *Laephotis, Neoromicia, Pipistrellus* and *Pseudoromicia*.

1992. *Attelepharca:* Corbet and Hill, The mammals of the Indomalayan Region: A systematic review, 131. (Lapsus).

1994. *Atellepharca:* Corbet and Hill, J. Mamm., 75 (1): 241. Publication date: February 1994. (Lapsus).

1999. *Pipistallus:* Salleh, Hang, Rahman and Abdulla, ASEAN Review of Biodiversity and Environmental Conservation (ARBEC), 1. Publication date: September - October 1999. (Lapsus).

2000. *Pipistrellis:* Qui, Han, Qi and Yufen, Acta Anthrop. Sin., 4 (1): 19. (Lapsus).

2007. *Pipistrellus (Afropipistrellus):* Thorn, Kock and Cuisin, Mammalia, 71 (1/2).

2008. *Pipistrillus:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Lapsus).

2008. *Pipstrillus:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Lapsus).

2018. *Pipistrelus:* Malekani, Musaba, Gembu, Bugentho, Toengaho, Badjedjea, Ngabu, Mutombo, Laudisoit, Ewango, Van Cakenberghe, Verheyen, Asimonyo, Masudi, Bongo and Ngbolua, Nat. Conserv. Res., 3 (2): 68. Publication date: January 2018. (Lapsus).

2019. *Pipistellus:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).

? *Pipistrellus sp. IVK-2011*

? *Pipistrellus sp.:*

? *Vansoni:* (Lapsus).

TAXONOMY:

For synonyms see Ellerman and Morrison-Scott (1951: 162); but also see Hill (1976: 25); Kitchener *et al.* (1986); and Menu (1984). *Hypsugo* was considered a full genus by Tiunov (1986). Hill and Harrison (1987) would transfer *Neoromicia* and *Vespadelus* to *Pipistrellus* from *Eptesicus*.

Based on the analysis of three nuclear genes (RAG2, APOB, and DMP1), Zhukova *et al.* (2023a: 302) found that the genus *Pipistrellus* is paraphyletic in respect to *Nyctalus* and *Glischropus*, and they suggest that the genus - as currently conceived - should probably be divided in two or three separate genera or that *Nyctalus* and *Glischropus* should be considered subgenera of *Pipistrellus*

Currently (Simmons and Cirranello, 2023b) recognized subgenera and species of the genus *Pipistrellus*:

Alionoctula Kruskop, Solovyeva and Kaznadzey, 2018: *stenopterus* (Dobson, 1875) – western Malaysia, Sumatra, Riau Arch., northern Borneo, Mindanao (Philippines) (Simmons, 2005: 478).

Pipistrellus Kaup, 1829: *abramus* (Temminck, 1838) – southern Ussuri region (Russia and China), Taiwan, southern and central Japan, Korea, Vietnam, Burma, India (Simmons, 2005: 473); *adamsi* Kitchener, Caputi and Jones, 1986 – Queensland and Northern Territory (Australia) (Simmons, 2005: 473); ***aero*** Heller, 1912; *angulatus* (Peters, 1880) – New Guinea, Bismarck Arch., Bougainville Isl and Solomon Isls, adjacent small islands (Simmons, 2005: 473); *ceylonicus* (Kelaart, 1852) – Pakistan, India, Sri Lanka, Bangladesh, Burma, Kwangsi and Hainan (China), Vietnam, Borneo (Simmons, 2005: 474); *collinus* Thomas, 1920 – Highlands of Papua New Guinea (Simmons, 2005: 474); *coromandra* (Gray, 1838) – Afghanistan, Bangladesh, India (including Nicobar Isls), Sri Lanka, Pakistan, Nepal, Bhutan, Burma, Cambodia, Thailand, southern China (Simmons, 2005: 474); *creticus* Benda, 2009 – Crete; *dhofarensis* Benda, Reiter, Uhrin and Varadínová, 2016 – E Yemen and SW Oman; *endoi* Imaizumi, 1959 – Honshu (Japan) (Simmons, 2005: 474); ***etula*** Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, 2025; ***hanaki*** Hulva and Benda, 2004; ***hesperidus*** (Temminck, 1840); ***inexspectatus*** Aellen, 1959; *javanicus* (Gray, 1838) – eastern Afghanistan, northern Pakistan, northern and central India, southeastern Tibet (China), Burma, Thailand, Vietnam, through southeast Asia to Lesser Sunda Isls and the Philippines (Simmons, 2005: 475); ***kuhlii*** (Kuhl,

1817); ***maderensis*** (Dobson, 1878); *minahassae* (A.B. Meyer, 1899) – northern Sulawesi (Simmons, 2005: 476); *murrayi* Andrews, 1900 – Christmas Island (extinct); ***nanulus*** Thomas, 1904; *nathusii* (Keyserling and Blasius, 1839) – western Europe to Urals and Caucasus and western Asia Minor, southern England (Simmons, 2005: 476); *papuanus* (Peters and Doria, 1881) – Seram, Aru Isls, Baik-Supiori, New Guinea, New Ireland (Bismarck Arch.) adjacent small islands (Simmons, 2005: 476); *paterculus* Thomas, 1915 – northern India, Burma, Thailand, Vietnam, and southwestern China (Simmons, 2005: 477); ***permixtus*** Aellen, 1957; ***pipistrellus*** (Schreber, 1774); *pygmaeus* (Leach, 1825) – British Isles, southern Scandinavia south to Spain, Portugal, Corsica, Sardinina, Italy, Slovenia and Greece, east to Ukaraine and western Russia, northern Algeria, Tunisia, Libya (Cyrenaica only) (Simmons, 2005: 477); ***raceyi*** Bates, Ratrimomanarivo, Harrison and Goodman, 2006; ***rusticus*** (Tomes, 1861); ***simandouensis*** Monadjem, Richards, Decher and Hutterer, 2020; *sturdeei* Thomas, 1915 – Bonin Isls (Japan) (Simmons, 2005: 478); *tenuis* (Temminck, 1840) – Afghanistan to the Moluccas, southern China, Laos, Vietnam, Cocos Keeling Isl and Christmas Isl (Simmons, 2005: 479); *wattsi* Kitchener, Caputi and Jones, 1986 – southeastern Papua New Guinea and Sanari Isl (Simmons, 2005: 479); *westralis* Koopman, 1984 – northern Australia from Kimberly to eastern Gulf of Carpentaria (Simmons, 2005: 479).

COMMON NAMES:
Czech: zakrslí netopýři. English: Pipistrelle Bats, Pipistrelles. French: Pipistrelles. German: Zwergfledermäuse, Pipistrellen. Italian: Pipistrèlli. Ukrainian: Нетопир [= Netopir].

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) line drawing of tragi of specimen DNSM 13220 referred to a *Pipistrellus* 1 from Mount Nimba, Liberia.

ECHOLOCATION:
Rakotondramanana *et al.* (2014: 80) studied the echolocation calls of Madagascan "*Pipistrellus sensu lato*" bat (including *Pipistrellus, Neoromicia* and *Hypsugo* in two different flight cages: A (12 x 3 x 3 m) and B (5.4 x 1.4 x 1.5 m), and found that the same bats used different types of calls depending on the cage they were flying in. In the large cage (A), the signal showed a frequency-modulated part followed by a short quasi-constant frequency (FM/QCF) component, whereas in the small cage (B) the QCF component was lacking. These authors, therefore, also warn against extrapolating the results of echolocation calls captured in flight cages.

PREDATORS:
Demeler (1981: 133) found remains of a "*Pipistrellus*" in pellets of *Bubo africanus* (Temminck, 1821) in the Yankari Game Reserve (Nigeria).

Mikula *et al.* (2016: Supplemental data) mention a *Pipistrellus* sp. being taken by a Grey-headed bushshrike (*Malaconotus blanchoti* Stephens, 1826).

In Algeria, Djilali *et al.* (2016: 161) found remains of 6 *Pipistrellus* specimens in 516 preys (1.2 %) captured by the Short-eared Owl (*Asio flammeus* (Pontoppidan, 1763)).

Goodman *et al.* (2015c: 78) found the remains of five *Pipistrellus/Neoromicia* sp. individuals in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023: 73) mentioned that *Basilia (Basilia) ansifera* Theodor, 1956 has been found on unidentified *Pipistrellus* bats from Côte d'Ivoire and Sudan. They also found *Basilia (Basilia) robusta* Theodor, 1956 on a *Pipistrellus aero* or *hesperidus* from Ol Jogi Conservancy (Kenya).

VIRUSES:
Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that twenty out of forty examined "*Pipistrellus*" specimens from the same colony in the DRC tested positive for *Paramyxovirus* sequences, all of which were nearly identical.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Angola, Burundi, Cameroon, Canary Islands (Spain), Central African Republic, Congo (Democratic Republic of the), Egypt, Ethiopia, Gabon, Ghana, Guinea-Bissau, Kenya, Liberia, Madagascar, Malawi, Namibia, Nigeria, Senegal, Sierra Leone, South Africa, South Sudan, Tanzania, Togo, Tunisia, Uganda.

Pipistrellus etula Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, 2025

*2025. *Pipistrellus etula* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, Zool. J. Linn. Soc., 204 (2): 13,14, figs 8 - 10, 12. Publication date: 13 June 2025.

Holotype: EBD 19203M: ad ♂, skull and alcoholic. Collected by: Javier Juste; collection date: 14 April 1989. Paratype: EBD 19086M: ♂. Collected by: Javier Juste; collection date: 13 April 1989. Paratype: EBD 19087M: ♂. Collected by: Javier Juste; collection date: 15 April 1989. Paratype: EBD 19088M: ♀. Collected by: Javier Juste; collection date: 15 April 1989. - Etymology: '*etula*' means island or nation in the language of the original Bubi people of Bioko Island (Torrent *et al.*, 2025b: 14)..

COMMON NAMES:
English: Bioko pipistrelle

DENTAL FORMULA:
I 2/3, C 1/1, P 2/3, M 2/3 = 34.

ECHOLOCATION:
Torrent *et al.* (2025b: 7) recorded the following values for three specimens: F_{max}: 40.1 ± 1.32 (37.5 - 42.0) kHz, F_{start}: 101.3 ± 6.19 (83.0 - 114.9) kHz and F_{end}: 31.5 ± 2.94 (24.2 - 35.3) kHz.

Subgenus *Pipistrellus (Pipistrellus)* Kaup, 1829

2004. *Pipistrellus sp. II:* Hulva, Horáček, Strelkov and Benda, Mol. Phylog. Evol., 32 (3): 1025. Publication date: September 2004. (Name Combination).
? *Pipistrellus (Pipistrellus):* (Name Combination).

TAXONOMY:
Zhukova *et al.* (2025: 15) reviewed the Pipistrellini and recognized two species groups in the subgenus *Pipistrellus,* containing the following species:
"*pipistrellus*": *hanaki, pipistrellus, pygmaeus*
"*kuhlii*": *hesperidus, kuhlii, maderensis, nanulus, raceyi, rusticus, simandouensis.*
They were unable to evaluate the status of i*nexspectatus.*

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea.

Pipistrellus (Pipistrellus) 'incertae-sedis'

1858. *Nannugo Kolenatii* Müller, Lotos (Prag), 8: 75, figs 1 - 4. Type locality: Egypt: "Egypt". [Goto Description].
1862. *Vespertilio (Nannugo) Kolenatii:* Koch, Nass. Naturw. Jahrb., 18: 397.
2013. *Pipistrellus cf. hesperidus:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. Torrent *et al.* (2025b: 20) found that these Senegalese specimens cluster with *Pipistrellus rusticus* and are unrelated to *Pipistrellus hesperidus* s.s. and might possibly be named *Pipistrellus marrensis* Thiomas and Hinton, 1923, but this qill require further investigation. (Name Combination).
? *Pipistrellus (Pipistrellus) 'incertae-sedis'*

TAXONOMY:
Müller (1858: 75) called *Nannugo Kolenati* one of the smallest Nord African bat species. Its German name "Die weissgesäumte Buschfledermaus" indicates that a white edge on the wing membrane was present.

Koch (1862: 397) considers this form a relative of *Nannugo marginatus*, which in turn is a synonym of *P. kuhlii*. Except for these two publications, no other references to this form were found.

The description does not enable us to assign this name to either *Pipistrellus kuhlii* Kuhl, 1817 or *Pipistrellus deserti* Thomas, 1902. In the latter case this name might be a senior synonym, provided *aegyptius* Fischer, 1829 is to be ignored. However, this name clearly does qualify for the status of "*nomen oblitum*", and should, therefore, probably be ignored.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

Pipistrellus (Pipistrellus) aero Heller, 1912

*1912. *Pipistrellus aero* Heller, Smiths. Misc. Coll., 60 (12): 3. Publication date: 4 November 1912. Type locality: Kenya: Mathews Range: Mount Gargues [00 57 N 37 24 E, 7 100 ft]. [Goto Description]. Holotype: USNM 181812: ad ♂, skin and skull. Collected by: Edmund Heller; collection date: 26 August 1911; original number: 4110.

1971. *Pipistrellus [(Pipistrellus)] aero:* Hayman and Hill, Mammals of Africa: Chiroptera, 41. (Name Combination, Current Combination).

1971. *Pipistrellus altae:* Hayman and Hill, Mammals of Africa: Chiroptera, 43. - Comments: Hayman and Hill (1971) refer to specimens in the NHMUK labelled as "*P. altae*" but do not mention an original author.

? *Pipistrellus (Pipistrellus) aero:* (Current Combination).

TAXONOMY:
The Ethiopian specimens in the British Museum are clearly *P. kuhlii*; see Hayman and Hill (1971: 41). Koopman (1994: 114) states that this species is probably a subspecies of *P. aegyptius* (= *deserti*).

COMMON NAMES:
Chinese: 东非伏翼. Czech: netopýr gargueský. English: Mt Gargues Pipistrelle Bat, Aerial Pipistrelle Bat, Mt Gargues Pipistrelle, Mount Gargues Pipistrelle, Kenya Pipistrelle. French: Pipistrelle du Kenya. German: Luftige Zwergfledermaus, Luftige Pipistrelle, Mount-Gargues Zwergfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Jacobs *et al.*, 2008q; IUCN, 2009; Jacobs *et al.*, 2019g).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019g). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008q; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Jacobs *et al.*, 2004ae; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs *et al.*, 2008q; IUCN, 2009; Jacobs *et al.*, 2019g).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008q) [in IUCN (2009)] and Jacobs *et al.* (2019g) report that it has been recorded in the Matthews Range Forest Reserve and Marsabit National Reserve. Further studies are needed into the distribution, natural history and possible threats to this little-known species.

GENERAL DISTRIBUTION:
Pipistrellus aero is endemic to northwestern Kenya, where it is known only from three localities (Mount Garguez; Marsabit Lake and Ngong). It is also present in adjacent Ethiopia.

Native: Ethiopia (Lavrenchenko *et al.*, 2004b: 135); Kenya.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 69 minutes, and the digestibility rate about 81.2 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008q; IUCN, 2009; Jacobs *et al.*, 2019g).

Trend
2018: Unknown (Jacobs *et al.*, 2019g). 2008: Unknown (Jacobs *et al.*, 2008q; IUCN, 2009).

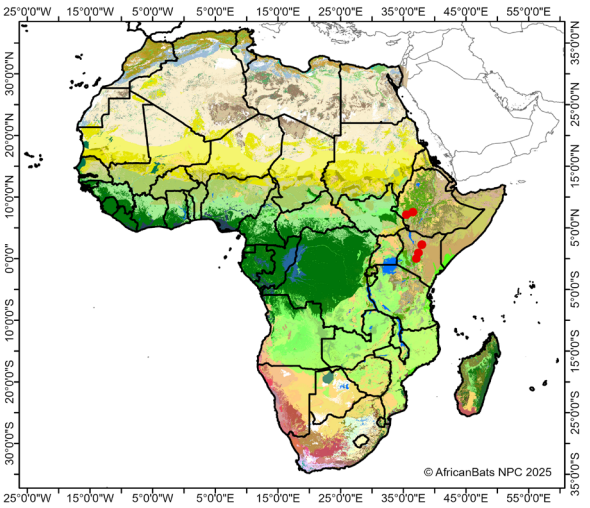

Figure 324. Distribution of *Pipistrellus (Pipistrellus) aero*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Kenya.

Pipistrellus (Pipistrellus) hanaki Hulva and Benda, 2004

*2004. *Pipistrellus hanaki* Hulva and Benda, in: Benda, Hulva and Gaisler, Acta Chiropt., 6 (2): 207. Type locality: Libya: Cyrenaica: Al Jabal Al Akhdar district:: (ca. 5 km) SW of Al Bayda: Wadi al Kuf [32 44 N 21 41 E, 495 m]. [Goto Description]. Holotype: NMP 49897: ad ♂, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 19 May 2002. 3 paratypes: see Benda *et al.* (2004b: 207). Paratype: NMP 49890: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 18 May 2002; original number: pb2135. Collected at: 'Arqub Ash Shafshaf, ca. 3 km south of Al Hilal, Cyrenaica, Libya; 32.87°N, 22.18°E. (see Benda in Mlíkovský *et al.*, 2011: 136). Paratype: NMP 49891: ad ♂, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 18 May 2002; original number: pb2136. Collected at: 'Arqub Ash Shafshaf, ca. 3 km south of Al Hilal, Cyrenaica, Libya; 32.87°N, 22.18°E. (see Benda in Mlíkovský *et al.*, 2011: 136). Paratype: NMP 49892: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 18 May 2002; original number: pb2137. Collected at: 'Arqub Ash Shafshaf, ca. 3 km south of Al Hilal, Cyrenaica, Libya; 32.87°N, 22.18°E. (see Benda in Mlíkovský *et al.*, 2011: 136). Paratype: NMP 49894: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 19 May 2002; original number: pb2142. Paratype: NMP 49895: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 19 May 2002; original number: pb2143. Paratype: NMP 49896: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 19 May 2002; original number: pb2144. Paratype: NMP 49902: sad ♂, alcoholic (skull not removed). Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2150. Collected at a small cave in the central part of Wadi Al Kuf, 8 km southwest of Massah, Cyrenaica, Libya; 32.70 N 21.58 E (see Benda in Mlíkovský *et al.*, 2011: 136). Paratype: NMP 49903: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2151. Collected a :a small cave in the central part of Wadi Al Kuf, 8 km southwest of Massah, Cyrenaica, Libya; 32.70 N 21.58 E (see Benda in Mlíkovský *et al.*, 2011: 136). Paratype: NMP 49904: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2152. Collected at a small cave in the central part of Wadi Al Kuf, 8 km southwest of Massah, Cyrenaica, Libya; 32.70 N 21.58 E (see Benda in Mlíkovský *et al.*, 2011: 136). - Etymology: In honour of prof. Vladimír Hanák (Prague, Czech Republic), who signficantly contributed to the knowledge of the Palaearctic bat fauna (see Benda *et al.*, 2004b: 208).

2004. *Pipistrellus sp. I:* Hulva, Horáček, Strelkov and Benda, Mol. Phylog. Evol., 32 (3): 1025. Publication date: September 2004. (Name Combination).

2020. *Pipistrellus (Pipistrellus) hanaki:* Simmons and Cirranello, BatNames.org. (Current Combination).

TAXONOMY:
See Benda *et al.* (2004b; 2009a).

Evin *et al.* (2011: 2095 - 2097) confirm that *hanaki* is composed of two different lineages: *P. hanaki hanaki* from Libya and *P. hanaki creticus* Benda, 2008 from Crete, which differ also in size and shape of the skull.

COMMON NAMES:
Albanian: Pipistrel i Hanak-ut. Armenian: Հանակի փոքրաչղջիկ. Azerbaijani: Hanaki cırtdan şəbpərəsi. Basque: Hanak pipistrelo. Belarusian: Нетапыр Ганака. Bosnian: Hanakov šišmiš. Breton: Pipistrell Libia. Bulgarian: Прилепче на Ханак. Castilian (Spain): Murciélago de Hanak. Catalan (Spain): Pipistrel·la de Hanak. Croatian: Hanakov patuljasti šišmiš. Czech: Netopýr Hanákův, Netopýr kyrénský. Danish: Hanaks flagermus. Dutch: Hanaks dwergvleermuis, Hanak's dwergvleermuis. English: Hanak's Pipistrelle. Estonian: Liibüa nahkhiir. Finnish: Libyanlepakko. French: Pipistrelle de Libye. Frisian: Hanaks dwerchflearmûs. Galician (Spain): Morcego de Hanak. Georgian: ჰანაკის ღამური. German: Hanaks Zwergfledermaus, Hanaks Pipistrelle. Greek: Ναvουχτερίδα του Hanak. Hungarian: Hanák-törpedenevér. Irish Gaelic: Ialtóg Hanak. Italian: Pipistrello di Hanak. Latvian: Hanaka sikspārnis. Lithuanian: Hanako šikšniukas. Luxembourgish: Libesch Zwergfliedermaus. Macedonian: Ханаков лилјак. Maltese: Pipistrell ta' Hanak. Montenegrin: Libijski patuljasti slijepi mišić. Norwegian: Kyrenaikaflaggermus. Polish: Karlik cyrenejski. Portuguese: Morcego de Hanak. Rhaeto-Romance: Pipistrel da Hanak. Romanian: Liliacul pitic a lui Hanak. Russian: Нетопырь Ганака. Serbian: Либијски сл[ij]епи мишић [= Libijski sl[ij]epi mišić]. Scottish Gaelic: Ialtag Hanak. Slovak: večernica Hanákova. Slovenian: Libijski drobni netopir. Swedish: Kretapipistrell. Turkish: Hanak'ın Cüce Yarasası. Ukrainian: Нетопир Ганака. Welsh: Ystlum lleiaf Hanak.

SIMILAR SPECIES:
Pipistrellus hanaki differs from its nearest relatives *P. pipistrellus* and *P. pygmaeus* chromosomally, and by its larger skull and teeth, and a number of other characters (Benda *et al.*, 2004b).

CONSERVATION STATUS:
Global Justification
This recently described species, little or no data is available on population size and trend, distribution, or potential threats. Assessed as Data Deficient DD ver 3.1 (2001) (Aulagnier and Palmeirim, 2008a; IUCN, 2009).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2008: DD ver 3.1 (2001) (Aulagnier and Palmeirim, 2008a; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Unknown (Aulagnier and Palmeirim, 2008a; Thorn *et al.*, 2009).

CONSERVATION ACTIONS:
Unknown (Aulagnier and Palmeirim, 2008a; IUCN, 2009).

GENERAL DISTRIBUTION:
Pipistrellus hanaki is known only from a small area on the Libyan coast (in the Cyrenaica area) (Benda *et al.*, 2004b), and from Crete (Greece) (see Benda *et al.*, 2009b).

Native: Greece (Benda *et al.*, 2009b); Libyan Arab Jamahiriya (Benda *et al.*, 2004b).

GEOGRAPHIC VARIATION:
Georgiakakis and Benda (2021: 2) indicate that the endemic Cretan population (representing the subspecies *creticus* Benda, 2009) differs from the northern African populations in both morphometric and genetic traits, but not significantly enough to represent separate species.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Penis
Georgiakakis and Benda (2021: 4) mention that the skin of the whole penis is pale greyish brown with unpigmented hairs. The glans penis is simple, without long medial stripe on dorsal side of praeputium.

DETAILED MORPHOLOGY:
Baculum
The baculum is a long thin bone (1.8 mm) bifurcated on both epiphyses. The proximal end is 0.4 mm wide and the distal one 0.1 mm (Georgiakakis and Benda, 2021: 4).

Herdina *et al.* (2013: 68) indicate that *P. hanaki* can not be separated from either *P. pipistrellus* or *P. pygmaeus* by the shape of its baculum. They found that the proximal third of the baculum shows the most interspecific variation between these three species, whereas the shape of the curve in lateral view shows the most individual variation.

ECHOLOCATION:
Georgiakakis and Russo (2012: 168) report that the echolocation call has a FM-QCF structure, consisting of a frequency modulated component followed by an almost constant frequency part. They (p. 169) also were able to distinguish two types of social calls: type 'A' (primarily emitted by foraging bats) with a maximum energy frequency (FMAXE) of about 27.7 kHz, and a duration of 19.9 ms, of which type 'B' had a maximum energy frequency of all components (Freq) of about 20.9 kHz and a bandwidth of 28 kHz, and a duration of 24.8 ms. The number of calls of type 'B' increased from July to October and then decreased again, whereas those of type 'A' decreased from July to November.

Russo *et al.* (2025a: 5) found that 21 of the *Pipistrellus hanaki* echolocation call recordings were classified as *Pipistrellus pipistrellus* in their discriminant function analyses. However, the thrills of *P. hanaki* were completely separate from all other species (*kuhlii, maderensis, nathusii, pipistrellus* and *pygmaeus*).

MOLECULAR BIOLOGY:
Genetics
See Benda *et al.* (2004b), Hulva *et al.* (2004).

DIET:
From Libya, Benda *et al.* (2014c: 60) reported the following food items: Smaller Lepidoptera and small Coleoptera (Scarabaeidae, Carabidae, Staphylinidae). Two digestive tracts contained high volumes of cockroaches (Blattodea), and small amounts of Nematocera (Culicidae and Chironomidae) as well as Hymenoptera (Ichneumonoidea).

Georgiakakis and Benda (2021: 9) indicate that the presence of diurnal brachyceran Diptera may isuggest that *P. hanaki* starts foraging very early and/or forages very close to vegetation and possibly glean the prey from foliage.

POPULATION:
Structure and Density
Unknown (Aulagnier and Palmeirim, 2008a; IUCN, 2009).

Trend
2008: Unknown (Aulagnier and Palmeirim, 2008a; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Smotherman *et al.* (2016: 537) refer to Georgiakakis and Russo (2012) in describing the song structure for this species as consisting of different syllable types in basic motif. These bats sing while flying.

REPRODUCTION AND ONTOGENY:
Benda *et al.* (2014c: 55) reported pregnant females (each containing one foetus) collected on 17, 18, and 19 May 2002 at different localities in Libya (see also Georgiakakis and Benda, 2021: 7).

Garbino *et al.* (2021: Suppl.), however, mention that this species has more than one young per litter.

PARASITES:
Benda *et al.* (2014c: 60) reported the presence of two Nycteribiid bat flies: *Basilia daganiae* Theodor and Moscona, 1954 and *Basilia mediterranea* Hůrka, 1970.

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following bat flies: Nycteribiidae: *Basilia daganiae* Theodor and Moscona, 1954, and *Basilia mediterranea* Hůrka, 1970.

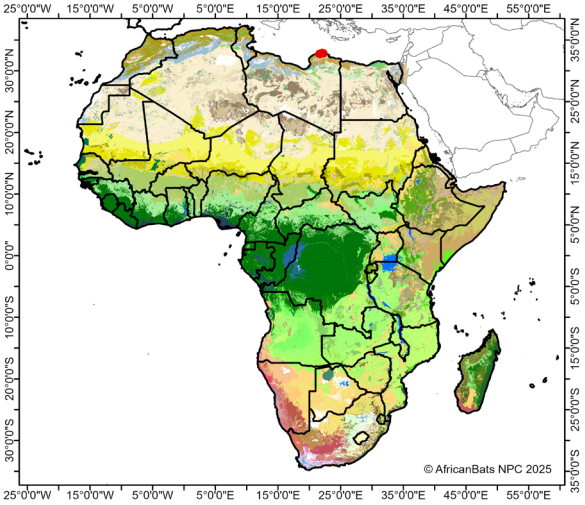

Figure 325. Distribution of *Pipistrellus (Pipistrellus) hanaki*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Libya.

Pipistrellus (Pipistrellus) hesperidus (Temminck, 1840)

1832. *Vespertilio platycephalus* Temminck, in: Smuts, Enumer. Mamm. Capensium, 107. Type locality: South Africa: Cape Town [33 56 S 18 28 E].

*1840. *Vespertilio hesperida* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe, 2 (13): 211. Publication date: 1840. Type locality: Eritrea: Abyssinia: Red Sea, shores of the [ca. 09 N 39 E]. [Goto Description]. Lectotype: SMF 12381: ad ♂, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1842. Old catalog number II.N.9*. - Etymology: From the feminine scientific Latin adjective *hespèrida*, meaning "evening animal", deriving from the feminine Greek substantive "*ἑσπέρα*" (hespèra), meaning "evening", as this bat, as almost all Chiroptera, begins to fly at dusk (see Lanza *et al.*, 2015: 410).

1969. *Vesperugo hespirida:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 206. (Name Combination, Lapsus).

2001. *Pipistrellus hesperidus:* Kock, Senckenb. biol., 81 (1/2): 277. (Name Combination).

2002. *Pipistrellus cf. kuhlii:* Kearney, Volleth, Contrafatto and Taylor, Acta Chiropt., 4 (1): 55. - Comments: Not of Kuhl, 1817.

2013. *Pipistrellus cf. hesperidus:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. Torrent *et al.* (2025b: 20) found that these Senegalese specimens cluster with *Pipistrellus rusticus* and are unrelated to *Pipistrellus hesperidus* s.s. and might possibly be named *Pipistrellus marrensis* Thiomas and Hinton, 1923, but this qill require further investigation. (Name Combination).

2013. *Pipistrellus hesperidares:* McCulloch, Barcoding of South African bat species and evaluation of their natural exposure to lyssaviruses, 120. Publication date: July 2013. (Lapsus).

2020. *Pipistrellus (Pipistrellus) hesperidus:* Simmons and Cirranello, BatNames.org. (Current Combination).

? *Pipistrellus (Pipistrellus) kuhlii:*

? *Pipistrellus hesperidus 3:*

? *Pipistrellus hesperidus fuscatus:* (Name Combination).

? *Pipistrellus kuhlii:* - Comments: Not of Kuhl, 1817.

TAXONOMY:
Pipistrellus hesperidus was separated from *kuhlii* by Kock (2001b: 277).

Vespertilio platycephalus Temminck, 1832 is according to Roberts (1951) a synonym of *P. kuhlii*, which would make this the senior synonym. However, both Allen (1939a) and Ellerman *et al.* (1953) regard this taxon as unidentifiable, besides which it seems to fall outside the known distribution of this species (Meester *et al.*, 1986: 52).

Koubínová *et al.* (2013: 8) suggest that three subspecies might deserve elevation to species rank: *hesperidus* (North-eastern Africa), *fuscatus* (Afro-tropical regions other than Southern Africa and Madagascar), and *subtilis* (Southern Africa and Madagascar), but they also indicate that the cyt *b* of Senegalese "*hesperidus*" differs considerably (13 %) from that in populations from South Africa, and might need to be considered a distinct species.

COMMON NAMES:
Chinese: 暗黑伏翼. Czech: netopýr jižní. English: African pipistrelle, Dusky pipistrelle. French: Pipistrelle hespéride, Pipistrelle sombre. German: Abendstern-Zwergfledermaus, Abendstern-Pipistrelle, Netzhäutigen Dämmerungsfledermaus, Flachköpfige Dämmerungsfledermaus. Italian: Pipistrèllo seràle.

ETYMOLOGY OF COMMON NAME:
Since sub-Saharan Africa populations are specifically distinct from Kuhl's pipistrelle occurring in the Palaearctic region (Kock 2001?a), the name African pipistrelle serves to distinguish it from Kuhl's pipistrelle (Bronner *et al.*, 2003; Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Mickleburgh *et al.*, 2008dp; IUCN, 2009; Piraccini, 2016e).

Assessment History
Global
2016: LC ver 3.1 (2001) (Piraccini, 2016e). 2008: LC ver 3.1 (2001) (Mickleburgh *et al.*, 2008dp; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as part of *P. kuhlii*] (IUCN, 2004).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016p). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004). 1986 - Indeterminate [assessed as *P. kuhlii*] (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Mickleburgh *et al.*, 2008dp; IUCN, 2009; Piraccini, 2016e).

CONSERVATION ACTIONS:
Mickleburgh *et al.* (2008dp) [in IUCN (2009)] and Piraccini (2016e) report that in view of the species wide range it is presumably present in a number of protected areas. It has been recorded from the Parc National de Kirindy-Mitea on Madagascar (Bates *et al.*, 2006). Additional taxonomic studies are needed to better define the extent of the species range relative to other species of *Pipistrellus*.

GENERAL DISTRIBUTION:
Pipistrellus hesperidus has been recorded over much of sub-Saharan Africa. It ranges from the Cape Verde Islands, to Liberia and Côte d'Ivoire, to Nigeria, Cameroon and Equatorial Guinea (Bioko), western Democratic Republic of the Congo, southern Sudan, Ethiopia, Eritrea and Somalia, into Kenya and Uganda, Rwanda, Burundi, Tanzania, Malawi, Mozambique, Zambia, Zimbabwe, Angola being found as far south as eastern and southern South Africa and possibly Swaziland. There are a few records of this species from central western Madagascar (Bates *et al.*, 2006: 317).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 820,815 km^2.

In the RSA, the species' distribution is strongly associated with annual precipitation (Babiker Salata, 2012: 49).

The current identity of bats from the Arabian Peninsula formerly allocated to *Pipistrellus kuhlii* is unclear and some records might refer to *P. hesperidus*. Simmons (2005) also indicates that this species is present in the Canary Islands (Spain). However, this distribution needs to be confirmed. Records from North Africa are referable to *Pipistrellus kuhlii*.

Taylor *et al.* (2018b: 63) predict the species might occur in Angola.

Benda *et al.* (2025: 88) indicate that the West African populations (Senegal to Cameroon) might might be erroneously assigned to this species,

Native: Botswana (Monadjem *et al.*, 2010d: 571); Burundi; Cameroon (Eisentraut, 1968: 171 - as "*P. kuhlii* - 1st record from West Africa); Cape Verde; Congo (The Democratic Republic of the); Equatorial Guinea (Bioko); Eritrea; Eswatini (Monadjem *et al.*, 2010d: 572, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 134); Kenya; Liberia (Fahr, 2007a: 104); Madagascar (Bates *et al.*, 2006: 317); Malawi (Ansell, 1974; Happold *et al.*, 1988; Monadjem *et*

al., 2010d: 571); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 571; Monadjem *et al.*, 2010c: 384); Nigeria; Rwanda; South Africa (Monadjem *et al.*, 2010d: 571); Tanzania (Stanley and Goodman, 2011: 47); Uganda; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 572); Zimbabwe (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 572).
Presence uncertain: Spain (Canary Islands).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) as *P. kuhlii* and Kearney *et al.* (2002) as *P* cf. *kuhlii*.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 8.5 Pa, aspect ratio 5.5 for a wingspan of 21 cm and a wing area of 80 cm^2 and a body mass of 7 g.

ECHOLOCATION:
Schoeman and Waddington (2011: 291) mention a peak frequency of 56.3 ± 2.1 kHz and a duration of 2.2 ± 0.2 ms for specimens from Durban, South Africa.

In Soutpansberg, South Africa, Taylor *et al.* (2013b: 17) recorded the following parameters for 19 calls: F_{max}: 66.9 ± 8.91 (48.5 - 82.0) kHz, F_{min}: 44.9 ± 1.53 (41.3 - 47.2) kHz, F_{knee}: 50.3 ± 2.50 (44.9 - 54.7) kHz, F_{char}: 45.8 ± 1.78 (41.5 - 49.1) kHz, duration: 2.6 ± 0.85 (1.7 - 5.0) ms.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg area (RSA): F_{min}:41 - 47 kHz, F_{char}: 42 - 49 kHz, F_{knee}: 45 - 55 kHz, slope: 154 - 829 OPS, duration: 2 - 5 ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 50 (45 - 55) kHz.

3871 calls of 129 bats from southern KwaZulu-Natal and Eastern Cape (RSA), reported by Moir (2020: 30) and Moir *et al.* (2021a: 371), had the following characteristics: F_{max}: 73.11 ± 7.87 (50.96 - 91.36) kHz, F_{min}: 45.63 ± 1.44 (42.60 - 49.81) kHz, F_{char}: 46.04 ± 1.42 (42.79 - 49.92) khz, F_{knee}: 49.65 ± 2.27 (44.11 - 54.55) kHz, and duration: 2.59 ± 0.66 (1.43 - 4.31) ms.

Monadjem *et al.* (2017c: 179) reported the following values for Eswatini: F_{min}: 45.3 ± 1.87 (41.7 - 49.1) kHz, F_{knee}: 49.6 ± 2.42 (44.6 - 54.3) kHz, F_c: 46.0 ± 1.83 (42.5 - 50.0) kHz, and duration: 3.1 ± 0.63 (2.3 - 4.5) ms.

Adams and Kwiecinski (2018: 4) recorded two calls in the Kalahari Desert: F_{char}: 43.3 ± 3.1 kHz, F_{max}: 53.6 ± 1.6 kHz, F_{min}: 42.9 ± 3.4 kHz, duration: 2.3 ± 0.3 ms.

16 "*Pipistrellus* cf. *hesperidus*" calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 51.75 ± 5.32 kHz, F_{min}: 40.87 ± 11.16 kHz, F_{knee}: 45.43 ± 0.74 kHz, F_{char}: 44.56 ± 0.96 kHz, slope: 22.01 ± 15.95 OPS, duration: 4.03 ± 1.48 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 59.1 kHz, F_{start}: NA kHz, F_{end}: NA kHz, Band width: NA kHz, and duration: 2.5 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 4 bats: F_{max}: 52.59 ± 4.32 kHz, F_{min}: 44.75 ± 3.24 kHz, F_{knee}: 46.89 ± 1.16 kHz, F_{char}: 45.46 ± 1.05 kHz, slope: 21.95 ± 2040.74 OPS, duration: 5.03 ± 1.75 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 3.35 ± 0.51 49 ms,.F_{min}: 13 ± 2.15 kHz, F_{max}: 62.43 ± 6.49 kHz, F_{knee}: 52.53 ± 1.32 kHz and F:50.28 ± 1.10 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 42 *Pipisrellus hesperidus* calls from the Kruger Park (RSA): F_{min}: 44.6 ± 1.6 (39.6 47.8) kHz, Duration: 3.3 ± 1.0 (2.0 5.9) ms, F_{max}: 63.0 ± 11.1 (48.7 86.6) kHz, F_{knee}: 48.5 ± 2.8 (44.3 54.9) kHz, F_{char}: 45.3 ± 1.6 (42.1 49.2) kHz,

61 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 41 - 47 kHz, F_{max}: 48 - 82 kHz, F_{char}: 42 - 49 kHz, F_{knee}: 45 - 55 kHz and duration 2 - 5 ms.

For 2 calls from 5 *Pipistrellus hesperidus* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 46.66 ± 0.79 kHz, F_{knee}: 48.33 ± 2.29 kHz, F_{min}: 46.48 ± 0.78 kHz, F_{max}: 78.24 ± 17.90 kHz, Bandwidth: 31.76 ± 17.70 kHz, Duration: 3.29 ± 1.14 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 55) reported F_{char}: 45.30 ± 1.60 kHz, F_{max}: 63.00 ± 11.1 kHz and F_{min}: 44.60 ± 1.60 kHz.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993), Volleth *et al.* (2001) and Kearney *et al.* (2002) all reported $2n$ = 42, FN = 50, BA = 10, and a metacentric X chromosome,

for specimens from South Africa and Madagascar. These results were the same as those obtained for *P. rusticus* (Kearney *et al.*, 2002). Rautenbach *et al.* (1993) also reported an acrocentric Y chromosome. GTG banding also identified that *P. hesperidus* and *P. rusticus* share the same Robertsonian fusion of chromosomes 11/12 (Kearney *et al.*, 2002). Volleth and Eick (2012: 169) indicate that the EMA segment order on chromosomal arm 2 of *P. hesperidus* is the same as that on human chromosome 4, but differs from that on chromosome 10 of *Rhinolophus hipposideros*, and conclude that the EMA segment order in the Vespertilioniformes is probably the ancentral one.

Koubínová *et al.* (2013: 3) report a different karyotype for 3 ♂♂ and 1 ♀ from Senegal: 2*n* = 46, Fna = 58, FN = 62, X = metacentric, and Y = dot-like. They also found that the cytochrome *b* in their specimens differed for about 13 % from that of South African specimens, which led them to the conclusion that Senegalese *P.* cf. *hesperidus* likely represents a different species.

Genetics
In South Africa, Moir *et al.* (2021c: 1595) found gene dispersal probably to be male-mediated and females were philopatric.

HABITAT:
Cooper-Bohannon *et al.* (2016: Table S2) indicate that, in southern Africa, *P. hesperidus* occurs primarily in Savanna (47 %), SW arid (20 %) and Afromontane (15 %) habitats.

Moir *et al.* (2021c: 1596) suggest that the removal of riparian vegetation by sugarcane farming and plantation forestry practices may deter this species from using watercourses, thereby hindering possible dispersal events.

In Madagascar, Ravelomanantsoa *et al.* (2019: 110) caught it in open spaces in a dry deciduous forest and near a banana plantation.

ROOST:
In South Africa, Czenze *et al.* (2021: 3) found these bats roosting in spots where the temperature approached normothermic body temperature.

Happold and Happold (2023: 155) mention these bats roost in groups of up to 12 individuals.

DIET:
Naidoo *et al.* (2011: 26) reported the following volume percentages from the Umbilo River (KwaZulu Natal, RSA): during summer: Lepidoptera (7.8 ± 2.8), Coleoptera (12.3 ± 5.5), Hemiptera (32.8 ± 2.8), Diptera (37.8 ± 8.1), and Trichoptera (9.2 ± 7.1); during winter: Lepidoptera (16.9 ± 19.0), Coleoptera (20.4 ± 20.3), Hemiptera (12.6 ± 13.2), Diptera (13.7 ± 5.1), and Trichoptera (36.4 ± 38.7). From the Westville River, they reported for the summer: Lepidoptera (10.0 ± 4.5), Coleoptera (8.0 ± 3.8), Hemiptera (31.2 ± 10.7), Diptera (42.7 ± 11.4), Trichoptera (2.7 ± 0), and Hymenoptera (5.4 ± 8.7).

From the Limpopo province (RSA), Taylor *et al.* (2017b: 245, 252 - 254) report the following food items, belonging to six insect orders: Lepidoptera (*Araeopteron* sp. + *Toxocampinae tathorhynchus* + *Eutelia polychorda* + *Chiasmia interrupta* + *Ennominae* sp. + *Isturgia roraria* + *Sena* sp. + *Sena prompta* + *Xenopseustis* sp. + *Athetis ignava* + *Copitarsia* sp. + *Cortyta canescens* + *Enmonodia capensis* + *Mythimna impura* + *Mythimna oxygala* + *Pandesma robusta* + *Pericyma atrifusa* + *Spodoptera exigua* + *Tycomarptes* sp. + *Maurilia arcuata* + *Pseudautomeris irene* + *Arotrura JFL201* + *Agrius convolvuli* + unmatched), Coleoptera (unmatched), Orthoptera (*Neoconocephalus spiza* + unmatched), Hemiptera (*Nezara viridula*), Diptera (*Culex quinquefasciatus* + 2 unmatched) and Blattodea (unmatched).

Bailey *et al.* (2019: 372) found that the Allotonic Frequency Hypothesis (eared moths are less available to syntonic bats due to their ability to detect these bat's echolocation, but become available around lights due to a reduction in efficacy of the moth's defences) is true for *Pipistrellus hesperidus*.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 63 minutes, and the digestibility rate about 82.1 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the following avian predators: Little sparrowhawk (*Accipiter minullus* (Daudin, 1800)); Southern fiscal (*Lanius collaris* Linnaeus, 1766). They also mention "*P. kuhli*" being preyed upon by the Lanner falcon (*Falco biarmicus* Temminck, 1825), the Eurasian hobby (*Falco subbuteo* Linnaeus, 1758), the Common kestrel (*Falco tinnunculus* Linnaeus, 1758), but some of these records might involve *P. hesperidus*. Their references to the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) probably all refer to *P. hesperidus* as these all point to sub-Saharan countries.

POPULATION:
Structure and Density

There is little information available on the abundance of this species, however, it is not very common in southern Africa (Skinner and Chimimba, 2005: 301; Mickleburgh *et al.*, 2008dp; IUCN, 2009; Piraccini, 2016e).

Trend
2016: Unknown (Piraccini, 2016e). 2008: Unknown (Mickleburgh *et al.*, 2008dp; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Stanley and Goodman (2011: 46 - 47) report on two females collected in early July 1991 in the West Usambara Mountains (Tanzania) of which one had an embryo in each uterine horn (leading to polytocy, see Garbino *et al.*, 2021: Suppl.). Three other females, collected on 1 September 1992, did not show any signs of reproduction.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned that pregnant females were collected in October.

In Malawi, the young were born in the wet season (Happold and Happold, 1990b: 567).

PARASITES:
Basilia robusta Theodor 1956 (Haeselbarth *et al.*, 1966: 111 - host recorded as *P. kuhlii*). Beaucournu and Noblet (1985: 635) also mention the possible presence of *Basalia daganiae* Theodor and Moscona, 1954 on a "*P. kuhlii*" from Kenya.

Clément *et al.* (2019a: 5) reported on one southern African bat infected by *Trypanosoma vespertilionis*_AF1. *T. vespertilionis* and *T. dionisii* were reported by Babyesiza *et al.* (2025: 4) from Uganda.

The bat fly "*Basilia* sp. 3" was reported from "*Pipistrellus* cf. *hesperidus*" by Ramasindrazana *et al.* (2017: 4).

Ramasindrazana *et al.* (2016: 6) report the presence of *Litosoma* Clade 2 (Nematoda: Onchocercidae) in Madagascan "*P.* cf. *hesperidus*".

The flea *Ischnopsyllus emminus* Jordan and Rothschild, 1921 was reported on "*P. kuhlii*" from Malawi by Beaucournu and Kock (1996).

The bat bugs *Cacodmus ignotus* Rothschild, 1912 and *Cacodmus sparsilis* Rothschild, 1914 (Hemiptera: Cimicidae) were reported from South Africa by Hornok *et al.* (2017a: 3). *Cacodmus villosus* (Stål, 1855) was reported from Ethiopia by Szentiványi *et al.* (2022: 12).

Hornok *et al.* (2017b: 3) found larvae of the tick *Argas transgariepinus* White, 1846 (Ixodida: Argasidae) on a *P. hesperidus* from Makhado, RSA. Hornok *et al.* (2019: 2) probably refer to the same bat and tick and indicate that the latter was infected with *Rickettsia* sp. bacteria.

Dick *et al.* (2023: 74) found the nycteribiid fly *Basilia (Basilia) robusta* Theodor, 1956 on Kenyan *Pipistrellus hesperidus*:and *Pipistrellus* cf. *hesperidus*.

VIRUSES:
Coronaviridae
Anthony *et al.* (2017b: Suppl.) mention the beta-coronavirus MERS_like_CoV. Anthony *et al.* (2017a: 1) described a MERS_like CoV (strain PREDICT/PDF-2180 - subgenus *Merbecovirus*; see Markotter *et al.*, 2020: 5) from *P.* cf. *hesperidus* from Uganda.

Paramyxoviridae
1 out of 11 Madagascan specimens tested by Mélade *et al.* (2016b: 4) was positive for paramyxoviruses.

Rhabdoviridae - Rabies like viruses
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested [as *P. kuhlii*] one individual brain, from Christiana, Free State Province South Africa by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), and this did not test positive.

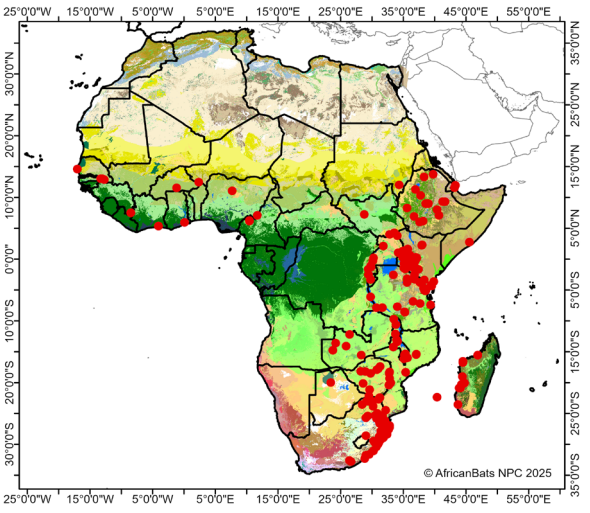

Figure 326. Distribution of *Pipistrellus (Pipistrellus) hesperidus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Botswana, Burkina Faso, Cameroon, Côte d'Ivoire, Djibouti, Eritrea, Eswatini, Ethiopia, French Southern and Antarctic Lands, Ghana,

Kenya, Liberia, Madagascar, Malawi, Mozambique, Niger, Nigeria, Rwanda, Senegal, Somalia, South Africa, South Sudan, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Pipistrellus (Pipistrellus) hesperidus broomi Roberts, 1948

*1948. *Pipistrellus (Romicia) kuhlii broomi* Roberts, Special Publication of the Royal Society of South Africa, Robert Broom Commemorative volume, 9. Type locality: South Africa: KwaZulu-Natal: Durban: Malvern [29 53 S 30 56 E, 275 m]. Holotype: TM 1085: ad ♀. Collected by: Henry Paul William Lyster Jameson; collection date: 10 January 1908; original number: 425. Smithers *et al.* (1987: 463) also mention that three specimens have the number TM 1085 (both other specimens are probably TM 1081 [*P. nanus*] and TM 1087 [*P.* cf. *fuscatus* -> *P. hesperidus*]. - Comments: Type locality more likely to be Tzaneen Estates, Tzaneen, northeastern Transvaal (R.H.N. Smithers, in litt): see Meester *et al.* (1986: 52). However, see also Smithers *et al.* (1987: 463) for a discussion on the type locality and type specimen. They confirm "Malvern" as type locality.
1951. *Romicia kuhlii broomi:* Roberts, Mammals of South Africa, 82. (Name Combination).
1953. *Pipistrellus (Pipistrellus) kuhli broomi:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1957. *P[ipistrellus] k[uhli] broomi:* Ansell, Ann. Mag. nat. Hist., ser 12, 10 (115): 538. Publication date: 29 October 1957. (Name Combination).
1968. *P[ipistrellus] k[uhlii] broomi:* Hill, Bonn. zool. Beitr., 19 (1/2): 44. (Name Combination, Alternate Spelling).
1969. *Pipistrellus (Romicia) kuhli broomi:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 167. - Comments: Alternate spelling for the name used by Roberts (1948). (Alternate Spelling).
1971. *Pipistrellus [(Pipistrellus)] kuhlii broomi:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Name Combination, Alternate Spelling).
1992. *Pipistrellus kuhli broomi:* Trujillo, Murcielagos de las Islas Canarias, 23. (Name Combination).
? *Pipistrellus (Pipistrellus) hesperidus broomi:* (Current Combination).
? *Pipistrellus hesperidus broomi:* (Name Combination).
? *Pipistrellus kuhlii broomi:* (Name Combination).

GENERAL DISTRIBUTION:
KwaZulu-Natal (RSA).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Africa.

Pipistrellus (Pipistrellus) hesperidus hesperidus (Temminck, 1840)

*1840. *Vespertilio hesperida* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe, 2 (13): 211. Publication date: 1840. Type locality: Eritrea: Abyssinia: Red Sea, shores of the [ca. 09 N 39 E]. [Goto Description]. Lectotype: SMF 12381: ad ♂, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1842. Old catalog number II.N.9*. - Etymology: From the feminine scientific Latin adjective *hespèrida*, meaning "evening animal", deriving from the feminine Greek substantive "*ἑσπέρα*" (hespèra), meaning "evening", as this bat, as almost all Chiroptera, begins to fly at dusk (see Lanza *et al.*, 2015: 410).
1901. *Pipistrellus Kuhlii fuscatus* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 34. Publication date: 1 July 1901. Type locality: Kenya: Naivasha [00 46 S 36 21 E]. [Goto Description]. Holotype: NHMUK 1901.8.9.96: ad ♂, skull and alcoholic. Collected by: Sir Harry Hamilton Johnston; collection date: 19 October 1900. Presented/Donated by: Sir Harry Hamilton Johnston.
1913. *Pipistrellus kuhli fuscatus:* Roberts, Ann. Transv. Mus., 4: 67. - Comments: Alternate spelling for the name used by Thomas, 1901. (Alternate Spelling).
1951. *Pipistrellus (Pipistrellus) kuhlii fuscatus:* Swynnerton and Hayman, J. East Afr. Nat. Hist. Soc., 20 (6-7) (90): 297 (for 1950).
? *Pipistrellus (Pipistrellus) hesperidus hesperidus:* (Current Combination).
? *Pipistrellus hesperidus hesperidus:* (Name Combination).

GENERAL DISTRIBUTION:
Sub-Saharan Africa with the exception of the extreme southeastern part of the continent.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Burundi, Djibouti, Ethiopia, Kenya, Malawi, South Sudan, Tanzania, Uganda.

Pipistrellus (Pipistrellus) hesperidus subtilis (Sundevall, 1846)

*1846. *Vesperugo subtilis* Sundevall, Öfvers. kongl. Sv. Vet.-Akad. Förhandl., 3 (4): 119. Type locality: South Africa: "Interior of Caffraria". [Goto Description]. Holotype: NRM 631076: ♂. Collection date: 1845. - Comments: Collector: J. Wahlberg.
1855. *Vespertilio (Vesperugo) subtilis:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 746. (Name Combination).
1860. *Hypsugo subtilis:* Kolenati, Monographie der Europäischen Chiroptern, 6. (Name Combination).

1878. *Vespertilio subtilis:* Dobson, Cat. Chiroptera Brit. Mus, 197. Publication date: 15 Jun 1878. (Name Combination).
1917. *Pipistrellus kuhlii subtilis:* G.M. Allen, Bull. Mus. comp. Zool., 83: 94. (Name Combination).
1931. *Pipistrellus subtilis:* Hewitt, A guide to the Vertebrate fauna of the Eastern Cape Province, 23. (Name Combination).
1951. *Eptesicops subtilis:* Roberts, Mammals of South Africa, 83. (Name Combination).
1953. *Pipistrellus (Pipistrellus) kuhli subtilis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1971. *Pipistrellus [(Pipistrellus)] kuhii subtilis:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Name Combination).
1978. *Pipistrellus kuhli subtilis:* Ansell, Mammals of Zambia, 27. (Name Combination).
1993. *subtilus:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 221. (Lapsus).
? *Pipistrellus (Pipistrellus) hesperidus subtilis:* (Current Combination).
? *Pipistrellus hesperidus subtilis:* (Name Combination).

GENERAL DISTRIBUTION:
SE Africa.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Africa.

Pipistrellus (Pipistrellus) inexspectatus Aellen, 1959

*1959. *Pipistrellus inexspectatus* Aellen, Archs Sci. Genève, 12 (2): 226. Type locality: Cameroon: Upper Benoue Valley: Ngaaouyanga [07 59 N 13 36 E]. [Goto Description]. Holotype: MHNC |TS324|: ad ♂, alcoholic (skull not removed). Collected by: Villy Aellen and Albert Monard; collection date: 11 July 1947; original number: 954. See Aellen (1959a: 226).
1966. *P[ipistrellus] inexpectatus:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 52. (Lapsus).
1971. *Pipistrellus [(Pipistrellus)] inexpectatus:* Hayman and Hill, Mammals of Africa: Chiroptera, 41. (Name Combination, Lapsus).
1987. *Nycterikaupius inexpectatus:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination, Lapsus).
1987. *Pipistrellus (Pipistrellus) inexspectatus:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination, Current Combination).
1993. *Pipistrellus (Hypsugo) inexspectatus:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 220. (Name Combination).
2020. *Pipistrellus cf. inexspectatus:* Monadjem, Richards, Decher, Hutterer, Mamba, Guyton, Naskrecki, Markotter, Wipfler, Kropff and Dalton, Zool. J. Linn. Soc., 191 (2): 553. Publication date: 4 September 2020. (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: netopýr kamerunský. English: Aellen's Pipistrelle Bat, Aellen's Pipistrelle, Central Africa Pipistrelle. French: Pipistrelle d'Aellen, Pipistrelle d'Afrique centrale. German: Unerwartete Zwergfledermaus, Unerwartete Pipistrelle.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Fahr, 2008q; IUCN, 2009; Fahr, 2019d).

Assessment History
Global
2018: DD ver 3.1 (2001) (Fahr, 2019d). 2008: DD ver 3.1 (2001) (Fahr, 2008q; IUCN, 2009). 2004: DD ver 3.1 (2001) (Fahr, 2004i; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known (Fahr, 2008q; IUCN, 2009; Fahr, 2019d).

CONSERVATION ACTIONS:
Fahr (2008q) [in IUCN (2009)] and Fahr (2019d) reports that it is not known if the species is present in any protected areas. Further field surveys are needed to better understand the distribution, natural history and possible threats to this little known bats species.

GENERAL DISTRIBUTION:
Pipistrellus inexspectatus has been recorded from a few localities in West and Central Africa. It has been reported from Sierra Leone, Ghana, Benin and Nigeria and Cameroon.

There are also uncertain records from east Sudan and Uganda, although the specimens in question are difficult to certainly allocate to *Pipistrellus*

inexspectatus (Koopman, 1975). The records of *P. inexspectatus* from the Democratic Republic of the Congo and Kenya are now allocated to *Pipistrellus eisentrauti* (Koopman *et al.*, 1995; Simmons, 2005).

Mamba *et al.* (2020: 135) reported a female specimen from Guinea as "*Pipistrellus* cf. *inexspectatus*", but its identity still needs to be confirmed.

Rudi Haslauer (pers. comm.) pointed out that the specimens from Kenya (mentioned in previous issues of ACR) might not represent this species either. The MCZ online catalogue showed that they were re-identified in early 2021 as belonging to "*Afropipistrellus grandidieri*".

In previous issues, we had this species mentioned as occurring on Madagascar. However, MCZ 45112 from near Cape Saint Vincent was originally part of the Grandidier collection and some other specimens supposedly collected on Madagascar by Grandidier were actually collected on the African mainland (e.g., coastal Kenya for the type of *Nycteris madagascariensis*, see Demos *et al.* (2021: 28-30). Demos *et al.* (2021: 28, 30) also state that Grandidier's second trip to Madagascar (in 1901) took him to the east coast of the island, whereas the coordinates for Cape Saint Vincent place this on the west coast. So possibly this specimen might also have been collected on the African mainland and not on the island of Madagascar. Given that this specimen only consists of a skull, its identification is uncertain.

Native: Benin; Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 621); Cameroon; Ghana; Nigeria; Sierra Leone.

Presence uncertain: Sudan; Uganda.

ECHOLOCATION:
One FM/QCF call from Maroua (Cameroon), reported by Manga Mongombe (2012: 79) had the following parameters: F_{max}: 54.7 kHz, F_{min}: 47.7 kHz, F_{mean}: 51.2 kHz, F_{knee}: 54.7 kHZ, F_{char}: 47.7 kHz, and duration: 0.46 ms.

HABITAT:
In Cameroon, Bakwo Fils *et al.* (2021b: 6) reported on one specimen that was found in disturbed habitats in the Afromontane forest biome.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 69 minutes, and the digestibility rate about 81.2 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Fahr, 2008q; IUCN, 2009; Fahr, 2019d).

Trend
2018: Unknown (Fahr, 2019d). 2008: Unknown (Fahr, 2008q; IUCN, 2009).

VIRUSES:
Coronaviridae
Gonzalez and Banerjee (2022: 8) reported HCoV-229E from this bat.

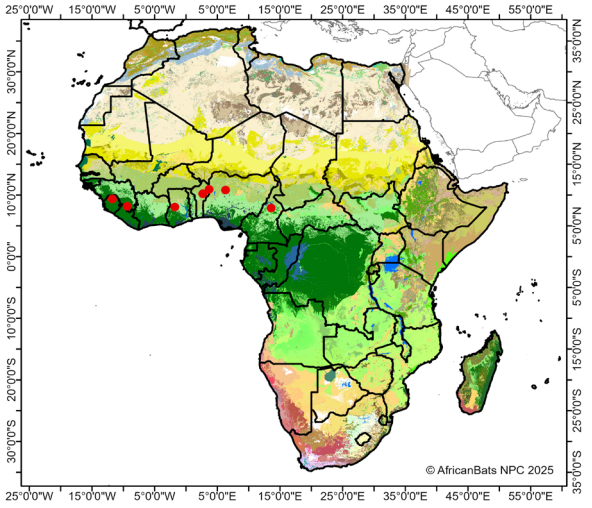

Figure 327. Distribution of *Pipistrellus (Pipistrellus) inexspectatus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Benin, Cameroon, Côte d'Ivoire, Ghana, Guinea, Kenya, Nigeria, Sierra Leone.

Pipistrellus (Pipistrellus) kuhlii (Kuhl, 1817)

*1817. *Vespertilio Kuhlii* Kuhl, Die Deutschen Fledermäuse, Hanau, 14. Type locality: Italy: Friuli-Venezia Giulia and Trieste. - Comments: Koopman (1993a: 221) mentioned 1817 as year of publication, whereas Meester *et al.* (1986: 51), Harrison and Bates (1991: 85), Corbet and Hill (1992: 137) and Bates and Harrison (1997: 179) mention "1819: Ann. Wetterau Ges. Naturk., 4 (2) 199".

1829. *[Vespertilio pipistrellus var.] ß Aegyptius* J.B. Fischer, Synopsis Mamm, 105. Publication date: 1829. Type locality: Egypt: Qena province: Luxor [25 41 N 32 39 E]. [Goto Description]. - Comments: Ellerman and Morrison-Scott (1951: 168) and Harrison (1964a: 151) mention Thebes as type locality.

1830. *Vespertilio marginatus* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 74, pl 29a. Type locality: "Africa": Nile valley or eastern desert of Egypt. [Goto Description]. Holotype: SMF 4307: ad

♀, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1822. Don 1882; old catalog II.N.10.a: see Mertens (1925: 21). - Comments: Kock (1969a: 167) mentions "Arabia Petraea (=Sinai) und Nubien" as type locality. The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831".

1838. *Scotophilus Kuhlii:* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 497. (Name Combination).
1839. *Vesperugo Kuhlii:* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 319. (Name Combination).
1853. *V[esperugo (Vesperugo)] Kuhlii:* Blasius, Arch. Naturgesch. Berlin, 19 (1): 46. (Name Combination).
1855. *Vespertilio (Vesperugo) Kuhlii:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 729. (Name Combination).
1856. *Nannugo Kuhlii:* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (4): 131. (Name Combination).
1857. *S[cotophilus] marginatus:* Tomes, Proc. zool. Soc. Lond., 1857, XXV (cccxxx): 50.
1862. *Vespertilio (Nannugo) Kuhlii:* Koch, Nass. Naturw. Jahrb., 18: 396. (Name Combination).
1862. *Vespertilio (Nannugo) marginatus:* Koch, Nass. Naturw. Jahrb., 18: 397.
1865. *V[espertilio] (Pipistrellus) marginatus:* De Filippi, Note di un viaggio in Persia nel 1862, 343. (Name Combination).
1866. *Vesperugo marginatus:* Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (6 - 10): 546.
1867. *Pipistrella marginata:* Loche, Exploration scientifique de l'Algerie pendant les années 1840, 1841, 1842. Mammifères, Cheiroptères, 77. (Alternate Spelling).
1867. *Pipistrella minuta:* Loche, Exploration scientifique de l'Algerie pendant les années 1840, 1841, 1842. Mammifères, Cheiroptères, 78. Publication date: 1867. Type locality: Algeria: Messad Oasis [34 11 N 03 31 E]. [Goto Description]. (Name Combination, Alternate Spelling).
1871. *Pipistrellus marginatus:* Dobson, J. Asiatic Soc. Bengal, 40 (2): 460.
1871. *V[esperugo] Kuhli:* Doderlein, Alcune generalita Intorno la Fauna Sicula de Vertebrati, 31. (Name Combination).
1878. *Vesperugo (Vesperugo) kuhlii:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 230. Publication date: 15 June 1878. (Name Combination).
1880. *Vesperugo Kühli:* Dobson, Bull. Soc. zool. France, 5: 235. (Name Combination).
1891. *Vesperugo (Vesperugo) kuhli:* Blanford, The fauna of British India, including Ceylon and Burma. Part II, 315. (Alternate Spelling).
1898. *P[ipistrellus] kuhli:* Thomas, Proc. zool. Soc. Lond., 1897, IV: 927. Publication date: April 1898. (Name Combination).
1899. *Vesperugo (Euvesperugo) kuhli:* Acloque, Faune de France, Mammifères, 36. (Name Combination).
1900. *Pipistrellus kuhlii:* Méhely, Monographia Chiropterorum Hungariae, 261. (Name Combination).
1902. *Pipistrellus deserti* Thomas, Proc. zool. Soc. Lond., 1902, II, I: 4. Publication date: October 1902. Type locality: Libya: Fezzan: Murzuk [25 56 N 13 57 E]. [Goto Description]. Holotype: NHMUK 1902.11.4.1: ad ♂, skin and skull. Collected by: Joseph Isaac Spadafora Whitaker; collection date: 30 May 1901; original number: 71. - Etymology: From *desèrti*, meaning "of the desert" (see Lanza *et al.*, 2015: 395).
1905. *Vespertilio (Pipistrellus) Kuhli:* Trouessart, Caus. sci. Soc. zool. France, 1 (10): 370/18. (Name Combination).
1909. *Pipistrellus kühli:* Satunin, Mitt. Kauk. Mus., 4: 299. (Name Combination).
1918. *Pipistrellus kuhli kuhli:* Wroughton, J. Bomb. nat. Hist. Soc., 25: 588. (Name Combination).
1936. *P[ipistrellus] k[uhlii] pallidus* Heim de Balsac, Supp. Bull. Biol. Fr. & Belg., 21: 43, 50, 180. Publication date: 1936. Type locality: Algeria: Northern Sahara: A'haggar, to the [ca. 23 30 N 06 00 E]. - Comments: Considered a nomen nudum by Allen (1939a: 94), Rode (1947: 138), Kock (1969a: 167). (Name Combination).
1936. *Pipistrellus kuhlii kuhlii:* Heim de Balsac, Supp. Bull. Biol. Fr. & Belg., 21: 91. (Name Combination).
1937. *[Pipistrellus Kühli] latastei* Laurent, Mammalia, 1: 157, footnote. Type locality: "Africa": Northern Africa. [Goto Description]. - Comments: New name for *Pipistrellus kuhlii albolimbatus* Lavauden non Kuster (see Laurent, 1937c: 157 footnote). - Etymology: In honour of Mr. Lataste (see Laurent, 1937c: 157).
1937. *Pipistrellus Kühli Kühli:* Laurent, Mammalia, 1: 157. (Name Combination).
1951. *Pipistrellus kuhlii albolimbatus:* Panouse, Trav. Inst. Sci. Cherifien, 1: 80. (Name Combination).
1953. *Pipistrellus (Pipistrellus) kuhli kuhli:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1953. *Pipistrellus (Pipistrellus) kuhli:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 81. (Name Combination).
1959. *Pipistrellus (Romicia) kuhli:* Anonymus, Koedoe, 3: 58. (Name Combination).
1966. *Pipistrellus (Pipistrellus) kuhli pallidus:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 169. (Name Combination).
1969. *[Pipistrellus kuhli] pallidus:* Aellen and Strinati, Rev. suisse Zool., 76 (16): 427. (Name Combination).
1971. *Pipistrellus [(Pipistrellus)] kuhlii kuhlii:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Name Combination).
1971. *Pipistrellus [(Pipistrellus)] kuhlii pallidus:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Name Combination).
1971. *Pipistrellus [(Pipistrellus)] kuhlii:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Alternate Spelling).
1972. *P[ipistrellus] k[uhli] marginatus:* Gaisler, Madkour and Pelikan, Acta sc. nat. Brno, 6 (8): 32. (Name Combination).
1975. *Pipistrellus kuhli aegyptius:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 400.
1976. *Pipistrellus (Pipistrellus) kuhli palludus:* Anciaux de Faveaux, Bull. Soc. Hist. nat. Afr. Nord, 67 (1-2): 73. (Lapsus).
1978. *Pipistrellus kuhli marginatus:* Madkour, Zool. Anz., 201 (5/6): 387. (Name Combination).
1984. *Pipistrellus (Pipistrellus) kuhli aegyptius:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch.
1985. *Pipistrellus aegyptius:* Qumsiyeh, Spec. Publ. Mus. Texas Tech. Univ., 23: 51.
1985. *Pipistrellus kuhlii marginatus:* Qumsiyeh, Spec. Publ. Mus. Texas Tech. Univ., 23: 47. (Name Combination).
1986. *Pipistrellus kunli:* Chastel, Launay, Le Lay, Bailly-Choumara, Hellal, Valle, Bach-Hamba and Beaucournu, Cah. ORSTOM, sér Ent. méd. et Parasitol., 24 (1): 71. (Lapsus).
1991. *Pipistrellus kuhlii deserti:* Kowalski and Rzebik-Kowalska, Mammals of Algeria: 100. - Comments: Kowalski and Rzebik-Kowalska (1991: 100) placed this name in the synonymy for *Pipistrellus kuhlii*, referring it to Thomas (1902) and Corbet (1978), but neither of these actually use this combination. (Name Combination).

1993. *Pipistrellus (Pipistrellus) aegyptius:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 219.
1994. *P[ipistrellus (Pipistrellus)] k[uhlii] marginatus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 114. (Name Combination).
1997. *Pipistrellus aegyptiacus:* Decher, Z. Säugetierk., 62: 132. (Lapsus).
2008. *Pipistrillus Kuhli:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Name Combination, Lapsus).
2008. *Pipstrillus Kuhli:* Selim, Nahla and Shelfeh, Tishreen Univ. J. Res. Sci. Stud. - Biol. Sci. Ser., 30 (1): 247. (Name Combination, Lapsus).
2019. *Pipistrellus cf. deserti:* Batsleer, Portelli, Borg, Kiefer, Veith and Dekeukeleire, Hystrix, It. J. Mamm., 30 (2): 175. (Name Combination).
2020. *Pipistrellus kulli:* Borloti, Dinis and Vasconcelos, Genes, 11 (2) 877: 9. Publication date: 1 August 2020. - Comments: The name *Pipistrellus kulli* was used in combination with a sonogram, of which Borloti *et al.* (2020) aren't certain it belongs to *Pipistrellus kuhlii*, but rather to *Pipistrellus hesperidus* or a *Neoromicia*. (Lapsus).
2023. *Pipestrellus kuhlii:* Weber, Nagy, Markotter, Schaer, Puechmaille, Sutton, Dávalos, Dusabe, Ejotre, Fenton, Knörnschild, López-Baucells, Medellin, Metz, Mubareka, Nsengimana, O'Mara, Racey, Tuttle, Twizeyimana, Vicente-Santos, Tschapka, Voigt, Wikelski, Dechmann and Reeder, Biol. Lett., 19 (11) (20230358): Suppl. Publication date: 15 November 2023. (Lapsus).
? *Nannugo marginatus:*
? *Pipistrellus (Pipistrellus) deserti:*
? *Pipistrellus (Pipistrellus) kuhlii:* (Name Combination).
? *Pipistrellus kuhli:* (Alternate Spelling).
? *Pipistrellus kuhlii pallidus:* (Name Combination).

GENERAL COMMENTS:
During their long-term study, Locatelli *et al.* (2019: 96) found that the body condition of bats carrying bands or PIT-tags did not differ from that of bats that were untagged.

TAXONOMY:
Koopman (1994: 114) states that the allocation of many populations to subspecies is uncertain. Additionally, sub-Saharan specimens belong to *hesperidus*.

Although most authors have considered *P. deserti* as a separate species (Heim de Balsac, 1934a, 1936, Allen, 1939a, Ellerman and Morrison-Scott, 1951, Kock, 1969a, Kock, 1999b, Hayman and Hill, 1971, Gaisler *et al.*, 1972, Koopman, 1975, 1993a, 1994, Anciaux de Faveaux, 1976b, Hanák and Elgadi, 1984, Qumsiyeh, 1985, Gaisler and Kowalski, 1986, Hill and Harrison, 1987, Le Berre, 1990, Kowalski and Rzebik-Kowalska, 1991, Horáček *et al.*, 2000), others (Corbet, 1978, Aulagnier and Thevenot, 1986, Pavlinov *et al.*, 1995, Benda and Ruedi, 2004, Benda *et al.*, 2004d, perhaps Rode, 1947) doubted the full species status and regarded it as conspecific with *P. kuhlii*, but *P. deserti* and *P. kuhlii* are two separate morphotypes which differ clearly in size (Gaisler *et al.*, 1972, Kowalski and Rzebik-Kowalska, 1991). As these forms do not occur in sympatry (but see Kowalski and Rzebik-Kowalska, 1991), they may perhaps represent two ecogeographic or ecomorphotypic forms of one species. However, this question requires profound revision of the whole *P. kuhlii* complex both on morphologic and genetic bases (see Kock, 2001b). Mayer *et al.* (2007) reported genetic evidence that *P. deserti* are not distinct from *P. kuhlii*, while García-Mudarra *et al.* (2009) found a differentiation in the cytochrome *b*. Benda *et al.* (2014c: 75) indicate that the presence of bats of the *deserti* morphotype within two separate lineages of *P. kuhlii*, the Libyan-Egyptian and Morrocan, suggests two directions of origin of this morphotype, the west-Saharan and east-Saharan, which in turn indicate that the *deserti* morphotype is a local variation (ecomorphotype) of *P. kuhlii*, which does not deserve taxonomic expression even at the subspecific level.

Benda *et al.* (2014a: 419) presented sufficient prove to support the view that significant differences between the two morphotypes are grouped by geographic origin, and that *P. deserti* should be considered a junior synonym of *P. kuhlii*.

However, Loumassine *et al.* (2020: 3) found both *P. kuhlii kuhlii* and *P. kuhlii deserti* active around streetlights in Ouahabi and Debdaba. This syntopic occurrence contradicts the geographic separation of both "subspecies".

The authorship and description date for *Vespertilio kuhlii* has been debated for years. It has been assigned to either Kuhl, Natterer or "Natterer (in Kuhl)". The publication year was mentioned as either 1817 or 1819. This confusing situation has been cleared by Bogdanowicz and Kock (1998), who fixed author and date to Kuhl, 1817.

Similarly, the authorship of *marginatus* has been assigned to various authors: Cretzschmar, 1826-1830, Rüppell, 1826, Wagner, 1840, Bonaparte, 1841, and Kolenati, 1856.

In the synonyms list for this species, we did not make a difference for the author and/or year of

publication mentioned by the various publications when dealing with *kuhlii*.

COMMON NAMES:
Afrikaans: Kuhl se vlermuis, Kuhl-vlermuis. Albanian: Pipistrel i Kuhl-it. Arabian: Khaffash. Armenian: Միջերկրածովային փոքրաչղջիկ. Azerbaijani: Küli şəbpərəsi. Basque: Kuhl pipistrelo, Kuhl saguzar. Belarusian: Нетапыр міжземнаморскі, Нетапыр Куля. Bosnian: Kulijev šišmiš. Breton: Pipistrell Kuhl. Bulgarian: Средиземноморско прилепче. Castilian (Spain): Murciélago de borde claro. Catalan (Spain): Pipistrel·la de vores clares, Rat penat de vores clares. Croatian: Bjelorubi šišmiš. Czech: Netopýr jižní, Netopýr vroubený, Nedopír celouchý, Netopýr červenohlavý. Danish: Kuhls flagermus. Dutch: Kuhls dwergvleermuis, Kuhl's dwergvleermuis. English: Kuhl's pipistrelle, Kuhl's Pipistrelle Bat, Kuhl's Bat, Great pipistrelle, Flitter Mouse, White stripe bat. Estonian: Vahemere nahkhiir. Finnish: Kapearäpyläpiippa. French: Pipistrelle de Kuhl, Pipistrelle géante, le vespertilion de Kuhl. Frisian: Wytrâne dwerchflearmûs. Galician (Spain): Morcego de borde claro, Morcego de beira branca. Georgian: ხმელთაშუაზღვიური ღამორი, კულის. German: Weißrandfledermaus, Weißrand-Pipistrelle, Haarbindigen Dämmerungsfledermaus, Kuhlische Fledermaus. Greek: Λευκονυχτερίδα. Hebrew: Atalfon Leven Shulayim. Hungarian: Fehérszélű törpedenevér, Nycteris i leukogyros. Irish Gaelic: Ialtóg Kuhl. Italian: Pipistrello albolimbato, Pipistrello de Kühli. Latvian: Kūla sikspārnis. Lithuanian: Kulio šikšniukas. Luxembourgish: Wäissbordfliedermaus. Macedonian: Белорабен лилјак [= Beloraben Liljak]. Maltese: Pipistrell ta' Kuhl. Montenegrin: Bijelorubi slijepi mišić. Norwegian: Hvitrandflaggermus. Polish: Karlik średni, Karlik Kuhla. Portuguese: Morcego de Kuhl, Morcego anao de Kuhl. Rhaeto-Romance: Pipistrel da Kuhl. Romanian: Liliacul pitic al lui Kuhl, Liliacul cu dungã albã. Russian: Нетопырь средиземноморский, Средиземноморский нетопырь [= Sredizemnomorskij netopyr], Нетопырь Куля. Serbian: Б[ј]елоруби слепи мишић [= B[j]elorubi slepi mišić]. Scottish Gaelic: Ialtag Kuhl. Slovak: Večernica južná. Slovenian: Belorobi netopir. Swedish: Parkpipistrell, Kuhls fladdermus. Turkish: Beyazşeritli Yarasa. Ukrainian: Нетопир білосмугий [= Netopir bilosmuhyy]. Welsh: Ystlum lleiaf Kuhl.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
González-Dionis *et al.* (2021: 9) reported the first fossil remains of *P. kuhll* on Lanzarote (Canary Islands).

CONSERVATION STATUS:
Global Justification
The species is widespread and abundant, and populations are increasing in parts of the range. Consequently, it is assessed as Least Concern (LC ver 3.1 (2001)) (Aulagnier *et al.*, 2008b; IUCN, 2009; Juste and Paunović, 2016d).

Assessment History
Global
2016: LC ver 3.1 (2001) (Juste and Paunović, 2016d). 2008: LC ver 3.1 (2001) (Aulagnier *et al.*, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessment included *P. hesperidus*] (Aulagnier, 2004c; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

For *P. deserti*, the Assessment History was:
2008: LC ver 3.1 (2001) (Benda *et al.*, 2008d; IUCN, 2009). 2004: LC ver 3.1 (2001) (Benda, 2004a; IUCN, 2004). 1996: LR/lc [assessed as *P. aegyptius*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
No major threats are known. Use of pesticides to eradicate mosquitos (especially in urban areas) may be a threat in places (Aulagnier *et al.*, 2008b; IUCN, 2009; Juste and Paunović, 2016d).

Sherwin *et al.* (2012: 174) name aerial hawking and its long-distance dispersal to be the most important risk factors related to climatic change. Bilgin *et al.* (2012: 434) indicate that climatic change is already influencing this species as it has been expanding its range northwards over the past 15 years.

CONSERVATION ACTIONS:
Juste and Paunović (2016d) supports Aulagnier *et al.* (2008b) [in IUCN (2009)] who report that it is protected by national law in most European range states. It is also protected under international legislation in parts of its range through the Bonn Convention (Eurobats) and Bern Convention, and is included in Annex IV of EU Habitats and Species Directive It is found in a number of protected areas. No specific conservation actions are known.

GENERAL DISTRIBUTION:
Pipistrellus kuhlii is widespread in North Africa, Europe and Asia. It has a large range extending from Iberia through southern Europe through the Near East and the Caucasus to Kazakhstan, Pakistan, and India (Molur *et al.*, 2002). There is a single record from China (Smith and Xie, 2008). The northern limit of its range in Europe was

formerly ca. 45°N, but the species has been expanding northwards. It arrived 1994 in Vienna/Austria (48°N) and was more recently recorded to 50°N in France and 51°N in Ukraine. It has been expanding northwards in Russia for the last half century from 46° N to c.53°N, with the highest record made at almost 57°N (S. Kruskop *pers. comm.*, 2006 in Aulagnier *et al.*, 2008b). It occurs from sea level to 2,000 m.

Borloti *et al.* (2020: 17) re-identified the only available *P. kuhlii* museum voucher specimen (MZUF 10597) as belonging to *Hypsugo savii* and indicated that the only evidence of *P. kuhlii* being present on the Cape Verdian Islands is a number of echolocation calls, which could be misclassified *P. hesperidus* or *Neoromicia*.

Native: Afghanistan; Albania; Algeria; Andorra; Angola; Armenia; Austria; Azerbaijan; Bosnia and Herzegovina; Burkina Faso (as *P. deserti*); Bulgaria; Croatia; Cyprus (Benda *et al.*, 2007: 71); Czech Republic (Reiter *et al.*, 2007: 47); Egypt; France [Corsica]; Georgia; Germany; Gibraltar; Greece [Crete]; Holy See [Vatican City State]; Hungary; India; Iran, Islamic Republic of; Iraq; Israel; Italy [Sardinia, Sicily]; Jordan; Kazakhstan; Kuwait; Lebanon (Horáček *et al.*, 2008: 59); Libyan Arab Jamahiriya; Macedonia, the former Yugoslav Republic of; Malta; Monaco; Montenegro; Morocco (Benda *et al.*, 2004d; 2010a: 158; El Ibrahimi and Rguibi Idrissi, 2015: 362; Dbiba *et al.*, 2025: 7); Oman; Pakistan; Palestinian Territory, Occupied; Portugal; Romania; Russian Federation; San Marino; Saudi Arabia; Serbia; Slovakia; Slovenia; Spain [Baleares, Canary Is.] (Azzaroli Puccetti and Zava, 1988); Sudan (as *P. deserti*); Switzerland; Syrian Arab Republic; Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26; 2023: 1); Turkey; Ukraine; United Arab Emirates (Anonymus, 2008: 38); Western Sahara (Benda *et al.*, 2010a: 161); Yemen.

Presence uncertain: China. Additionally, its presence (as *P. deserti*) was reported as uncertain from Cape Verdian Islands, Ghana, Kenya, Nigeria, Senegal, and Somalia.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Alagaili *et al.* (2011: 466) describe the timing and moulting patterns of *P. kuhlii* specimens from Saudi Arabia. They found that males were moulting from the end of April to the end of August, whereas females were moulting from the end of May/beginning of June to the end of August. The later moulting in females was probably related to the fact that females gave birth between mid-April and mid-May. The moulting itself starts at the back of the head and on the lower back and spreads from there over the entire head and back. Ventrally, the moult starts on the neck, around the nipples and along the sides of the body, then making its way to the centre of the chest.

DENTAL FORMULA:
Dorst (1949: 45-46, fig. 1) provides a description of the milk dentition of *P. kuhlii*. He also indicated (p. 47) that the milk teeth show some sort or heterodonty with the premolars being of different shape when compared with the incisors and canines, which look more similar to one another. These latter teeth help the young to cling to the mother's nipples.

DETAILED MORPHOLOGY:
Ibraheem and Shelfeh (2008) report on the anatomy and histology of the digestive tract of Syrian *P. kuhlii*.

Selim *et al.* (2008: 247) studied the microscopical structure of the tongue of Egyptian and Syrian *P. kuhlii* specimens and found some differences between them.

Massoud and Abumandour (2020: 1) examined the structure of the tongue of nine bats from Egypt. These have a lingual prominence on the dorsum of lingual body. The lingual epithelium had an outer covering of nucleated epithelium, and they also found entoglossal plates which consisted of a cartilaginous element. The ligual root of the tongue has two laterally situated circumvallate papillae.

The retinal structure was investigated by Aboelnour *et al.* (2020), who did not find any aberrant structures. The structure of the eye lens was examined by Aboelnour *et al.* (2024).

FUNCTIONAL MORPHOLOGY:
Gearhart *et al.* (2019: 1) studied the evaporative water loss of these bats in Israel and found that the total evaporative water loss was lower in hyperarid environments (deserts) as compared with bats from more mesic environments. This difference was especially noticeable in the significantly lower cutaneous water loss, which might be the result of modified lipids in the outer layer of the skin.

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 8.5 Pa, aspect ratio 6.3 for a wingspan of 19 cm and a wing area of 54 cm^2 and a body mass of 5 g.

Eitan *et al.* (2022: 5) found that *P. kuhlii* widens it gape to narrow the vertical echolocation beam

width and reduce the zone of ensonification. The gape can be adjusted rapidly according to the particular task (search versus approach beams).

SEXUAL DIMORPHISM:
In a year-round study in Tunisia, Dalhoumi *et al.* (2016a: 157) found adult females to be significantly heavier than males.

ECHOLOCATION:
For 31 Greek specimens, Papadatou *et al.* (2008b: 133) report a start frequency of 59.8 ± 14.75 kHz, a terminating frequency of 37.5 ± 1.33 kHz, a peak frequency of 39.7 ± 1.46 kHz, and a bandwidth of 9.4 ± 2.85 kHz. The duration of the call is 6.4 ± 1.38 ms, and the interpulse interval is 124.7 ± 44.55 ms.

Walters *et al.* (2012: suppl.) mention the following numbers for 47 calls of bats from France, Greece, Italy and Switzerland: duration: 5.62 ± 1.43 ms, F_{max}: 53.57 ± 10.08 kHz, F_{min}: 36.87 ± 2.15 kHz, bandwidth: 16.70 ± 9.93 kHz, F_{peak}: 39.77 ± 2.63 kHz.

In Jordan, Benda *et al.* (2010b: 204) reported the following parameters for 76 calls: F_{start}: 51.7 ± 6.2 (41.4 - 65.6) kHz, F_{end}: 39.1 ± 1.1 (41.4 - 65.6) kHz, F_{peak}: 41.1 ± 1.1 (37.2 - 43.2) kHz, duration: 6.4 ± 1.7 (3.4 - 10) ms, interpulse interval: 112.9 ± 38.0 (70.0 - 279.0) ms. For 37 calls from Iran, Benda *et al.* (2012a: 183) report: F_{start}: 48.9 ± 4.5 (43.26 - 60.5) kHz, F_{end}: 41.1 ± 1.6 (38.7 - 44.3) kHz, F_{peak}: 42.2 ± 1.9 (39.1 - 46.8) kHz, duration: 6.1 ± 1.3 (4.0 - 9.0) ms, and interpulse interval: 106.5 ± 38.7 (54.4 - 231.9) ms.

In Israel, the following values were recorded by Hackett *et al.* (2016: 223) for 84 calls: Pulse duration: 4.57 ± 2.05 ms, F_{start}: 51.27 ± 4.54 (40 - 71.2) kHz, F_{end}: 40.58 ± 1.54 (37 - 43.9) kHz, F_{peak}: 41.48 ± 1.53 (37 - 42.8) kHz.

Luo *et al.* (2019a: Supp.) reported the following data (from 2 calls): F_{peak}: 41.4, 39.7 kHz, F_{start}: 72, 59.8 kHz, F_{end}: 39.6, 37.5 kHz, Band width: 32.4, 22.3 kHz, and duration: 5.7, 6.4 ms.

Boonman *et al.* (2013b: 6) determined the detection range to be between 2 and 3.5 m at 20 dB and 4 and 7 m at 0 dB.

Corcoran and Moss (2017: 4560) refer to Amichai *et al.* (2015), who found that *P. kuhlii* solved the jamming problem of extreme acoustic interference from conspecifics not by adjusting call frequency but by emitting calls of hither intensity, longer duration, and calling more often. This suggests that the bats try to increase the signal-to-noise ratio rather than avoiding spectral overlap.

In the Bechar region (Algeria), Loumassine *et al.* (2020: 2) reported F_{max} and F_{end} for *P. kuhlii kuhlii* and *P. kuhlii deserti* to be respectively 42.59 ± 1.14, 38.72 ± 1.63 kHz and 46.32 ± 1.56, 41.43 ± 1.92 kHz. *Pipistrellus kuhlii* bats from Constantine emit call with an F_{max} of 38.71 ± 1.03 kHz (Ait-Abdesselam *et al.*, 2025: 40).

Bats from Tunisia were found to have F_{start}: 59.60 ± 10.97 (39.7 - 101.6) kHz, F_{end}: 42.13 ± 1.91 (36.8 - 48.4) kHz, F_{max}: 42.91 ± 1.91 (36.9 - 49.5) kHz, duration: 6.10 ± 1.18 (3.6 - 11.8) ms and Interpulse interval: 181.81 ± 82.16 (8.4 - 716.5) ms (Dalhoumi *et al.*, 2023: 5). Dalhoumi *et al.* (2023: 9) also found profound differences in the call parameters between various locations, which they suggest might be adaptations to different habitat types.

MOLECULAR BIOLOGY:
Karyotype
Both Baker *et al.* (1974) and Iliopoulou-Georgudaki and Giagia (1986) reported 2*n* = 44, FN = 50, and BA = 8. However, Baker *et al.* (1974) reported a submetacentric X chromosome and an acrocentric Y chromosome, whereas Iliopoulou-Georgudaki and Giagia (1986) reported metacentric X and Y chromosomes. Rushton (1970: 465) reported 2*n* = 44, FN = 50, X = metacentric and Y = acrocentric. Arslan and Zima (2014: 13) indicate that the autosomal set consists of three large and one small metacentric pairs, 15 acrocentric pairs and two dot-like pairs, and both sex chromosomes are medium-sized. According to Capanna and Manfredi Romanini (1971: 474) the autosomal chromosomes consist of 3 metacentric pairs, 1 submetacentric and 17 acrocentrics.

Protein / allozyme
Andriollo *et al.* (2015: 1) examined the COI gene in in European and North African *P. kuhlii* populations and found that all North African nuclear genotypes were grouped in a highly distinct subpopulation when compared with European samples sharing the same mitochondrial barcodes. In their figure 1 (p. 3), they show that the North African populations (including *deserti* have very similar haplotypes with the eastern European populations from the Balkan and Italy but differ considerably from the western lineage found in France and Spain. Batsleer *et al.* (2019: 172) analysed part of the 16S rRNA from some Maltese specimens and found them to belong to a lineage occurring in northern Africa.

Genetics
See Mayer *et al.* (2007), García-Mudarra *et al.* (2009).

Locatelli *et al.* (2016: 423) determined the complete mitogenome and found it to contain 16,991 base pairs with 37 genes (13 protein-coding genes, 22 tRNA genes, 2 rRNA) and 1 control region.

Bray *et al.* (2013: 5) indicate that widespread species - such as *P. kuhlii* - have extensive genetic diversity.

HABITAT:
In Tunisia, Dalhoumi *et al.* (2018: 1) found this species to forage mainly around water bodies and streetlights. During summer, they also foraged in open Acacia woodlands (*Acacia tortilis raddiana*).

ROOST:
All of the roost found in Libya by Benda *et al.* (2014c: 64) were in ruins, with one exception for a single male in a rock fissure in an overhang.

DIET:
Benda *et al.* (2012a: 448) report that the diet is very variable over the species' distribution range: Diptera, Lepidoptera, Hymenoptera (particularly Formicoidea), Auchenorrhyncha, Coleoptera, and Heteroptera comprised a major part of the diet. For Iran, they found Coleoptera, Heteroptera, and Auchenorrhyncha to be the most important food items.

Also in Libya, Benda *et al.* (2014c: 77) report a very variable diet for *P. kuhlii*, where smaller moths (Lepidoptera) and beetles (Coleoptera) were the most important types of prey. The beetles belonged to the families Scarabaeidae, Carabidae (frequently Harpalini), Staphylinidae, Tenebrionidae, Chrysomelidae. Furthermore, ants (Hymenoptera: Formicoidea) formed a major part of the diet. Additionally, medium-sized brachyceran Diptera (Muscidae, Asilidae) were identified, as well as Neuroptera (Chrysopidae and Hemerobiidae).

Abdel-Hamid and Alqahtani (2022: 103494-103495) reported that in the Nile Valley, the diet of this bat consisted of (volume/frequency %) 29/87.3 % Hymenoptera, 9/36.5 % Coleoptera, 27/74.6 % Lepidoptera and 32 % unknown materials. They also found 3/4.8 % of fruits.

A long-term study (17 years) by Locatelli *et al.* (2019) in southern Europe indicated that *P. kuhlii* specimens had an optimal body condition when there was a combination of warmer spring-summers and cooler winters. They also found that higher spring humidity combined with intermediate precipitation and humidity levels recorded during the summers prior to the capture were favourable for these bats. These conditions are probably linked with a larger abundance of insect prey.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 67 minutes, and the digestibility rate about 81.4 %.

PREDATORS:
Reuven (1991: 79) reported on *P. kuhlii* being captured by a Lanner Falcon (*Falco biarmicus* Temminck, 1825) in Israel. Mikula *et al.* (2016: Supplemental data) furthermore mention the same predator from either Botswana, Egypt, Ethiopia, Kenya, Nigeria, Sudan or South Africa. Part of these records might actually be for *P. hesperidus*. This is also the case for their record involving the Peregrine falcon (*Falco peregrinus* Tunstall, 1771).

Souttou *et al.* (2018: 136) found *P. kuhlii* to be a major part of the diet of the Common Kestrel (*Falco tinnunculus* Linnaeus, 1758) in Dergana (Algeria), where it made up to 16.4 % of the birds prey. In a second locality (El Harrach) if made up 0.7 % of the prey (and 0 % in seven other localities). In another locality in Algeria, Souttou *et al.* (2006: 177) found that *P. kuhlii* made up 4.7 to 9.4 % of the prey of fledgling common kestrels, making it the third most frequent prey species.

POPULATION:
Structure and Density
It is a relatively abundant species in the Mediterranean region and Middle East. Populations in South Asia seem to be stable and doing well (Molur *et al.*, 2002). Summer colonies typically number 30-100 individuals. In Iran and the Caucasus, the species' range is increasing, and it is displacing *P. pipistrellus* (M. Sharifi and K. Tsytsulina *pers. comm.*, 2005 in Aulagnier *et al.*, 2008b). The northern border of the species' range is also expanding. It is very numerous in urban areas across much of its range (Aulagnier *et al.*, 2008b; IUCN, 2009; Juste and Paunović, 2016d).

As *P. deserti*, it was reported to be the most common species in Sahara oases (Benda *et al.*, 2008d; IUCN, 2009).

Trend
2016: Unknown (Juste and Paunović, 2016d). 2008: Unknown (Aulagnier *et al.*, 2008b; IUCN, 2009). *P. kuhlii* populations within the Asia Minor and Levant region are unknown population trend,

under predictive climate change scenarios (Bilgin *et al.*, 2012: 433).

LIFESPAN:
Szekely *et al.* (2015: Suppl.) and Lagunas-Rangel (2019: 2) report a maximum longevity of 8 years.

ACTIVITY AND BEHAVIOUR:
In the Negev Desert, Polak *et al.* (2011: 24) found that *P. kuhlii* had a significantly higher flight speed when flying in areas with streetlamps, than in in dark areas. They also found that flight height was higher in dark areas than in lighted areas (> 1 m).

Smotherman *et al.* (2016: 537) refer to Barak and Yom-Tov (1991) and Russo and Jones (1999) in describing the song-like structure for *P. kuhlii* as simple syllable type in a basic motif. Singing occurs while flying.

REPRODUCTION AND ONTOGENY:
Deleuil and Labbe (1955b: 238) reported three lactating females from El Hamaïn (Tunisia) on 24 July 1955. From the same country, Dalhoumi *et al.* (2018: 1) reported pregnant females from March to June, lactating females in June, and flying juveniles from June to August. Dalhoumi *et al.* (2015: 265) found that females were most often pregnant in May and lactating in June.

In Libya, Benda *et al.* (2014c: 71) report on four pregnant females collected on 16 April, 16 on 20 April, 2 on 8 May, 3 on 22 May, and 1 on 23 May. Lactating females were found on 8, 21, 26 and 27 May. Szekely *et al.* (2015: Suppl.) report that weaning occurs after 60 days.

In the United Arab Emirates, Davis (2007: 8) indicates that females are sexually mature in their first year, and that two young are born (= polytocy, see Garbino *et al.*, 2021: Suppl.).

POSTNATAL DEVELOPMENT:
Sharifi *et al.* (2012: 1235) studied the development of Iranian *P. kuhlii* specimens born in captivity and found that, at birth, young had a mean body mass of 1.04 ± 0.08 g and a forearm length of 11.48 ± 0.45 mm. During the first 23 days of their live, their body mass and forearm length increased on average with 0.10 ± 0.10 g/d and 0.64 ± 0.61 mm/d. Wingspan, handwing length and area, armwing length and area, and total wing area increased linearly until the age of the 1st flight (at 33 days), after which growth rates significantly declined. At the age of 60 d, the young had an average weight of 5.47 ± 0.07 g (87.56 % of the adult) and the mean forearm length of 35.97 ± 0.86 mm (89.46 % of the adult length).

PARASITES:
Kock *et al.* (1998b: 236) reported *Cacodmus villosus* (Stål, 1855) (Cimicidae) from bats from Malawi.

Korine *et al.* (2012: 1435) experimentally infested *P. kuhlii* specimens with the flea *Xenopsylla ramesis*, whose normal host is Sundevall's jird (*Meriones crassus*). They found that both male and female fleas engorged less blood from the bats than from the jird (and less than from *R. aegyptiacus* specimens tested during the same study). They also found that the survival time of the fleas was shorter when fed on *P. kuhlii* blood. Furthermore, fleas feeding from torpid bats were found to engorge more blood than those feeding from normothermic bats.

From Algeria, Bendjeddou *et al.* (2013: 325) reported *Phthiridium biarticulatum* Hermann, 1804 (Diptera: Nycteribiidae), *Cimex pipistrelli* Jenyns, 1839 (Hemiptera: Cimicidae), and *Ischnopsyllus octactenus* (Kolenati, 1856) (Siphonaptera: Ischnopsyllidae).

Bendjeddou *et al.* (2017: 15) mention the following ectoparasites: Siphonaptera: *Nycteridopsylla longiceps* Rothschild, 1908 and *Ischnopsyllus octactenus* (Kolenati, 1856); Heteroptera: *Cimex pipistrelli* Jenyns, 1839 and *Cacodmus vicinus* Horváth, 1934; Arachnida: *Hyalomma dromedarii* Koch, 1844.

Bendjoudi *et al.* (2019: 71) and Khelfaoui *et al.* (2018: 68) furthermore reported *Ixodes ricinus* (Linnaeus, 1758), *Steatonyssus occidentalis* (Ewing, 1933)

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Carios vespertilionis* Latreille, 1802, *Ornithodoros coniceps* (Canestrini, 1890); Cicimidae: *Cacodmus vicinus* Horváth, 1934, *Cimex lectularius* Linnaeus, 1758, *Cimex pipistrelli* Jenyns, 1839; Ischnopsyllidae: *Ischnopsyllus consimilis* (Wahlgren, 1904), *Ischnopsyllus octactenus* (Kolenati, 1856), *Nycteridopsylla longiceps* Rothschild, 1908; Ixodidae: *Ixodes ricinus* (Linnaeus, 1758), *Ixodes vespertilionis* Koch, 1844; Macronyssidae: *Hyalomma dromedarii* Koch, 1844, *Steatonyssus occidentalis* (Ewing, 1933); and Spinturnicidae: *Spinturnix acuminata acuminata* (C.L. Koch, 1836).

Selmi *et al.* (2021: 1) reported on a Tunisian "*Pipistrellus pipistrellus*" infested by the rat flea (*Xenopsylla cheopis*) and mites of the genus

Macronyssus. Spleen and liver samples of that bat contained DNA of *Anaplasmataceae* bacteria, more specifically *Ehrlichia canis*. However, fig 1a clearly shows the presence of a white margin at the edge of the wing membrane, which suggests that the bat involved is actually a representative of *Pipistrellus kuhlii*.

Benda *et al.* (2014c: 80) report the following ectoparasites from Libya: Argasidae: *Argas vespertilionis* (Latreille, 1802); Macronyssidae: *Steatonyssus periblepharus* Kolenati, 1858; Spinturnicidae: *Spinturnix acuminata* group; Cimicidae: *Cimex lectularius* Linnaeus, 1758, *Cacodmus vicinus* Horváth, 1934; Ischnopsyllidae: *Ischnopsyllus consimilis* (Wahlgren, 1904)

From Jordan, Benda *et al.* (2010b: 285) mention *Argas vespertilionis* (Latreille, 1802) (Argasidae), *Steatonyssus periblepharus* Kolenati, 1858 (Macronyssidae), and *Cacodmus vicinus* Kolenati, 1858 (Cimicidae).

Other parasites that were previously reported from the Middle East include the bat flies: *Nycteribia schmidlii* Schiner, 1853, *N. vexata* Westwood, 1835, *Penicillidia conspicua* Speiser, 1901, and *Basilia daganiae* Theodor and Moscona, 1954; the bat fleas *Ischnopsyllus octactenus* (Kolenati, 1856) (also from Tunisia by Beaucournu and Kock, 1996), *I. consimilis* (Wahlgren, 1904) *Xenopsylla cheopis* (Rothschild, 1903) and *Leptopsylla sengis* (Schoenherr, 1911); and the mite species *Spinturnix acuminatus* (Koch, 1836) and *Steatonyssus periblepharus* Kolenati, 1858.

Benda *et al.* (2012a: 449) report the following ectoparasites from Iran: Spinturnicidae: *Spinturnix* sp., *Meristaspis lateralis* Kolenati, 1857; Macronyssidae: *Steatonyssus periblepharus* Kolenati, 1858; Ischnopsyllidae: *Ischnopsyllus octactenus* (Kolenati, 1856). They also mention the presence of the bat flies *Basilia daganiae* Theodor et Moscona, 1954 in the Levant, *Ischnopsyllus consimilis* (Wahlgren, 1904) in Egypt, Israel and Lebanon, the bed bug *Cimex lectularius* Linnaeus, 1758 in Iraq, and *Cacodmus vicinus* Horváth, 1934 in Cyprus, Syria, Israel, Jordan, and Egypt.

Trypanosoma (Schizotrypanum) vespertilionis Battaglia, 1904 was reported from *P. kuhlii* specimens from the Assiut Governate, Egypt by Fahmy *et al.* (1978: 251). Based on older references, Austen and Barbosa (2021: 7) reported *Trypanosoma (Megatrypanum) heybergi* Rodhain, 1923 from the DRC, and *Trypanosoma (Megatrypanum) megadermae* Wenyon, 1909 from either Sudan or Egypt.

Duszynski (2002: 16) indicates that Arabian *P. kuhlii* is the type host of *Eimeria chiropteri* Alyousif, 1999, *Eimeria kuhliensis* Alyousif, 1999, and *Eimeria pipistrellus* Alyousif, Al-Dakhil and Al-Shawa, 1999.

Greiman *et al.* (2016: 1006) reported the presence of a Trematode belonging to the genus *Lecithodendrium* Looss, 1896 in *P. kuhlii marginatus* from Egypt.

DIPTERA
Nycteribiidae
Basilia bathybothyra from Palestine, Egypt and Cyprus (Haeselbarth *et al.*, 1966: 110).

Ševčík *et al.* (2012: 35) report on the presence of the bat fly *Basilia daganiae* Theodor and Moscona, 1954 on bats from Cyprus. Beaucournu and Noblet (1985: 636) also plot a record for this bat fly in Egypt.

VIRUSES:
Astroviridae
El Taweel *et al.* (2020: 5) found viruses belonging to the genus Mamastrovirus in "*P. aegyptius*" bats from Egypt.

Coronaviridae
SARS-CoV
During Febuary 2008 in Ghana, one fecal sample of "*P. deserti*" tested negative for coronavirus (CoV) RNA by Pfefferle *et al.* (2009).

Alphacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from Spain and Italy.

Betacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from Italy.

Paramyxoviridae
Drexler *et al.* (2012a: Suppl. Table S1) indicated that the single specimen of "*P. deserti*" they examined from Ghana did not test positive for *Repirovirus, Henipavirus, Morbillivirus, Rubulavirus* or *Pneumovirus*.

Phenuiviridae
Phlebovirus
de Jong *et al.* (2011: 11), Luis *et al.* (2013: suppl.), and Kohl and Kurth (2014: 3111) report the occurrence of Toscana virus.

Saeed *et al.* (2021b: 1004, 1005) found two "*P. deserti*" bats testing positive for Rift Valley Fever

phlebovirus, and suggested that this bat might play a role in the maintenance, transmission, and evolution of RVFV in humans and domestic animal populations.

Reoviridae
Orthoreovirus
Kohl and Kurth (2014: 3113) reported this virus from Germany and Italy.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Canary Islands (Spain), Chad, Egypt, Libya, Madagascar, Morocco, Sudan, Tunisia.

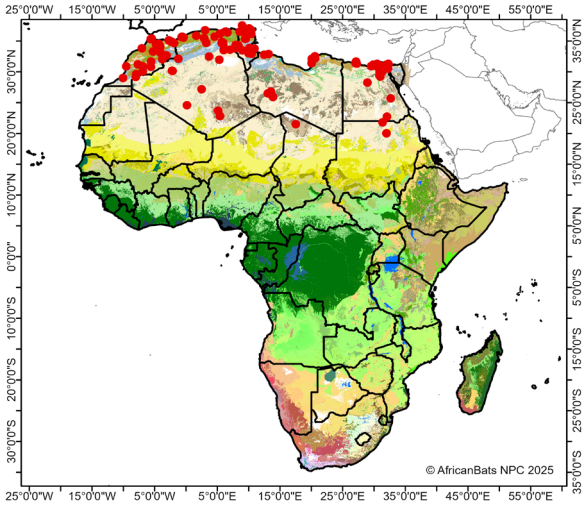

Figure 328. Distribution of *Pipistrellus (Pipistrellus) kuhlii*.

Pipistrellus (Pipistrellus) maderensis (Dobson, 1878)

*1878. *Vesperugo [(Vesperugo)] maderensis* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, p xxxix, 211, 231, pl 12, fig 5. Publication date: 15 June 1878. Type locality: Madeira (Portugal): "Madeira" [32 44 N 15 58 W]. [Goto Description]. Holotype: NHMUK 1855.8.16.34: ad ♀, skull and alcoholic. Collected by: William S. MacGillivray. - Etymology: The name refers to the island where the type specimen was collected.
1908. *P[ipistrellus] maderensis:* K. Andersen, Ann. Mag. nat. Hist., ser 8, 1 (5): 435. (Name Combination, Current Combination).
1922. *Pipistrellus maderensis:* Bannerman. - Comments: They Canary Islands: 153. (Name Combination).
1966. *Pipistrellus (Pipistrellus) maderensis:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 171. (Name Combination, Current Combination).
1999. *Pipistrellus madarensis:* Ohlendorf, Nyctalus (N.F.), 7: 193 - 195. (Lapsus).
2020. *Pipistrellus madeirensis:* Borloti, Dinis and Vasconcelos, Genes, 11 (8) 844: 3. Publication date: 1 August 2020. (Lapsus).

TAXONOMY:
Pestano *et al.* (2003b: 61) indicate that *P. maderensis* is more closely related to the Canary Island *P. kuhlii* clade than the latter is to *P. kuhlii* from outside the Canaries.

Jesus *et al.* (2013: 179) analyzed cytochrome b from Madeiran and Canary bats and found these to be sufficiently different to warrant subspecific distinction. However, as their data were preliminary, they did not officialize this view (see also Rocha, 2023: 522).

Evin *et al.* (2010: 35) suggest that a Kuhl's pipistrelle-like bat colonized the Canary Islands and differentiated during the middle Pleistocene to give rise to the *maderensis* clade.

COMMON NAMES:
Albanian: Pipistreli i Madeiras. Armenian: Մադեյրական փոքրաչղջիկ. Azerbaijani: Maderiya və ya Kanar şəbpərəsi. Basque: Pipistrelo madeirar. Belarusian: Нетапыр мадэрскі. Bosnian: Madeirski šišmiš. Breton: Pipistrell Madeira. Bulgarian: Мадейрско прилепче. Castilian (Spain): Murciélago de Madeira. Catalan (Spain): Pipistrel·la de Madeira, Rat penat de Madeira. Croatian: Madeirski mali šišmiš. Czech: Netopýr makaronéský, Netopýr madeirský. Danish: Madeiraflagermus. Dutch: Madeira dwergvleermuis, Madeiradwergvleermuis. English: Madeiran Pipistrelle Bat, Madeira pipistrelle. Estonian: Madeira nahkhiir. Finnish: Madeiranpiippa. French: Pipistrelle de Madère. Frisian: Madeira dwerchflearmûs. Galician (Spain): Morcego de Madeira. Georgian: მადეირული ღამორი. German: Madeira-Fledermaus, Madeira-Zwergfledermaus, Madeira-Pipistrelle. Greek: Νυχτερίδας της Μαδέρας. Hungarian: Madeirai törpedenevér. Irish Gaelic: Ialtóg Mhaidéarach. Italian: Pipistrello di Madeira. Latvian: Madeiras sikspārnis. Lithuanian: Madeirinis šikšniukas. Luxembourgish: Madeira-Zwergfliedermaus. Macedonian: Медеирски лилјак. Maltese: Pipistrell ta' Madejra. Montenegrin: Slijepi mišić sa Madeire. Norwegian: Madeiraflaggermus. Polish: Karlik maderski. Portuguese: Morcego da Madeira. Rhaeto-Romance: Pipistrel da Madeira. Romanian: Liliacul pitic din Madeira. Russian: Нетопырь мадейрский. Serbian: Атлантски

сл[иј]епи мишић [= Atlantski sl[ij]epi mišić]. Scottish Gaelic: Ialtag Mhaideurach. Slovak: Večernica madeirská. Slovenian: Madeirski mali netopir. Swedish: Madeirapipistrell. Turkish: Maderia Cüce Yarasası. Ukrainian: Нетопир мадейрський. Welsh: Ystlum lleiaf Madeira.

SIMILAR SPECIES:
Based on fossil material, González-Dionis *et al.* (2021: 13) were able to distinguish *P. maderensis* from *P. kuhlii* occurring on the Canary Islands. In the former, the paraloph, metaloph and metaconule in M1 and M2 are more developed than in the latter.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
No fossil records of *Pipistrellus maderensis* are known (Rocha, 2023: 523).

CONSERVATION STATUS:
Global Justification
The species is restricted to few islands in the Canaries and the Madeira islands (and possibly the Azores). The population numbers < 1,000 individuals and it is suspected to be declining as a result of habitat loss, use of agricultural pesticides, and disturbance to roosts. This species is also severely fragmented. It is assessed as Vulnerable (VU C2a(i)) but may be approaching the Endangered category (Alcaldé and Juste, 2016).

P. maderensis is protected under the Bern Convention and included in Annex IVof the EU Habitats Directive (Rocha, 2021: 7).

Assessment History
Global
2016: VU C2a(i) ver 3.1 (2001) (Alcaldé and Juste, 2016). 2008: VU A2c, B1 + 2c ver 2.3. 1994: VU A2c, B1 + 2c ver 2.3.

Regional
Portugal: 2005: CR; Spain: 2008: NT

MAJOR THREATS:
Sherwin *et al.* (2012: 174) name the small distribution range, water stress, the aerial hawking feeding style and the long-distance dispersal to be the most important risk factors linked with climatic change.

Jesus *et al.* (2013: 177) indicate that human activities (e.g., large-scale land use change, the use of biocids/pesticides and roost disturbance and destruction) as well as some natural events (e.g., floods and wildfires) form the major threats for this species. Additionally, introduced species such as *Rattus rattus* and *Felis catus* might pose important threats. The latter is also illustrated by Rocha (2015: 17), who reported on a domestic cat, which brought home three bats (of which one was identified as *P. maderensis*) over a period of one year.

Rocha (2021: 8) indicated that, on Madeira, the use multiple-funnel traps used to control pinewood nematodes (*Bursaphelenchus xylophilus* (Steiner & Buhrer 1934)) have been reported to capture Madeiran pipistrelles. The bats can not exit these traps as the walls are too smooth and subsequently die.

Sagot and Chaverri (2015: 1670) mention roost loss or disturbance, and habitat degradation or loss as major threats for this species.

Restoration of buildings, covering cracks where it roosts, is a threat to the species. Rain-gauges attract dozens of bats which are trapped there and die (Trujillo, 2007). Loss of natural habitat may be a threat, although the species is apparently adapted to man-made habitats. The use of agricultural pesticides may be a problem, and disturbance to roosts in buildings may also be of concern (Alcaldé and Juste, 2016).

CONSERVATION ACTIONS:
The species is protected through Bern Convention, and included in Annex IV of EU Habitats & Species Directive. Rainho and Palmeirim (2002) proposed the following actions: identification, protection and monitoring of roosts; preservation and restoration of natural habitats, reduction of pesticide use; and, study of the species' biology, ecology, genetics, and systematics. Trujillo (2002) additionally recommend a public awareness campaign aimed at reducing disturbance of breeding colonies in private houses.

GENERAL DISTRIBUTION:
Madeira Islands (Portugal, where Rainho (2017: 161) reports its presence on six islands); Canary Islands (Spain).

Borloti *et al.* (2020: 3) [referring to R(1383)] indicate that *P. maderensis* is only found on the western Canary Islands and Madeira, whereas the other islands are inhabited by *P. kuhlii*.

Rocha (2021: 4,2023: 524) and Teixeira *et al.* (2023: 4) reported this species from the Atlantic islands of Madeira and Porto Santo (?), the Azores and the Canary Islands.

GEOGRAPHIC VARIATION:
When comparing cytochrome *b* sequences from Madeiran and Canary Island specimens, Jesus *et al.* (2013: 119) found that the populations from

both island groups represent "sister populations", showing a much higher sequence divergence than that observed within groups.

Rocha (2021: 4) mentions that the animals from La Palma are slightly larger than those from other Canary Islands.

The study by Teixeira *et al.* (2023: 1) - covering bats from Madeira, the Canary Islands and the Azores - proved that these populations formed distinct Evolutionary Significant Units, with the haplotypes of bats from Madeira and the Canary Islands showed genetic differences between 2.4 and 3.3 %. (The Azoran population was not included as no GenBank material was available from that archipelago).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 329. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1955.8.16.34, holotype of *Vesperugo maderensis* Dobson, 1878.

SEXUAL DIMORPHISM:
Rocha (2021: 4) [referring to Trujillo and González (2011)] mentioned that the forearms of females are slightly larger than in males.

ECHOLOCATION:
Luo *et al.* (2019a: Supp.) reported the following data (from two calls): F_{peak}: 47.8, 44.6 kHz, F_{start}: 67, 50.9 kHz, F_{end}: 45.9, 43.7 kHz, Band width: 21.1, 7.2 kHz, and duration: 4.9, 6.7 ms.

Rocha (2021: 7) mentioned a peak frequency between 41.3 - 51.7 kHz. In open areas F_{peak} ranges from 41.3 to 48.9 kHz and a duration 2.5 - 9.5-ms. In cluttered environments, the calls are shorter (2.1 - 5.8 ms) and F_{peak} 42.3 - 51.7 kHz. Social calls on Madeira have peak frequencies between 14.9 and 28.9 kHz and a duration of 21 to 57 ms.

MOLECULAR BIOLOGY:
Genetics
See Pestano *et al.* (2003b), Mayer *et al.* (2007).

Nóbrega *et al.* (2023: 94) mention that the bats from Madeira and Porto Santo have a genetic distance of 0.04 %, suggesting gene flow between these two islands, although they can not exclude recent re-colonisation of Porto Santo by bats from Madeira.

HABITAT:
Ferreira *et al.* (2022a: 1) found *P. maderensis* to be the most common and widespread bat species on the island of Madeira and also found it was positively associated with landscape-scale shrubland, cropland and Laurisilva (primary forest) cover.

ROOST:
Rocha (2021: 6) mentioned that nursery colonies of these bats are generally found in buildings (wall fissures and under roofing tiles).

Nóbrega *et al.* (2023: 88) mention it is proned to roost in cliffs, tree holes and human-made structures.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 69 minutes, and the digestibility rate about 81.2 %.

Nóbrega *et al.* (2023: 92, 93) found insect prey belonging to five order, 12 families, 13 genera and 11 identified species in faecal samples from *P. maderensis* collected on Porto Santo (Madeira), including: Culicidae: *Culex pipiens* Linnaeus, 1758, *Culex theileri* Theobald, 1903; Chironomidae: *Chironomus transvaalensis* Kieffer, 1908, *Polypedilum nubifer* (Skuse, 1889); Depressariidae: *Depressaria marcella* Rebel, 1901; Tortricidae: *Epiphyas postvittana* (Walker, 1863); Noctuidae: *Peridroma saucia* (Hübner, 1808); Hemerobiidae: *Wesmaelius subnebulosus* (Stephens, 1836); Tineidae: *Oinophila v-flava* (Haworth, 1828), *Psychoda alternata* Say, 1824; Ichneumonidae: *Campoletis* Förster, 1868; Formicidae: *Nylanderia* Emery, 1906; Cicadellidae: *Psammotettix confinis* (Dahlbom, 1850); Tephritidae: *Capitites ramulosa* (Loew, 1844).

Gonçalves *et al.* (2024: 4) found that most of they prey belonged to the Lepidoptera (47.1 %), followed by Diptera (29.9 %), Trichoptera, Coleoptera, and Araneae (all 4.6 %). The Lepidopteran family Blastobasidae was the most consumed (23.0 %), followed by Limoniidae (13.8 %), Tineidae (8.0 %), and Psychodidae (6.9 %). At species level, *Blastobasis vittata* (Wollaston, 1858) was recorded the most (12.6 %) , followed by *Dicranomyia* sp. 1 (Limoniidae - 8.0 %), and *Opogona sacchari* (Tineidae - 4.6 %). Of the 31 prey species, 19.3 % were agricultural pests, 6.4 % were possible agricultural pests and 3.2 % were species with human health implications.

POPULATION:
Structure and Density
Queiroz *et al.* (2005) [in Jesus *et al.* (2013: "1")] indicate that the population on Madeira consists of about 1,000 individuals. They also indicate that on the Azores the total population is probably less than 300 (but they point out that the identity of these bats is uncertain). On Madeira and associated islands, it is abundant but very rare on Porto Santo (Alcaldé and Juste, 2016). The total population is estimated to be less than 1,000 individuals, and trends are unknown (Rainho *et al.*, 2002). On the Canary Islands it is relatively common and is the most frequently reported bat on all islands of occurrence, although no bat is abundant on the islands. Population size and trend have not been quantified (Trujillo, 2002), although declines are suspected as a result of threats including loss and degradation of habitats, pesticide use, and disturbance and destruction of roosts. On the Azores, *Pipistrellus* bats are rare or very rare on all islands of occurrence, and the total number of individuals is probably less than 300 (Rainho *et al.*, 2002).

Trend
2016: Decreasing (Alcaldé and Juste, 2016).

ACTIVITY AND BEHAVIOUR:
Referring to Russo *et al.* (2009), Smotherman *et al.* (2016: 537) indicate that the song-like structure for this species consists of a simple syllable type in a basic motif. Singing occurs while flying.

PARASITES:
When describing *Steatonyssus (Steatonyssus) balcellsi*, Estrada-Peña and Sanchez (1988: 305) also mentioned the presence of this mite on *P. maderensis* specimens from El Lagar and Aguamansa, Canary Islands.

Sándor *et al.* (2021a: 4) reported the presence of the argasid tick *Carios vespertilionis* Latreille, 1802.

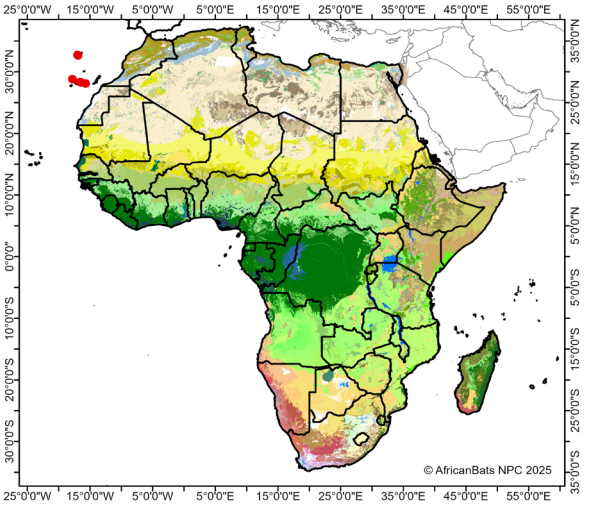

Figure 330. Distribution of *Pipistrellus (Pipistrellus) maderensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Canary Islands (Spain), Madeira (Portugal).

Pipistrellus (Pipistrellus) nanulus Thomas, 1904

*1904. *Pipistrellus nanulus* Thomas, Ann. Mag. nat. Hist., ser 7, 14 (81): 198. Publication date: 31 August 1904. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1904.2.8.8: ad ♂, skull and alcoholic. Collected by: George Latimer Bates Esq.
1966. *Pipistrellus (Pipistrellus) nanulus:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 16. (Name Combination, Current Combination).
1994. *Pipistrellus (Vansonia) nanulus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116. (Name Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Castilian (Spain): Pipistrelo. Chinese: 中非小伏翼. Czech: netopýr efulenský. English: Tiny Pipistrelle Bat, Dwarf Pipistrelle Bat, Tiny Pipistrelle. French: Pipistrelle minuscule. German: Kleine Zwergfledermaus, Kleine Pipistrelle.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008r; IUCN, 2009; Monadjem and Fahr, 2017g).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Pipistrellus nanulus*] (Monadjem and Fahr, 2017g). 2008: LC ver 3.1 (2001) (Fahr, 2008r; IUCN, 2009). 2004: LC ver 3.1 (2001) (Fahr, 2004h; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Fahr, 2008r; IUCN, 2009; Monadjem and Fahr, 2017g).

CONSERVATION ACTIONS:
Fahr (2008r) [in IUCN (2009)] and Monadjem and Fahr (2017g) report that *Pipistrellus nanulus* has been reported from the Mole National Park in Ghana (Grubb *et al.*, 1998). No direct conservation measures are currently needed for this widespread and seemingly adaptable species as a whole.

GENERAL DISTRIBUTION:
Pipistrellus nanulus is widespread in West and Central Africa, with an apparently disjunct population in East Africa. It ranges from Senegal eastwards, through most West African countries to Cameroon, from here it has been recorded from Equatorial Guinea (including the island of Bioko) and Gabon. In the east of the species range it has been recorded from eastern Democratic Republic of the Congo, Uganda and western Kenya (north of Lake Victoria).

Kruskop *et al.* (2016: 64) report two specimens from Ethiopia, which look very similar to *P. nanulus* from other parts of Africa, and although they do not mention any "cf." or "aff." as they do for other species, they hint that the identification need further confirmation.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2015a: 621); Cameroon; Central African Republic; Congo (Bates *et al.*, 2013: 329 - 1st authenticated record); Congo (The Democratic Republic of the) (Monadjem *et al.*, 2010d: 572); Côte d'Ivoire; Equatorial Guinea (Bioko); Ethiopia (Kruskop *et al.*, 2016: 64); Gabon; Ghana (Decher and Fahr, 2007: 18); Guinea (Decher *et al.*, 2016: 274); Kenya; Liberia; Nigeria; Senegal; Sierra Leone; Uganda.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) line drawing of tragi of specimen DNSM 13234 from Mount Nimba, Liberia.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

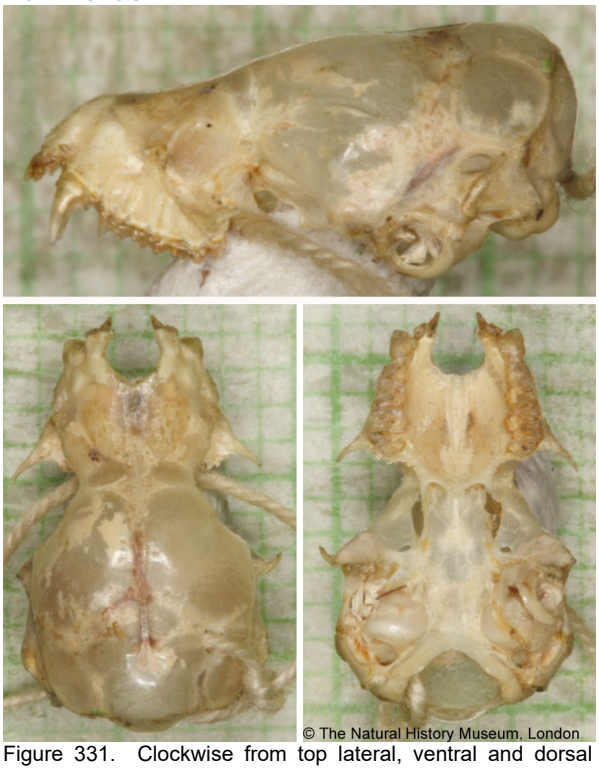

Figure 331. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1904.2.8.8, holotype of *Pipistrellus nanulus* Thomas, 1904.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987). *P. nanulus* and *H. c. bellieri* were much longer in total length than any of the *Neoromicia* species examined by Monadjem *et al.* (2013c). The shaft tip has a bifurcated structure with one projection that was slightly more distended than the other baculum shaft in both species was moderately ventrally curved, ending in a fluted base that was broader in *P. nanulus* (0.71 - 0.82 mm) than in *H. c. bellieri* (0.38 - 0.41 mm), a broad projection was clearly visible midway down the ventral surface of the shaft in *P. nanulus* (Monadjem *et al.*, 2013c: 197). Line drawing of dorsal and ventral bacula of specimen DNSM 13230 from Mount Nimba, Liberia are shown in Monadjem *et al.* (2013c: 204).

ECHOLOCATION:
Manga Mongombe (2012: 79) reported a FM/QCF call type for 1 calls from Maroua (Cameroon) and F_{max}: 65.5 kHz, F_{min}: 45.6 kHz, F_{mean}: 51.3 kHz, F_{knee}: 49.2 kHZ, F_{char}: 45.8 kHz, and duration: 2.89 ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 27 calls of 2 bats: F_{peak}: 57.3 ± 0.6 (57.0 - 58.0) kHz, F_{min}: 54.0 ± 1.6 (51.3 - 55.2) kHz, F_{max}: 106.0 ± 6.0 (100.6 - 113.5) kHz, duration: 2.4 ± 0.3 (2.2 - 2.9) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Grunwald *et al.* (2025: 303) indicate that the populations from West and Central Africa differ slightly in their cyt *b* sequences (p- distance: 0.04) and further research is required to evaluate their exact relationship. They also found some dental differences between the animals from Cameroon and West Africa, which also require further investigation.

HABITAT:
The specimens recorded by Monadjem *et al.* (2016y: 371) from the Mount Nimba area were found in lowland forest habitats (420 - 480 m).

DIET:
Faecal pellets of 2 bats from Cameroon examined by Waghiiwimbom *et al.* (2019a: 156), contained the following volume (± SD) and frequency percentages: Lepidoptera (64 ± 7.11; 100), Diptera (19.7 ± 3.9; 73.6), Diptera (19.7 ± 3.9; 73.6), Coleoptera (14.3 ± 5.2; 67.7), Hymenoptera (1.2 ± 0.5; 25), Hemiptera (0.8 ± 0.4; 5).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 43 minutes, and the digestibility rate about 86.5 %.

POPULATION:
Structure and Density
This species is relatively common (Fahr, 2008r; IUCN, 2009; Monadjem and Fahr, 2017g).

Trend
2016: Unknown (Monadjem and Fahr, 2017g).
2008: Unknown (Fahr, Fahr, 2008r; IUCN, 2009).

PARASITES:
PROTOZOA
Thiombiano *et al.* (2023: 4) reported that one of the10 bats from Burkina Faso they examined had *Trypanosoma* cf. *dionisii* parasites.

VIRUSES:
Coronaviridae - Coronaviruses
SARS-CoV
During February 2008 in Ghana, Pfefferle *et al.* (2009) tested negative one faecal sample for coronavirus (CoV) RNA.

Herpesviridae
Cameron *et al.* (2020: 1) reported a new Herpesvirus from the Republic of Congo, belonging to the Gammaherpesvirinae

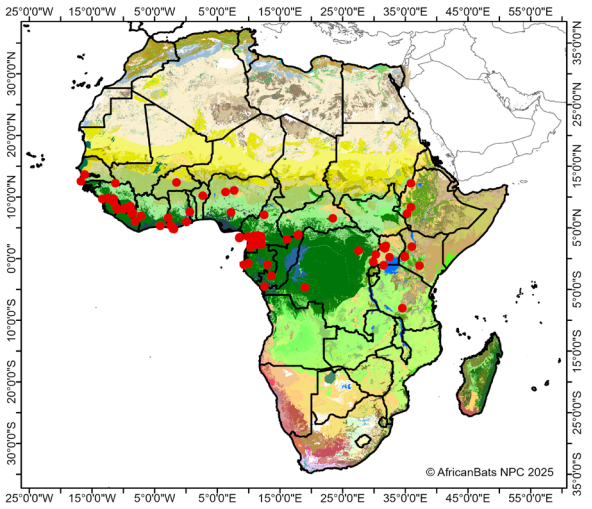

Figure 332. Distribution of *Pipistrellus (Pipistrellus) nanulus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Mali, Nigeria, Senegal, Sierra Leone, Tanzania, The Gambia, Togo, Uganda.

Pipistrellus (Pipistrellus) permixtus Aellen, 1957

*1957. *Pipistrellus (Pipistrellus) permixtus* Aellen, Rev. suisse Zool., 64 (6): 200. Type locality: Tanzania: Dar-es-Salaam [06 48 S 39 18 E]. [Goto Description]. Holotype: MZS 12c: ad ♀, skull and alcoholic. Collected by: Hürstel; collection date: 1905. (Current Combination).
1966. *[Pipistrellus] permixtus:* Koopman, The Puku, 4: 159. (Name Combination, Current Combination).
1982. *Pipistrellus permixtus:* Seal and Makey, ISIS Mammalian Taxonomic Director, ???. (Name Combination).

TAXONOMY:
This is a very illusive species. It is only known from the type specimen, which shows more affiliation to the European *P. nathusii* than to any of the African species. Since the type specimen was collected in Dar-es-Salaam, a port, it cannot be excluded that this animal was transported by ship from Europe to Africa.

COMMON NAMES:
Czech: netopýr tanganjický. English: Dar-es-Salaam Pipistrelle Bat, Dar-es-salaam Pipistrelle, Tanzania Pipistrelle. French: Pipistrelle de Tanzanie. German: Verwechselte Zwergfledermaus, Verwechselte Pipistrelle.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, ecological requirements, threats and conservation status (Jacobs *et al.*, 2008v; IUCN, 2009; Jacobs *et al.*, 2019h).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019h). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008v; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004ac; IUCN, 2004). 1996: DD (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are poorly known. However, it may be confined to dry coastal forest habitat, which is significantly threatened by conversion to agricultural use and extraction of firewood and timber (Jacobs *et al.*, 2008v; IUCN, 2009; Jacobs *et al.*, 2019h).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008v) [in IUCN (2009)] and Jacobs *et al.* (2019h) report that there appear to be no direct conservation measures in place for this species, and it is not known if the species is present within any protected areas. Additional studies are needed into the distribution, abundance, breeding biology and general ecology of this species. There is a need to conserve remaining areas of dry coastal forest in much of East Africa.

GENERAL DISTRIBUTION:
Pipistrellus permixtus is known only from a single specimen collected close to Dar es Salaam in Tanzania.

Native: Tanzania.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 70 minutes, and the digestibility rate about 81.0 %.

POPULATION:
Structure and Density
No information available on the abundance of this bat (Jacobs *et al.*, 2008v; IUCN, 2009; Jacobs *et al.*, 2019h).

Trend
2018: Unknown (Jacobs *et al.*, 2019h). 2008: Unknown (Jacobs *et al.*, 2008v; IUCN, 2009).

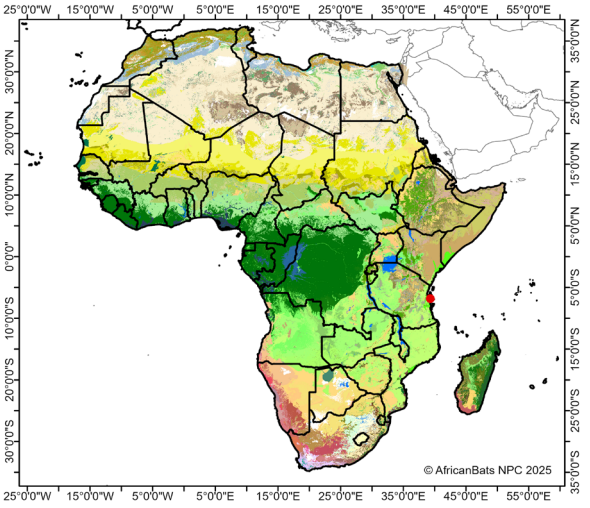

Figure 333. Distribution of *Pipistrellus (Pipistrellus) permixtus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Tanzania.

Pipistrellus (Pipistrellus) pipistrellus (Schreber, 1774)

*1774. *Vespertilio pipistrellus* Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, 1 (7): pl 54 + 1 (9): 167. Publication date: 1774. Type locality: France: "France". Neotype: NHMUK 1997.81: ad ♂. Collection date: October 1996. Designated by Anonymus (2003: 85). Locality of neotype: France: Normandy: Beauvais cathedral.

1839. *V[esperus (Vesperugo)] Pipistrellus:* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 321. (Name Combination).

1853. *V[esperugo (Vesperugo)] Pipistrellus:* Blasius, Arch. Naturgesch. Berlin, 19 (1): 36. (Name Combination).

1855. *Vespertilio (Vesperugo) pipistrellus:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 730. (Name Combination).
1856. *Vesperugo (Nannugo) pipistrellus:* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (5): 170. (Name Combination).
1857. *S[cotophilus] pipistrellus:* Tomes, Proc. zool. Soc. Lond., 1857, XXV (cccxxx): 5x. (Name Combination).
1860. *Nannugo pipistrellus:* Kolenati, Monographie der Europäischen Chiroptern, 8. (Name Combination).
1862. *Vesperugo (Vesperugo) pipistrellus:* Römer, Nass. Naturw. Jahrb., 18: ???. (Name Combination).
1863. *Vespertilio (Nannugo) pipistrellus:* Koch, Nass. Naturw. Jahrb., 18: 339. (Name Combination).
1867. *Scotoph[ilus] pipistrellus:* H. Allen, Proc. Acad. nat. Sci. Philad., 18 (4): 287 (for 1866). Publication date: prior to 13 February 1867. - Comments: The publication date of this issue uncertain. Nolan (1913: vii) mentions issue 3 containing pages 225 - 279 and issue 4 containing pages 280 - 336. The receipt of the latter was acknoldged on 13 February 1867, whereas no receipt date was given for issue 3. The problem is that H. Allen's paper starts on page 279 and ends on page 288. (Name Combination).
1871. *Vesperugo pipistrellus:* Doderlein, Alcune generalita Intorno la Fauna Sicula de Vertebrati, ???. (Name Combination).
1899. *Vesperugo (Euvesperugo) pipistrellus:* Acloque, Faune de France, Mammifères, 36. (Name Combination).
1900. *Pipistrellus pipistrellus:* Méhely, Monographia Chiropterorum Hungariae, 262. (Name Combination).
1928. *Pipistrellus pipistrellus pipistrellus:* Ognev, Mammals of eastern Europe and Northern Asia, 481. (Name Combination).
1959. *Pipistrellus (Pipistrellus) pipistrellus pipistrellus:* Aellen, Rev. suisse Zool., 66 (2): 381. (Name Combination).
1966. *Pipistrellus (Pipistrellus) pipistrellus:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 163. (Name Combination, Current Combination).
1970. *P[ipistrellus] pipistrelli:* Rushton, Ann. Génét. Sél. anim., 2 (4): 465. (Lapsus).
2023. *P[ipistrellus] pipestrellus:* Sidhoum, Boucheikhchoukh, Mechouk and Deak, Acta Trop., 247 (107004): 6. Publication date: 22 August 2023. (Lapsus).

Taxonomy:

Does not contain *pygmaeus* Leach, 1821. Genetic studies (e.g., Benda *et al.*, 2004b) provided evidence for a North-African lineage, possibly identified as a subspecies. Evin *et al.* (2011: 2096) also show that the shape of the skull of the Moroccon specimens differs from that of specimens from continental Europe and Corsica, and to a lesser extent, from the Middle East. Boston *et al.* (2014: 268) found *P. pipistrellus* to form a monophyletic group, but with a split between *P. pipistrellus* s. stricto and a possible paraphyletic group in Morocco, Algeria, Tunisia, Malta, Sicily, Corsica and Italy. Hulva *et al.* (2004; 2010) called this latter group "*P. pipistrellus* SW" and Puechmaille *et al.* (2012) suggest this group might represent a new species.

Common Names:

Albanian: Pipistrel i zakonshëm. Arabian: Khaffash. Armenian: Թզուկ փոքրաչղջիկ. Azerbaijani: Cırtdan şəbpərə. Basque: Pipistrelo arrunt, Saguzar. Belarusian: Нетапыр-карлік. Bosnian: Mali šišmiš, Patuljasti slijepi mišić. Breton: Pipistrell voutin. Bulgarian: Кафяво прилепче. Castilian (Spain): Murciélago comúin, Murciélago enan, Murciélago enano. Catalan (Spain): Rat penat comú, Pipistrel·la comuna. Croatian: Patuljasti šišmiš, Mali šišmiš. Czech: Netopýr hvízdavý, Nedopír hvízdavý, Netopýr malý, Letouň zakrpený, Netopýr pisklavý. Danish: Pipistrelflagermus, Dværgflagermus. Dutch: Gewone dwergvleermuis. English: Common Pipistrelle, Common Pipistrelle Bat, 45 kHz pipistrelle, Small house-bat. Estonian: Kääbus-nahkhiir. Finnish: Vaivaislepakko. French: Pipistrelle commune. Frisian: Gewoane dwerchflearmûs. Galician (Spain): Morcego común. Georgian: ჯუჯა ღამორი. German: Zwergfledermaus, Kahlschienige Dämmerungsfledermaus. Greek: Ναvονυχτερίδα. Hebrew: עטלפון אירופי, atalefon eropi, Atalfon Aeropi. Hungarian: Törpe denevér, Közönséges törpedenevér, Nycteris i kini. Irish Gaelic: Ialtóg fheascrach. Italian: Pipistrello nano. Latvian: Pundursikspārnis. Lithuanian: Šikšniukas nykštukas. Luxembourgish: Kleng Fliedermaus, Zwergfliedermaus. Macedonian: Мал лилјак, Dzudzest Liljak. Maltese: Pipistrell, Pipistrell Komuni. Montenegrin: Mali slijepi mišić. Norwegian: Tusseflaggermus, Dvergflaggermus. Polish: Karlik malutki. Portuguese: Morcego-anão. Rhaeto-Romance: Pipistrel nanin. Romanian: Liliacul pitic. Russian: Нетопырь-карлик [= Netopyr karlik]. Serbian: Обични сл[ij]епи мишић [= Obični sl[ij]epi mišić]. Scottish Gaelic: Ialtag fheasgarach. Slovak: Večernica hvízdavá, Večernica malá. Slovenian: Mali netopir. Swedish: Sydpipistrell, Pipistrell. Turkish: Cüce Yarasa. Ukrainian: Нетопир карлик, Нетопир малийНетопир пігмей [= Netopyr malyy, Netopir pihmey]. Welsh: Ystlum-lleiaf cyffredin.

Conservation Status:

Global Justification

The species is widespread and abundant, and there is no evidence of current significant population decline. Consequently, it is assessed as Least Concern (LC ver 3.1 (2001)) (Hutson *et al.*, 2008l; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008l; IUCN, 2009). 2004: LC ver 3.1 (2001) (Aulagnier and Benda, 2004a; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
In parts of the range there is deliberate persecution as people do not want thousands of bats roosting in their buildings. As a high proportion of colonies are found in buildings, the species may be particularly vulnerable to other anthropogenic factors, such as disturbance, timber treatment and building renovation (Battersby, 2005; Hutson *et al.*, 2008l; IUCN, 2009).

Sherwin *et al.* (2012: 174) indicate that the aerial hawking feeding style and the long-distance dispersal are the most important risk factors related to climatic change.

CONSERVATION ACTIONS:
Hutson *et al.* (2008l) [in IUCN (2009)] report that it is protected under national law in most range states. It is also protected under international law through the Bonn Convention (Eurobats) and Bern Convention in parts of its range where these apply and is included in Annex IV of the EU Habitats and Species Directive. It occurs in many protected areas. No specific conservation actions are known.

Adoption of bat-friendly practices in the construction and maintenance of buildings is a proposed action.

GENERAL DISTRIBUTION:
Pipistrellus pipistrellus is a widespread western Palaearctic species with a range extending from the British Isles through southern Scandinavia, much of Europe (including all the Mediterranean countries, but with the exception of northern Fennoscandia) to the Volga and Caucasus; and through parts of north-western Africa (mountainous areas of Morocco, Algeria and Tunisia, also in Cyrenaica in Libya) and south-west Asia to central and eastern Asia (China, India, Myanmar). Its detailed distribution, as distinct from that of the recently differentiated *P. pygmaeus*, is still to be established. It occurs from sea level to 2,000 m.

A dubious record from Taiwan by Kishida (1924) is rejected by Lin *et al.* (2002: 509). A record from Myanmar by Bates and Harrison (1997: 167) is rejected by Bates *et al.*, 2005: 220).

Native: Afghanistan; Albania; Algeria; Andorra; Armenia; Austria; Azerbaijan; Belarus; Belgium; Bosnia and Herzegovina; Bulgaria; China; Croatia; Cyprus (Benda *et al.*, 2007: 71); Czech Republic; Denmark; Estonia; Finland; France [Corse]; Georgia; Germany; Gibraltar; Greece [East Aegean Is., Kriti]; Holy Seat [Vatican City State]; Hungary; India (Jammu-Kashmir); Iran, Islamic Republic of; Ireland; Israel; Italy (Sardinia, Sicily); Jordan (Benda *et al.*, 2010b: 185), Kazakhstan; Latvia; Lebanon (Horáček *et al.*, 2008: 59); Libyan Arab Jamahiriya; Liechtenstein; Lithuania; Luxembourg; Macedonia, the former Yugoslav Republic of; Malta; Moldova (Bondarenko, 2007: 23); Monaco; Montenegro; Morocco (Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 361; Dbiba *et al.*, 2025: 7); Myanmar; Netherlands; Norway; Pakistan; Poland; Portugal; Romania; Russian Federation; San Marino; Serbia; Slovakia; Slovenia; Spain [Baleares]; Sweden; Switzerland; Taiwan, Province of China; Tunisia (Dalhoumi *et al.*, 2016b: 867); Turkey; Ukraine (Tyshchenko *et al.*, 2005: 181); United Kingdom.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

Other
Madej *et al.* (2012: 478) studied the skin structure and hair morphology of different body parts and found a number of areas with thin skin (wing and tail membrane) and other areas with thick skin (head and dorsum, abdomen, footpad). They also found that the density of the hairs was higher on the head than in the dorsal and ventral body parts. These differences might play a role for ectoparasites when choosing their preferred body region.

ECHOLOCATION:
The data for 47 animals from Greece are the following: F_{start}: 78.9 ± 15.79 kHz, F_{end}: 47.5 ± 1.43 kHz, F_{peak}: 48.6 ± 1.46 kHz, bandwidth: 6.5 ± 1.31 kHz, duration 5.7 ± 1.53 ms and interpulse interval: 94.9 ± 29.90 ms (Papadatou *et al.*, 2008b: 132).

Benda *et al.* (2010a: 163) report for 50 Moroccan specimens a starting frequency of 53.3 ± 4.6 (45.6 - 62.7) kHz, a maximum energy frequency of 47.9 ± 2.9 (42.9 - 51.8) kHz, an end frequency of 46.3 ± 3.0 (40.0 - 50.7) kHz, with a duration of 7.4 ± 1.7 (5.2 - 12.4) ms, and an inter-pulse interval of 123.9 ± 46.2 (73.4 - 250.1) ms.

Data presented by Walters *et al.* (2012: suppl.) for 47 calls by bats from France, Switzerland and the UK include: duration: 6.02 ± 2.10 ms, F_{max}: 58.06 ± 10.34 kHz, F_{min}: 44.77 ± 1.92 kHz, bandwidth: 13.29 ± 9.25 kHz, F_{peak}: 45.75 ± 2.03 kHz.

In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for 70 calls: F_{start}: 69.3 ± 14.8 (53.1 - 110.0) kHz, F_{end}: 48.4 ± 0.9 (46.8 - 50.5) kHz, F_{peak}: 51.2 ± 2.0 (48.2 - 57.9) kHz, duration: 5.7 ± 1.5 (2.8 - 8.0) ms, and Interpulse interval: 81.7 ± 22.2 (49.0 - 169.0) ms. For 54 Iranian calls, Benda *et al.* (2012a: 182) report: F_{start}: 57.1 ± 4.2 (50.2 - 60.8) kHz, F_{end}: 46.6 ± 2.2 (42.6 - 50.8) kHz, F_{peak}: 48.6 ± 2.4 (44.1 - 54.0) kHz, duration: 6.8 ± 1.5 (3.4 - 10.4) ms, and interpulse interval: 100.5 ± 26.5 (62.3 - 162.7) ms.

Götze *et al.* (2013: 61) indicate that frequency shifts occurring when *P. pipistrellus* specimens are flying together, are not linked with jamming avoidance, but with a switch from search calls to shorter approach calls, which have higher frequencies. The other bats are perceived as moving targets, hence the switch to the approach call.

In Morocco, Disca *et al.* (2014: 226) reported for "*Pipistrellus* cf. *pipistrellus*" a FM-QFC type of call with the following parameters: F_{start}: 75.5 ± 12.8 kHz, F_{end}: 47.7 ± 2.3 kHz, F_{peak}: 50.4 ± 2.4 kHz, $F_{QFC\text{-}peak}$: 49.9 ± 2.5 kHz, bandwidth: 27.8 ± 12.3 kHz, duration: 6.4 ± 1.1 ms.

Ait-Abdesselam *et al.* (2025: 40) reported an F_{max} of 47.72 ± 5.17 kHz for Algerian bats.

Molecular Biology:

Karyotype

Rushton (1970: 465) mentioned a diploid number (2*n*) of 42. Arslan and Zima (2014: 12) report 2*n* = 42-44, FNa = 48-50, FN = 52-54, a medium-sized (sub)metacentric X, and a dot-like acrocentric Y. The autosomal component contains three large metacentric, one small metacentric and 16/17 acrocentric pairs. However, they cannot exclude that some of the "aberrant" sets might represent *P. pygmaeus*.

Tolera *et al.* (2021: 127) reported the karyotype of Ethiopian bats with 2n = 36 and FN = 50. However, the identification as *Pipistrellus pipistrellus* seems highly unlikely.

Genetics

See Benda *et al.* (2004b), Hulva *et al.* (2004), Mayer *et al.* (2007), García-Mudarra *et al.* (2009). Batsleer *et al.* (2019: 172) analyses a fragment of the 16S rRNA, and found this to belong to two haplotypes, which clustered within a northern African clade, clearly differing from the European haplotypes.

Diet:

Benda *et al.* (2012a: 425 - 427) indicate that in Europe, *P. pipistrellus* mainly feeds on small swarming nematoceran Diptera, followed by Lepidoptera, Heteroptera and Hymenoptera. In the Middle East, the diet seems to be more variable and is dominated by smaller Coleoptera, Formicoidea, Heteroptera, smaller Lepidoptera, Ephemeroptera, Plecoptera, and Blattodea. In Iran, the most important food items are: Nematocera, Hymenoptera (Formicoidea), and Auchenorrhyncha.

Population:

Structure and Density

A widespread and abundant species, one of the most common bats in many parts of its range. Summer maternity colonies generally number 25 - 50 individuals, although colonies of as many as 200 have been recorded. In winter, it tends to occur singly or in small groups, although some very large groups have been recorded (e.g., up to 45,000 in caves in Romania and Slovakia) (Seamark, 2006d). Significant declines have been recorded in some European countries (e.g., Britain), although in Britain at least the trend may now have stabilised (Battersby, 2005). In Serbia, in the urban areas, *P. pipistrellus* has become less common due to displacement by *P. kuhlii* (M. Paunovic *pers. comm.*, 2007 in Hutson *et al.*, 2008l). The same is also reported from the Russian Federation.

Trend

2008: Stable (Hutson *et al.*, 2008l; IUCN, 2009).

Activity and behaviour:

Referring to amongst others Barlow and Jones (1997a,1997b), Smotherman *et al.* (2016: 537) describe the song-like structure for this species as simple syllable type in a basic motif. Singing occurs while flying.

Reproduction and ontogeny:

Ginther (1967: 580) mentioned that the embryo is more frequently located in the right uterine horn, whereas the Corpus luteum is about 50 % in the left ovary.

At birth, the young weights about 23.7 % of its mother's body mass (1.4 g versus 5.9 g), and its forearm length is about 35.6 % of that of its mother (11.4 versus 32.0 mm) (see Kurta and Kunz, 1987: 83).

PARASITES:
In Europe, Genov *et al.* (1992) reported the following Nematodes: *Molinostrongylus vespertilionis* Morosov and Spassky, 1961 (of which *P. pipistrellus* is the type host) and *M. alatus* (Ortlepp, 1932).

Benda *et al.* (2010b: 278) found the following ectoparasites on Jordanian *Pipistrellus pipistrellus*: Ticks: Argasidae: *Argas vespertilionis* (Latreille, 1802); mites (Macronyssidae): *Macronyssus* sp., *Steatonyssus periblepharus* Kolenati, 1858, *Parasteatonyssus hoogstraali* Keegan, 1956; bugs: Cimicidae: *Cacodmus vicinus* Keegan, 1956; bat flies: Nycteribiidae: *Basilia daganiae* Keegan, 1956; and fleas: Ischnopsyllidae sp. The latter might possibly belong to *Ischnopsyllus octactenus* (Kolenati, 1856), *I. dolosus* Dampf, 1912 or *I. consimilis* (Wahlgren, 1904) which were previously reported from *P. pipistrellus* from Turkey and Lebanon.

From Iran, Benda *et al.* (2012a: 428) reported the following ectoparasites: Ticks: Argasidae: *Argas vespertilionis* (Latreille, 1802), Ixodidae: *Dermacentor marginatus* (Sulzer, 1776), *Ixodes redikorzevi* Olenev, 1927; mites: Macronyssidae: *Steatonyssus* sp., Trombiculidae: *Schoutedenichia chilmirica* Kudrâšova, 1975; fleas: Ischnopsyllidae: *Ischnopsyllus octactenus* (Kolenati, 1856), Pulicidae: *Xenopsylla nuttalli* Ioff, 1930. From Azerbaijan, they mention another bat flea: *Ischnopsyllus dolosus* Dampf, 1912.

From Algeria, Bendjeddou *et al.* (2013: 325) reported the following parasites: *Cimex pipistrelli* Jenyns, 1839 (Hemiptera: Cimicidae) and *Ischnopsyllus octactenus* (Kolenati, 1856) (Siphonaptera: Ischnopsyllidae). Bendjeddou *et al.* (2017: 15) mentioned the following Heteroptera: *Cimex pipistrelli* Jenyns, 1839, *Cimex lectularius* Linnaeus, 1758 and *Cacodmus vicinus* Horváth, 1934.

The checklist of arthropod parasites of North African bats provided by Bendjeddou *et al.* (2023: 4 - 7) mentions the following species: Argasidae: *Carios vespertilionis* Latreille, 1802; Cicimidae: *Cacodmus vicinus* Horváth, 1934, *Cimex lectularius* Linnaeus, 1758, *Cimex pipistrelli* Jenyns, 1839; and Ischnopsyllidae: *Ischnopsyllus hispanicus* (Rothschild, 1898), *Ischnopsyllus octactenus* (Kolenati, 1856).

Beaucournu and Noblet (1985: 636) refer to Hůrka (1982) in plotting a record of *Basalia mediterranea* Hurka, 1970, parasitizing on *P. pipistrellus*.

VIRUSES:
Adenoviridae
Mastadenovirus
Reported from Germany by Kohl and Kurth (2014: 3111).

Bornaviridae
An unclassified genus belonging to this family was reported by Kohl and Kurth (2014: 3111) from France.

Coronaviridae
None of five Kenyan bats tested by Tao *et al.* (2017: Suppl.) tested positive for CoV.

Betacoronavirus
This virus was reported from the Netherlands by Kohl and Kurth (2014: 3112).

Herpesviridae
Betaherpesvirus
Reported by Kohl and Kurth (2014: 3113) from Germany.

Gammaherpesvirus
Reported by Kohl and Kurth (2014: 3113) from Germany.

Orthomyxoviridae
Despite sampling and testing of 44 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

Paramyxoviridae
An unassigned virus was reported from Germany by Kohl and Kurth (2014: 3113).

Reoviridae
Orthoreovirus
Kohl and Kurth (2014: 3113) reported this virus from Germany.

Rhabdoviridae
"Various European bat lyssaviridae" were reported from various European countries by Kohl and Kurth (2014: 3114).

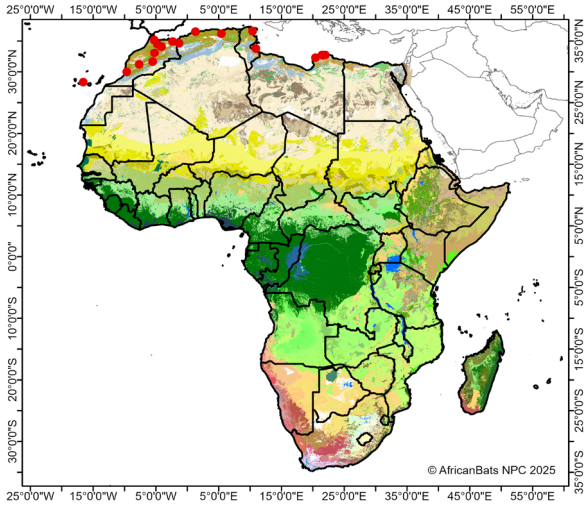

Figure 334. Distribution of *Pipistrellus (Pipistrellus) pipistrellus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Algeria, Canary Islands (Spain), Egypt, France, Libya, Morocco, Tunisia.

Pipistrellus (Pipistrellus) pygmaeus (Leach, 1825)

*1825. *Vespertilio Pygmæus* Leach, Zool. Journ., 1: 560. Type locality: United Kingdom: Chew valley. - Comments: Type locality: The original type locality was "England, Devonshire, near forest of Dartmoor, Spitchweek". The Neotype was collected in NE Somerset, Bath, Chew valley.

1999. *Pipistrellus pygmaeus:* Jones and Barratt, Bull. Zool. Nomencl., 56 (3): 182. Publication date: September 1999. (Name Combination).

2020. *Pipistrellus (Pipistrellus) pygmaeus:* Simmons and Cirranello, BatNames.org. (Name Combination).

TAXONOMY:
One of the most outspoken examples of cryptic species is formed by the "*Pipistrellus pipistrellus / pygmaeus*" species complex. Originally, both taxa were considered to represent one single species, but with the growing use of bat detectors, it became clear that two forms were present. In a first stage, these were called the "45 kHz phonic type" and the "55 kHz phonic type". Jones and van Parijs (1993) and Barratt *et al.* (1995) proved that two separate species were involved: *Pipistrellus pygmaeus* and *Pipistrellus pipistrellus*.

Based on López-Baucells *et al.* (2012), Disca *et al.* (2014: 211) include *P. pygmaeus* as a member of the Moroccan bat fauna, but they indicate that more prove (e.g., photos, detailed descriptions, echolocation data, …) would be welcome.

Herdina *et al.* (2014: 157) indicate that *P. pipistrellus* and *P. pygmaeus* specimens can be discriminated by measuring the projected length, height, and width of the baculum. Other morphological discrimination traits commonly used are "wing vein" pattern and shape and color of the penis, but these have not been validated on sets of genetically identified specimens.

COMMON NAMES:
Albanian: Pipistrel xhuxh. Armenian: Գաջաճ փոքրաչղջիկ. Azerbaijani: Kiçik şəbpərə. Basque: Pipistrelo mediterraneo. Belarusian: Нетапыр-пігмей. Bosnian: Patuljasti šišmiš. Breton: Pipistrell gorr. Bulgarian: Малко кафяво прилепче. Castilian (Spain): Murciélago pigmeo, Murciélago de Cabrera. Catalan (Spain): Pipistrel·la nana. Croatian: Močvarni patuljasti šišmiš. Czech: Netopýr nejmenší, Nedopír kařelný. Danish: Dværgflagermus. Dutch: Kleine dwergvleermuis. English: Midge Bat, Soprano Pipistrelle, Pygmy pipistrelle bat, 55 kHz pipistrelle, Mediterranean Lesser pipistrelle. Estonian: Pügmee-nahkhiir. Finnish: Kääpiölepakko. French: Pipistrelle soprane, Pipistrelle pygmée, le vespertilion pygmée. Frisian: Lytse dwerchflearmûs. Galician (Spain): Morcego anano. Georgian: პაწია ღამორი. German: Mückenfledermaus. Greek: Μικρονυχτερίδα. Hungarian: Szoprán törpedenevér. Irish Gaelic: Ialtóg shopránach. Italian: Pipistrello soprano, Pipistrello pigmeo, Pipistrello soprano. Latvian: Pigmejsikspārnis. Lithuanian: Šikšniukas mažylis. Luxembourgish: Méckefliedermaus. Macedonian: Џуџест лилјак, Kafeav Dzudzest Liljak. Maltese: Pipistrell Żgħir. Montenegrin: Patuljasti slijepi mišić. Norwegian: Dvergflaggermus. Polish: Karlik drobny. Portuguese: Morcego-pigmeu. Rhaeto-Romance: Pipistrel pigmeic, Pipistrel muschin.

Romanian: Liliacul pigmeu. Russian: Нетопырь малый (пигмей), Малый нетопырь [=Malyj Neopyr]. Serbian: Патуљасти сл[ij]епи мишић [= Patuljasti sl[ij]epi mišić]. Scottish Gaelic: Ialtag shopràn ach. Slovak: Večernica Leachova. Slovenian: Drobni netopir, Liliacul-pitic mediteranean. Swedish: Dvärgpipistrell, Dvärgfladdermus. Turkish: Akdeniz Cüce Yarasası. Ukrainian: Нетопир пігмей. Welsh: Ystlum-lleiaf soprano.

CONSERVATION STATUS:

Global Justification

The species is widespread and abundant, and there is no evidence of current significant population decline. Consequently, it is assessed as Least Concern (Benda *et al.*, 2016a).

Assessment History

Global

2016: LC ver. 3.1 (2001) (Benda *et al.*, 2016a).

Local

None known.

Legal Status

Benda *et al.* (2016a) report it is protected under national law in most range states. It is also protected under international law through the Bonn Convention (Eurobats) and Bern Convention in parts of its range where these apply and is included in Annex IV of the EU Habitats and Species Directive. It occurs in many protected areas.

MAJOR THREATS:

As maternity colonies tend to be found in buildings, the species may be vulnerable to anthropogenic factors, such as disturbance, timber treatment and building renovation (Battersby, 2005). However, this is not thought to be a major threat (Benda *et al.*, 2016a).

CONSERVATION ACTIONS:

Benda *et al.* (2016a) report that no specific conservation actions are known. They suggest that adoption of bat-friendly practices in the construction and maintenance of buildings is a proposed action. Although this species was only recently described, it is apparently widespread and abundant. However, further clarification of its distribution, population size and trend, habitat preferences, and ecology is required (Benda *et al.*, 2016a).

GENERAL DISTRIBUTION:

Native: Albania; Azerbaijan; Belarus; Belgium; Bosnia-Herzogovina; Bulgaria; Croatia; Cyprus; Czech Republic; Denmark; Estonia; Georgia; Germany; Great Britain; Greece; Iran; Ireland; Latvia; Lebanon (?); Moldova; Montenegro; Morocco (Dbiba *et al.*, 2025: 7); Portugal; Romania; Serbia; Slovakia; Spain; Sweden; Switzerland; Slovenia; The Netherlands; Turkey.

López-Baucells *et al.* (2012: 43) reported this species from the northern African Spanish enclave Ceuta, which is the first report of this species on the African continent.

POPULATION:

Structure and Density

Benda *et al.* (2016a) reports that *Pipistrellus pygmaeus* generally appears to be less abundant than *P. pipistrellus*, although it is nevertheless a widespread and abundant species. Summer colonies may be larger than *P. pipistrellus*, numbering up to 250 (or occasionally up to 3,000) individuals. It is not known if the species congregates in winter, or what size its winter colonies attain. Recent evidence of hybridisation with *P. pipistrellus* has been found in Central Europe by Sztencel-Jablonka and Bogdanowicz (2012).

Trends

2016: Unknown (Battersby, 2005).

VIRUSES:

Coronaviridae

Alphacoronavirus

Kohl and Kurth (2014: 3112) report this virus from German bats.

Orthomyxoviridae

Despite sampling and testing of 132 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

Pipistrellus (Pipistrellus) raceyi Bates, Ratrimomanarivo, Harrison and Goodman, 2006

*2006. *Pipistrellus raceyi* Bates, Ratrimomanarivo, Harrison and Goodman, Acta Chiropt., 8 (2): 301. Type locality: Madagascar: Fianarantsoa province: Kianjavato [21 22.84 S 44 40.49 E, 75 m]. Holotype: FMNH 185567: ad ♂, skull and alcoholic. Collected by: Fania H. Ratrimomanarivo and E.N. Rakotonandrasana; collection date: 22 May 2005; original number: RHF 1281. - Etymology: In honour of Prof. Paul A. Racey, Regius professor of natural history, University of Aberdeen, UK, in recognition of his longstanding commitment to the study and conservation of bats worldwide and in particular to his on-going programme of capacity building and bat research in Madagascar (see Bates *et al.*, 2006: 305).

2020. *Pipistrellus (Pipistrellus) raceyi:* Simmons and Cirranello, BatNames.org. (Current Combination).

TAXONOMY:
Goodman *et al.* (2015a: 992) suggest that the eastern population (specimens from the Provinces of Fianarantsoa and Toamasina) and the western population (specimens from Province of Toliara) might warrant separation.

See also Bates *et al.* (2006).

COMMON NAMES:
English: Racey's Pipistrelle Bat. French: Pipistrelle de Racey. German: Raceys Zwergfledermaus, Raceys Pipistrelle.

CONSERVATION STATUS:
Global Justification
This species is listed as Data Deficient (DD ver 3.1 (2001)) because although preliminary evidence suggests that it is widely distributed in lowland areas of parts of eastern and western Madagascar and it exists in a range of vegetation types, there are insufficient data on its habitat requirements and major threats (Jenkins *et al.*, 2008j; IUCN, 2009; Jenkins *et al.*, 2019a).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jenkins *et al.*, 2019a).
2008: DD ver 3.1 (2001) (Jenkins *et al.*, 2008j; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
No major threats are documented, but forest degradation may conceivably reduce availability of suitable foraging and roosting habitat in the west where this species presumably roosts in trees and appears to be associated with forest habitats (Jenkins *et al.*, 2008j; IUCN, 2009; Jenkins *et al.*, 2019a).

CONSERVATION ACTIONS:
Jenkins *et al.* (2008j) [in IUCN (2009)] and Jenkins *et al.* (2019a) report that even though this species roosts synanthropically in the east and may therefore be expected to be relatively common given the abundance of suitable roosting sites, it is only known from four locations across Madagascar despite the large survey effort on Malagasy bats in recent years. Of the four known localities, all receive some form of active forest management, and it is expected that deforestation at these sites has been and will be less than for non-protected forest. Further studies of this species are needed to investigate why it appears to be forest-dependent in the west but not in the east of its range.

GENERAL DISTRIBUTION:
Pipistrellus raceyi is an endemic species to Madagascar that is currently known from four localities (Bates *et al.*, 2006), two in the west (Mikea forest and Kirindy CFPF) and two in the east (Kianjavato and Tampolo forests), all below 80 m elevation (from 16 - 70 m asl.).

Native: Madagascar (Bates *et al.*, 2006).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
See Bates *et al.* (2006).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
See Bates *et al.* (2006).

DETAILED MORPHOLOGY:
Other
For a description of the crania, teeth, ears and tragus see Bates *et al.* (2006).

HABITAT:
P. raceyi occurs In humid forest and agricultural areas in the east, and in intact and degraded dry forest in the west (Bates *et al.*, 2006; Garbutt, 2022: 102).

ROOST:
Synanthropic structures and vegetation for the typical roosting sites for this species on Madagascar according to Wilkinson *et al.* (2012: 160).

DIET:
Rakotondramanana *et al.* (2015: 77) reported the following volume percentages of food items: Coleoptera: 27.8 ± 20.00; Hymenoptera: 12.5 ± 17.15; Lepidoptera: 26.1 ± 23.05; Trichoptera: 1.9 ± 4.80; Isoptera: 30.0 ± 40.71; Homoptera: 1.5 ± 3.31; Arachnida: 0.1 ± 0.24. Expressed as frequency percentages, the values are: Coleoptera: 78.9 ± 29.48; Hymenoptera: 47.8 ± 41.81; Lepidoptera: 65.6 ± 44.35; Trichoptera: 10.0 ± 23.01; Isoptera: 37.8 ± 48.94; Homoptera: 12.2 ± 27.56; Arachnida: 1.7 ± 4.71. Based on the faeces of three animals, Rasoanoro *et al.* (2015: 64) found the following volume percentages: Aranea: 6.8 ± 1.47, Coleoptera: 32.5 ± 1.36, Diptera: 28.9 ± 4.15, Homoptera: 11.7 ± 2.18, Hymenoptera: 3.9 ± 2.20, and Lepidoptera: 16.3 ± 1.95.

PREDATORS:
Razakaratrimo *et al.* (2019: 114) mention the bat hawk (*Macheiramphus alcinus anderssoni* (Gurney, 1866)).

POPULATION:
Structure and Density
This recently described species is currently known only from 15 specimens (Bates *et al.*, 2006); however, with further survey work, it may be shown to more common (Jenkins *et al.*, 2008j; IUCN, 2009; Jenkins *et al.*, 2019a).

Trend
2018: Unknown (Jenkins *et al.*, 2019a). 2008: Unknown (Jenkins *et al.*, 2008j; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
See Bates *et al.* (2006).

VIRUSES:
Paramyxoviridae
Wilkinson *et al.* (2012: 160) tested 1 individuals from the Madagascar using RT-PCR specific for *Respirovirus*/*Morbillivirus*/*Henipahvirus* (RMH) and *Paramyxovirinae* (PMV) and found 0 positive results for viral nucleic acids.

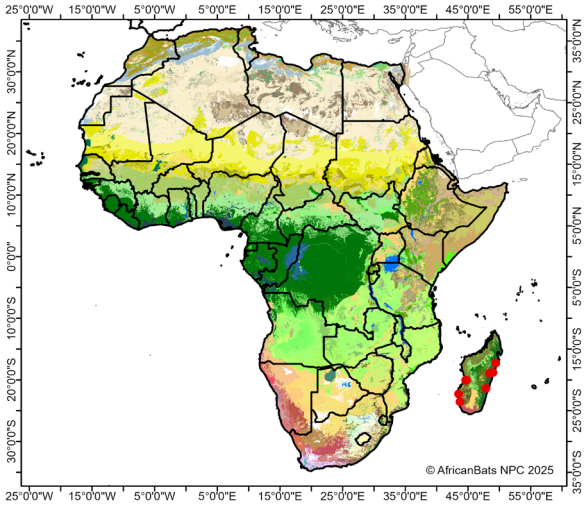

Figure 335. Distribution of *Pipistrellus (Pipistrellus) raceyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Pipistrellus (Pipistrellus) rusticus (Tomes, 1861)

*1861. *Scotophilus rusticus* Tomes, Proc. zool. Soc. Lond., 1861, I: 31, 35. Publication date: May 1861. Type locality: Namibia: Ovamboland: Olifants Vlei [18 00 S 17 30 E]. [Goto Description]. Lectotype: NHMUK 1907.1.1.419: ad ♀, skin and skull. Collected by: 1 Anderson; original number: 176a. Paralectotype: NHMUK 1907.1.1.420: ad, skin and skull. Collected by: 1 Anderson; collection date: November 1899; original number: 176b. - Etymology: Lanza *et al.* (2015: 441) mention "The masculine Latin adjective *rùsticus* actually means "rural, country" i. e. farmland-loving. Tomes (1861b: 35) apparently used this adjective erroneously instead of the masculine Latin adjective *robiginosus* "rusty", referring to the fur dorsal colour of the species: 'On the upper surface it is dark brown at the roots, with the terminal half light cinnamon-brown […].' ".
1913. *Pipistrellus rusticus:* Roberts, Ann. Transv. Mus., 4: 67. (Name Combination).
1923. *Pipistrellus marrensis* Thomas and Hinton, Proc. zool. Soc. Lond., 1923, II: 249. Publication date: 6 July 1923. Type locality: Sudan: foothills S Jebel Marra: Darfur [12 54 N 24 21 E, 4 000 ft]. [Goto Description]. Holotype: NHMUK 1923.1.1.15: ad ♂. Collected by: Captain/Rear-Admiral Hubert Lynes and Willoughby P. Lowe; collection date: 3 April 1924; original number: 633.
1934. *Eptesicops rusticus:* Shortridge, Mammals of South West Africa, 60. (Name Combination).
1953. *Pipistrellus (Pipistrellus) rusticus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination, Current Combination).
1959. *Pipistrellus (Eptesicops) rusticus:* Anonymus, Koedoe, 3: 58. (Name Combination).
1968. *Pipistrellus (Pipistrellus) rusticus rusticus:* Smithers, A check list and atlas of the mammals of Botswana (Africa), ???. (Name Combination).
1971. *Pipistrellus [(Pipistrellus)] rusticus marrensis:* Hayman and Hill, Mammals of Africa: Chiroptera, 40. (Name Combination).
1975. *P[ipistrellus] r[usticus] rusticus:* Wilson, Mus. Mem., Salisbury, 5: 141. (Name Combination).
2019. *Pipistellus rusticus:* Hranac, Marshall, Monadjem and Hayman, Epidemics, Suppl. Publication date: 16 November 2019. (Lapsus).
? *Pipistrellus rusticus marrensis:* (Name Combination).
? *Pipistrellus rusticus phasma:* (Name Combination).
? *Pipistrellus rusticus rusticus:* (Name Combination).

TAXONOMY:



Figure 336. A male *Pipistrellus (Pipistrellus) rusticus* (TM 48130) caught at Makalali-GR, Limpopo, South Africa.

See Simmons (2005).

COMMON NAMES:
Afrikaans: Roeskleurvlermuis. Chinese: 锈色伏翼. Czech: netopýr damarský. English: Rusty Bat, Rusty Pipistrelle Bat, Rusty Pipistrelle. French: Pipistrelle rustique, Pipistrelle rouille. German: Rostfarbene Zwergfledermaus, Rostfarbene Pipistrelle. Italian: Pipistrèllo rugginóso.

ETYMOLOGY OF COMMON NAME:
The colloquial name refers to the rusty colour of their fur (Taylor, 2005).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008am; IUCN, 2009; Monadjem *et al.*, 2017cx).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Pipistrellus rusticus* (Monadjem *et al.*, 2017cx). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008am; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004ao; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016r). 2004: NT ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Jacobs *et al.*, 2008am; IUCN, 2009; Monadjem *et al.*, 2017cx).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008am) [in IUCN (2009)] and Monadjem *et al.* (2017cx) report that this species has been recorded from Mole National Park in Ghana (Grubb *et al.*, 1998). No direct conservation measures are currently needed for this species as a whole.

GENERAL DISTRIBUTION:
Pipistrellus rusticus has been widely, but patchily, recorded throughout much of sub-Saharan Africa. It is distributed from Senegal and The Gambia in the west, with easternmost records from Ethiopia close to the Somalia border area. It is found as far south as northern South Africa (where its distribution is mostly affected by precipitation seasonality; Babiker Salata (2012: 49)) and central Namibia. Other than records from southern Chad and northern Central African Republic, the species has not been recorded in Central Africa.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 842,481 km^2.

Fahr (2007a: 105) assigns the Liberian *rusticus* specimens tentatively to *hesperidus*.

Native: Angola (Taylor *et al.*, 2018b: 60); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 572); Burkina Faso (Kangoyé *et al.*, 2015a: 621); Central African Republic (Kock *et al.*, 2002b: 87); Chad; Eswatini (Monadjem *et al.*, 2021: 5); Ethiopia; Gambia (Kock *et al.*, 2002b: 87); Ghana; Kenya; Malawi (Ansell and Dowsett, 1988: 40; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 572); Mozambique; Namibia (Monadjem *et al.*, 2010d: 572); Nigeria; Senegal; South Africa (Monadjem *et al.*, 2010d: 572); Sudan (Kock *et al.*, 2002b: 87); Tanzania (Kock *et al.*, 2002b: 87); Uganda; Zambia (Ansell, 1969; Ansell, 1973; Monadjem *et al.*, 2010d: 572); Zimbabwe (Monadjem *et al.*, 2010d: 572).

DETAILED MORPHOLOGY:
Penis
Fasel *et al.* (2020: 1394) indicated that the penis if *Pipistrellus rusticus* could easily be separated from those of the five other pipistrelloid species they examined by means of its robust width, which is approximately 40 % of its length (in the other species this is less than 35 %). Its dorsal side is completely covered by short hairs, and the proximal section is violet in colour, which is also the case for the central line that ends at the distal end. In erect status, the penis is violet in colour (in the other species it is red) and curved.

Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

ECHOLOCATION:
In Waterberg, South Africa, Taylor *et al.* (2013b: 17) recorded the following parameters for 1 call: F_{max}: 62.1 kHz, F_{min}: 55.3 kHz, F_{knee}: 57.6 kHz, F_{char}: 55.4 kHz, duration: 3.1 ms. 19 calls recorded at Mapungubwe National Park (RSA) by Parker and Bernard (2018: 57) had the following features: F_{char}: 55.20 ± 0.92 kHz, F_{max}: 64.41 ± 3.75 kHz, F_{min}: 54.00 ± 1.05 kHz, F_{knee}: 57.68 ± 1.34 kHz, duration: 4.70 ± 1.59 ms, and 6.11 ± 3.12 calls/sec.

Weier *et al.* (2020: Suppl.) reported on 11 calls from the Okavango River Basin with the following characteristics: F_{max}: 59.44 ± 5.07 kHz, F_{min}: 52.34 ± 0.99 kHz, F_{knee}: 53.55 ± 1.63 kHz, F_{char}: 52.87 ± 1.03 kHz, slope: 15.95 ± 30.29 OPS, duration: 3.24 ± 1.27 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 9 *Pipistrellus rusticus* calls from the Kruger Park (RSA): F_{min}: 50.8 ± 2.9 (46.8 55.2) kHz, Duration: 2.4 ± 0.4 (2.1 3.1) ms, F_{max}: 70.3 ± 7.0 (62.7 82.0) kHz, F_{knee}: 48.2 ± 16.0 (5.9 57.9) kHz, F_{char}: 51.9 ± 2.4 (48.5 55.5) kHz.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 55.7 kHz and duration: 4.5 ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

56 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 55 kHz, F_{max}: 62 kHz, F_{char}: 55 kHz, F_{knee}: 58 kHz and duration 3 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 55) reported F_{char}: 55.20 ± 0.92 kHz, F_{max}: 64.41 ± 3.75 kHz and F_{min}: 54.00 ± 1.05 kHz.

For 14 calls from 2 *Pipistrellus rusticus* bats from Telperion Nature Reserve (RSA), De Jong *et al.* (2025: 322) reported the following parameters: F_{char}: 48.66 ± 0.83 kHz, F_{knee}: 52.76 ± 2.26 kHz, F_{min}: 48.26 ± 1.66 kHz, F_{max}: 79.26 ± 8.95 kHz, Bandwidth: 31.00 ± 8.26 kHz, Duration: 6.40 ± 1.84 ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 55.20 ± 0.92 kHz, F_{max}: 64.41 ± 3.75 kHz, F_{min}: 54.00 ± 1.05 kHz.

From Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 18 calls: Interpulse interval: 69.9 ± 13.5 (44.2 - 98.7) ms; F_{max}: 61.5 ± 4.5 (57.3 - 72.1) kHz; Start slope: -23.9 ± 4.3 (-12.0 - -29.3) kHz/ms; End slope: -7.2 ± 3.8 (-1.7 - -9.8) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.3 - 0.6) ms.

MOLECULAR BIOLOGY:
Karyotype
Both Rautenbach *et al.* (1993) and Kearney *et al.* (2002) reported 2*n* = 42, FN = 50, BA = 10, and an acrocentric Y chromosome, for specimens from South Africa. However, while Rautenbach *et al.* (1993) reported a submetacentric X chromosome, Kearney *et al.* (2002) reported a metacentric X chromosome. GTG banding identified that *P. hesperidus* and *P. rusticus* share the same Robertsonian fusion of chromosomes 11/12 (Kearney *et al.*, 2002).

HABITAT:
In southern Africa, *P. rusticus* occurs in Savanna habitats (84 %; Cooper-Bohannon *et al.*, 2016: Table S2).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 59 minutes, and the digestibility rate about 83.0 %.

PREDATORS:
Malan *et al.* (2022: 167) reported ten individuals found in pellets from a bat hawk pair (*Macheiramphus alcinus* Bonaparte, 1850 from the RSA.

POPULATION:
Structure and Density
This species is locally common (Jacobs *et al.*, 2008am; IUCN, 2009; Monadjem *et al.*, 2017cx).

Trend
2016: Unknown (Monadjem *et al.*, 2017cx).
2008: Unknown (Jacobs *et al.*, 2008am; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
P. rusticus displays a clear disassociation between male and female gamete production (van der Merwe and Mostert, 2005: 45). Spermatogenesis occurs during summer, and by late autumn the testes have regressed and the caudae epididymidis are full of stored spermatozoa (van der Merwe and Rautenbach, 1990). Mating is initiated in autumn, and

spermatozoa from these inseminations are stored throughout the winter in the uteri of females (van der Merwe and Rautenbach, 1990; van der Merwe, 1994). Ovulation occurs late in winter to early spring and the released ova are fertilized by the spermatozoa stored within the female (van der Merwe and Mostert, 2005: 45).

van der Merwe and Rautenbach (1990: 538) found that 1 to 5 embryos might be present, but a maximum of two become implanted. The other embryos (up to morula stage) are resorbed (p. 540).

P. rusticus are seasonally monoestrous breeders and normally give birth to twins during the middle of November (van der Merwe and Rautenbach, 1990: 539; van der Merwe, 1994). However, occasional singletons have been recorded by van der Merwe and Rautenbach (1990). The uterus is bicornuate and a single foetus is carried in each of the uterine horns (van der Merwe and Rautenbach, 1990). *P. rusticus* is unique, in that although implantation is superficial, the amnion is formed by means of cavitation (van der Merwe, 1994). According to van der Merwe and Rautenbach (1990), embryonic development seems to be retarded just after implantation.
van der Merwe and Mostert (2005) investigated the reproductive pattern of female *P. rusticus* in South Africa by means of a histological examination of the ovarian follicles as well as early embryonic development. Female *P. rusticus* are seasonal monestrous breeders, initiating copulation in mid-autumn (April), storing sperm until the time of ovulation in late winter (August), and giving birth to twins in late spring (November). The period April until mid-August was characterized by sperm storage and increased follicular development. During mid-August the females ovulate, and excess sperm was discarded. Females released between three and five ova, while a maximum of two embryos implanted successfully. Only a single embryo implanted per uterine horn. Embryo movement through the Fallopian tubes appeared to be a rapid process. Redundant embryos were resorbed before implantation. The period from the end of August until mid-November was marked by Pregnancy. Females invariably carried twins (one foetus in each uterine horn). Large-scale follicle atresion, and very low levels of follicle development, characterized the period end of August until March. High incidences of polyovular follicles were recorded for all months of the year. No obvious form of reproductive asymmetry was recorded in *P. rusticus* (van der Merwe and Mostert, 2005).

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births taking place in November.

MATING:
For Northern Transvaal (RSA), van der Merwe and Rautenbach (1990: 538) indicate that copulation was initiated during April, and ovulation and fertilization takes place in the second half of August.

PARASITES:
HEMIPTERA
Cicimidae
Kock *et al.* (1998b: 236, 137) reported *Cacodmus sparsilis* Rothschild, 1914 and *Cacodmus villosus* (Stål, 1855).

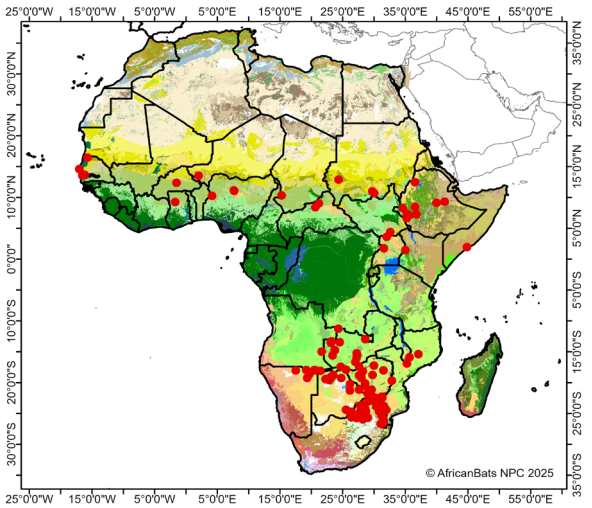

Figure 337. Distribution of *Pipistrellus (Pipistrellus) rusticus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Burkina Faso, Cameroon, Central African Republic, Egypt, Eswatini, Ethiopia, Ghana, Kenya, Malawi, Mozambique, Namibia, Niger, Nigeria, Senegal, Somalia, South Africa, South Sudan, Sudan, The Gambia, Uganda, Zambia, Zimbabwe.

Pipistrellus (Pipistrellus) simandouensis Monadjem, Richards, Decher and Hutterer, 2020

*2020. *Pipistrellus simandouensis* Monadjem, Richards, Decher and Hutterer, Zool. J. Linn. Soc., 191 (2): 556, 559, figs 4A-B, 5 - 9. Publication date: 4 September 2020. Type locality: Guinea: N'Zérékoré region: Beyla prefecture: Whiskey 1 [08 32 56 N 08 53 57 W, 950 m]. Holotype: ZFMK MAM-2008.0302: ad ♂, skull and alcoholic. Collected by: Jan Decher *et al.*; collection date: 25 February 2008; original number: JD 614. Paratype: ZFMK MAM-2008.0300: ad ♀. Collected by: Jan Decher *et al.*; collection date: 8 March 2008; original number: JD 656. Paratype: ZFMK MAM-2008.0301: ad ♂. Collected by: Jan Decher *et al.*; collection

date: 9 March 2008; original number: JD 661. - Etymology: Referring to the region where the type specimen was collected: the Simandou mountain range in eastern Guinea (Monadjem *et al.*, 2020d: 562).

? *Pipistrellus (Pipistrellus) simandouensis:* (Current Combination).

? *Pipistrellus cf. grandidieri:* (Name Combination).

TAXONOMY:
Based on cyt-*b* analyses and morphologic data, Monadjem *et al.* (2020d: 565) recognized the West African specimens formerly included in "*Pipistrellus grandidieri*" as a separate species.

COMMON NAMES:
English: Simandou serotine

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Monadjem *et al.* (2020d: 563) indicate that this species is only known from two localities: Mount Nimba (Liberia) and the Simandou Range (Guinea). Specimens from Fouta Djallon might belong to this species, but genetic confirmation is still required.

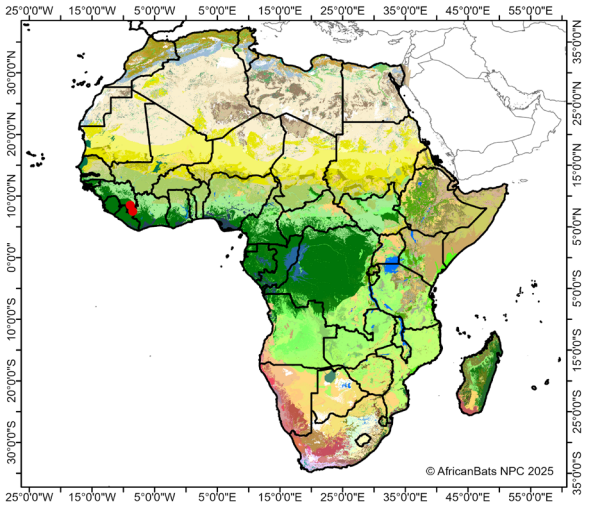

Figure 338. Distribution of *Pipistrellus (Pipistrellus) simandouensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Guinea, Liberia.

Pipistrellus (Pipistrellus) sp. aff. kuhlii Kuhl, 1817

*2001. *Pipistrellus cf kuhlii* Volleth, Bronner, Göpfert, Heller, von Helversen and Yong, Chromosome Res., 9 (1): 26. (Current Combination).

? *Pipistrellus (Pipistrellus) sp_aff_kuhlii*

TAXONOMY:
Volleth *et al.* (2001: 25) report a *Pipistrellus kuhlii*-like species from Madagascar, which they separated from the European *Pipistrellus* based on a different diploid chromosome number. This form might possibly be conspecific with *Pipistrellus hesperidus* Temminck, 1840, since Bates *et al.* (2006: 299) mention *P. hesperidus* from Madagascar.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

Genus ***Scotoecus*** Thomas, 1901

*1901. *Scotœcus* Thomas, Ann. Mag. nat. Hist., ser 7, 7 (39): 263. Publication date: 1 March 1901 [Goto Description]. - Comments: Type species: *Scotophilus albofuscus* Thomas, 1890. - Etymology: From the Greek "*σκόοτος*", meaning darkness and "*όικέω*", meaning to dwell (see Palmer, 1904: 627).

1917. *Scotæcus:* Thomas, Ann. Mag. nat. Hist., ser 8, 19 (111): 280. (Lapsus).

? *Scotoecus sp.*
? *Scotoecus sp. DMR-2017*
? *Scotoecus sp. IVK-2011*
? *Scotoecus:* (Current Spelling).

TAXONOMY:
Scotoecus has been treated as a subgenus of *Nycticeius* (Ellerman *et al.*, 1953; Hayman and Hill, 1971), but more often as a full genus (Allen, 1939a; Rosevear, 1965; Kock, 1969a; Hill, 1974b; Koopman, 1975, 1978; Corbet and Hill, 1980; Swanepoel *et al.*, 1980; Honacki *et al.*, 1982). Of the two (Honacki *et al.*, 1982) or three (Corbet and Hill, 1980) recognized African species only *albofuscus* occurs in Southern Africa, having been recorded from a single locality in Mozambique.

Bronner *et al.* (2003) report the light-winged lesser house bat (*Scotoecus albofuscus*) in South Africa. This represents a significant extension in the known ranges of both species and testifies to the need for more intensive field surveys targeting poorly known taxa. Cotterill (2001d) also recorded *Scotoecus albigula* and *S. hindei* from Zinave, Mozambique, based on the re-identification of two museum specimens originally assigned to *Scotophilus viridis*. Compared with the light-winged *albofuscus*, species identification of the dark-winged taxa of *Scotoecus* (*albigula, hindei, hirundo, falabae*) is more complicated. Indeed, Koopman (1993a) included all these taxa in *S. hirundo*. A study of cranial variation involving a small sample of Malawian specimens (Taylor and van der Merwe (1998) revealed that *hindei, hirundo* and *albigula* are distinguishable on morphometric grounds, with *albigula* and *hindei* apparently having larger canines and cheekteeth (as well as larger skulls) than *hirundo*, while *albigula* and *hindei* differ from each other in skull proportions. However, we provisionally retain these within *S. hirundo*, pending a broader study of the dark-winged forms including a larger sample of specimens from across the range.

Benda *et al.* (2025: 92) reiterate that the taxonomy of the dark-winged species of the genus Scotoecus remains unresolved.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Scotoecus*: ***albigula*** Thomas, 1909; ***albofuscus*** (Thomas, 1890); ***hindei*** Thomas, 1901; ***hirundo*** (de Winton, 1899); *pallidus* (Dobson, 1876) – Pakistan, northern India (Simmons, 2005: 465). Additionally, there is also the extinct ***†olduvensis*** Gunnell, Butler, Greenwood and Simmons, 2015.

COMMON NAMES:
Czech: vlaštovčí netopýři. English: Lesser House Bats, House Bats. French: Scotoèques, Chauves-souris des maisons. German: Kleine Hausfledermäuse. Italian: Scotoèchi.

GENERAL DISTRIBUTION:
Monadjem *et al.*, 2010d could not distinguish between *S. hindei* and *S. albigula* therefore they were combined for the distribution being recorded from Angola; Congo (Democratic Republic of the); Malawi; Mozambique; Zambia.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Patterson and Webala (2012: 43) indicate that male *Scotoecus* can easily be distinguished from any other Vespertlionid by the large size of its penis.

HABITS:
Rainho *et al.* (2023: 7) assigned the *Scotoecus* bats in Meru county (Kenya) to a medium-to-high flying bats guild occurring at altitudes between 3 and 15 m.

VIRUSES:
Coronaviridae
None of the 24 *Scotoecus* specimens tested by Tao *et al.* (2017: Suppl.) in Kenya were positive for CoV.

Alphacoronavirus
Tong *et al.* (2009) identified coronavirus RNA from the fecal material of *Scotoecus* spp.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Mozambique, South Sudan, Tanzania, Uganda.

Scotoecus albigula (Thomas, 1909)

*1909. *Scotœcus albigula* Thomas, Ann. Mag. nat. Hist., ser 8, 4 (24): 544. Publication date: 1 December 1909. Type locality: Kenya: Mount Elgon: Kirui [04 43 S 39 13 E, 6 000 ft]. [Goto Description]. Holotype: NHMUK 1910.4.1.24: ad ♂. Collected by: Robert ("Robin") Kemp Jr. Collection date: 5 September 1909; original number: 200. Formerly Rudd Collection. - Comments: Type locality coordinates mentioned as 00 50 N 34 40 E by Thorn *et al.* (2009: 58). - Etymology: From the feminine Latin adjective *àlba*, meaning "white" and the feminine Latin substantive *gùla*, meaning "throat", referring to the colour of the throat fur (see Lanza *et al.*, 2015: 460).

2010. *Scotoecus hindei/albigula:* Monadjem, Taylor, Cotterill and Schoeman, Bats of Southern and Central Africa. A biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, 510.
? *Nycticeius (Scotoecus) hirundo albigula:* (Name Combination).
? *Scotoecus albigula:* (Current Combination, Current Spelling).
? *Scotoecus hindei albigula:* (Name Combination).
? *Scotoecus hirundo albigula:* (Name Combination).

TAXONOMY:
Considered a subspecies of *hindei* by Hill (1974b: 182), and Thorn and Kerbis Peterhans (2009: 58). Included in *hirundo* by Koopman (1993a: 226), but considered a valid species by Ansell and Dowsett (1988: 44), Simmons (2005).

COMMON NAMES:
Czech: netopýr bělohrdlý. English: White-throated Lesser House Bat, White-bellied Lesser House Bat. French: Scotoèque à gorge blanche. German: Weisskehl-Hausfledermaus. Italian: Scotoèco golabiànca. Tshokwe (Angola): Kafukufuku.

CONSERVATION STATUS:
Global Justification
Scotoecus albigula was included in *Scotoecus hirundo* by Jacobs *et al.* (2008af) in IUCN (2009) for the global assessment. Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008af; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) [assessed as part of *Scotoecus hirundo*] (Jacobs *et al.*, 2008af; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs and Cotterill, 2004c; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
While the threats to this species are not well known, it is presumed not to have any major threats in view of the species wide distribution in habitats that are not rapidly declining throughout much of its recorded range (Jacobs *et al.*, 2008af; IUCN, 2009).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008af) [in IUCN (2009)] report that further studies are needed into the natural history and possible threats to this poorly known species.

GENERAL DISTRIBUTION:
Native: Angola; Kenya; Malawi; Mozambique (Monadjem *et al.*, 2010c: 384 as *S. hindei/albigula*); Somalia; Uganda; Zambia.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
See Taylor *et al.* (2005).

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 89 minutes, and the digestibility rate about 78.5 %.

POPULATION:
Structure and Density
It is very rarely recorded, and there is little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008af; IUCN, 2009).

Trend
2008: Unknown (Jacobs *et al.*, 2008af; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Happold and Happold (1990b: 567) reported births in Malawi to take place early in the wet season.

PARASITES:
HEMIPTERA
Cimicidae
Kock *et al.* (1998b: 237) reported *Cacodmus sparsilis* Rothschild, 1914 on bats from Malawi.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Kenya, Malawi, Mozambique, Somalia, Tanzania, Uganda, Zambia.

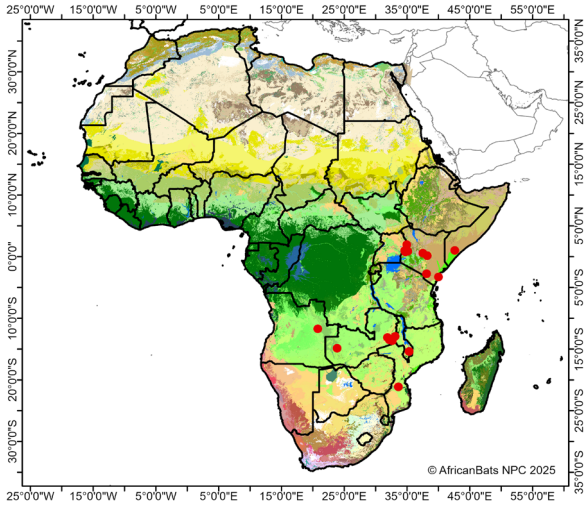

Figure 339. Distribution of *Scotoecus albigula*.

Scotoecus albofuscus (Thomas, 1890)

*1890. *Scotophilus albofuscus* Thomas, Ann. Mus. civ. Stor. nat. Genova, ser 2a, (OS 29) 9: 84. Publication date: 3 February 1890. Type locality: The Gambia: Bathurst [=Banjul] [13 28 N 16 39 W]. [Goto Description]. Holotype: NHMUK 1889.12.12.2: ad ♂, alcoholic (skull not removed). Collected by: Dr. Percy John Rendall.

1917. *Scotoecus woodi* Thomas, Ann. Mag. nat. Hist., ser 8, 19 (111): 280. Publication date: 1 March 1917. Type locality: Malawi: Shiré valley: Chiromo [16 32 S 35 09 E, 200 ft]. [Goto Description]. Holotype: NHMUK 1917.2.1.1: ad ♂. Collected by: Rodney Carrington Wood Esq. Collection date: 2 October 1916; original number: 173. Presented/Donated by: Rodney Carrington Wood Esq.

? *Scotoecus albofuscus albofuscus:* (Name Combination).

? *Scotoecus albofuscus woodi:* (Name Combination).

? *Scotoecus albofuscus:* (Name Combination, Current Combination).

TAXONOMY:

See Simmons (2005).

COMMON NAMES:

Afrikaans: Thomas se vlermuis, Thomas-vlermuis. Chinese: 淡翼宽吻. Czech: netopýr gambiánský. English: Thomas' House Bat, Light-winged Lesser House Bat, Thomas's Lesser House Bat. French: Scotoèque à ailes pâles, Scotophile du crépuscule, Chauve-souris de Thomas. German: Weißflügel-Hausfledermaus. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego pequeno das casas.

CONSERVATION STATUS:

Global Justification

Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Jacobs, 2008l; IUCN, 2009; Jacobs, 2019b).

Assessment History

Global

2018: DD ver 3.1 (2001) (Jacobs, 2019b). 2008: DD ver 3.1 (2001) (Jacobs, 2008l; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs, 2004h; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: NT D2 ver 3.1 (2001) (Richards *et al.*, 2016f). 2004: VU D2 ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

The threats to this species are not known (Jacobs, 2008l; IUCN, 2009; Jacobs, 2019b).

CONSERVATION ACTIONS:

Jacobs (2008l) [in IUCN (2009)] and Jacobs (2019b) reports that there appear to be no direct conservation measures in place. It has been recorded from Zinave National Park on the Save River in Mozambique, and presumably is present in additional protected areas. Further studies are needed into the distribution, natural history and possible threats to this widespread but seemingly very poorly known species.

GENERAL DISTRIBUTION:

Scotoecus albofuscus has been widely, but patchily recorded over much of West Africa and East Africa, with some records from Central Africa. It ranges from The Gambia and Senegal in the west, through West Africa to eastern Nigeria, it is then distributed from northern Uganda and southern Kenya, through Tanzania, southeastern Democratic Republic of the Congo,

southern Malawi, Mozambique and southeastern South Africa. The range is poorly known, and the species might be more widespread.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 626); Cameroon (Waghiiwimbom *et al.*, 2019b: 6), Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 573); Côte d'Ivoire; Gambia; Ghana; Kenya; Malawi (Happold and Happold, 1997b: 819; Cotterill, 2001d; Monadjem *et al.*, 2010d: 573); Mozambique (Cotterill, 2001d; Monadjem *et al.*, 2010d: 573); Nigeria; Senegal; Sierra Leone; South Africa (Kearney and Taylor, 1997: 53; Monadjem *et al.*, 2010d: 573); Sudan; Tanzania; Uganda (Kityo and Kerbis, 1996: 62); Zambia (Monadjem *et al.*, 2010d: 573).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 39.3 kHz and duration: 3.3 ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 58 minutes, and the digestibility rate about 83.0 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs, 2008l; IUCN, 2009; Jacobs, 2019b).

Trend
2018: Unknown (Jacobs, 2019b). 2008: Unknown (Jacobs, 2008l; IUCN, 2009).

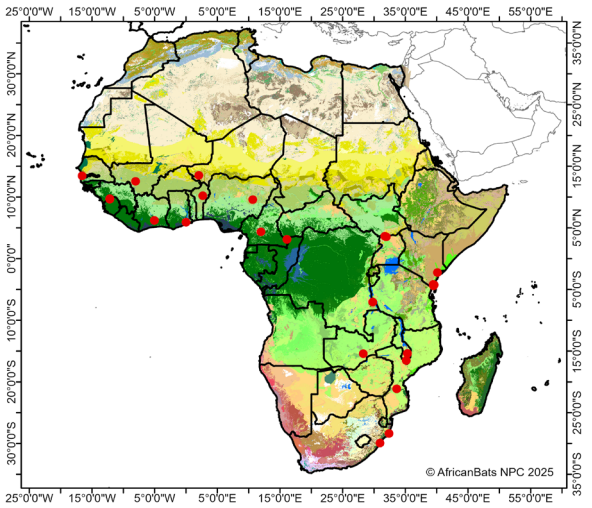

Figure 340. Distribution of *Scotoecus albofuscus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Cameroon, Central African Republic, Congo (Democratic Republic of the), Côte d'Ivoire, Ghana, Kenya, Malawi, Mali, Mozambique, Niger, Nigeria, Sierra Leone, South Africa, Tanzania, The Gambia, Uganda, Zambia.

Scotoecus hindei (Thomas, 1901)

*1901. *Scotœcus Hindei* Thomas, Ann. Mag. nat. Hist., ser 7, 7 (39): 264. Publication date: 1 March 1901. Type locality: Kenya: Kitui [01 22 S 38 01 E, 3 500 ft]. [Goto Description]. Holotype: NHMUK 1901.2.5.1: ♂. Collected by: Dr. Sidney Langford Hinde; collection date: 26 November 1900; original number: 63. - Etymology: In honour of Sidney Langford Hinde (1863 - 1931), English Medical Officer of the Interior in the former British East Africa, Captain in the Congo Free State Forces, Provincial Commissioner in Kenya, naturalist and collector of the type specimen (see Allen, 1939a: 98; Lanza *et al.*, 2015: 466).
1911. *Scotoecus hindei:* G. M. Allen, Bull. Mus. comp. Zool., 54 (9): 330. Publication date: December 1911. (Current Combination, Current Spelling).
1915. *Scotoecus falabæ* Thomas, Ann. Mag. nat. Hist., ser 8, 16 (95): 447. Publication date: 1 November 1915. Type locality: Nigeria: Northern Nigeria, Bauchi plateau: Kabwir [09 24 N 09 34 E, 2 500 ft]. [Goto Description]. Holotype: NHMUK 1915.10.8.1: sad ♀. Collected by: Dr. J.C. Fox; collection date: 28 July 1915; original number: 70. Presented/Donated by: Dr. J.C. Fox. - Etymology: Thomas (1915d: 448) mentoined "The specific name is given in commemoration of Dr. Fox's escape from the peaceful liner 'Falaba', barbarously sunk on its way out to Africa.".
2010. *Scotoecus hindei/albigula:* Monadjem, Taylor, Cotterill and Schoeman, Bats of Southern and Central Africa. A biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, 510. (Name Combination).
? *Scotoecus hindei falabae:* (Name Combination).
? *Scotoecus hindei hindei:* (Name Combination).
? *Scotoecus hirundo hindei:* (Name Combination).

TAXONOMY:
Included in *hirundo* by Kock (1969a: 192), Koopman (1993a: 226), but considered a valid species by Ansell and Dowsett (1988: 44), Simmons (2005).



Figure 341. *Scotoecus hindei* (ECJS-36/2008), from Lafupa camp, Zambia.

COMMON NAMES:
Czech: netopýr Hindeův. English: Hinde's Lesser House Bat. French: Scotoèque de Hinde. German: Hindes Hausfledermaus. Italian: Scotoèco di Hìnde.

CONSERVATION STATUS:
Global Justification
Scotoecus hindei was included in *Scotoecus hirundo* by Jacobs *et al.* (2008af) in IUCN (2009) for assessment. Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008af; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) [assessed as part of *Scotoecus hirundo*] (Jacobs *et al.*, 2008af; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004q; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
While the threats to this species are not well known, it is presumed not to have any major threats in view of the species wide distribution in habitats that are not rapidly declining throughout much of its recorded range (Jacobs *et al.*, 2008af; IUCN, 2009).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008af) [in IUCN (2009)] report that further studies are needed into the natural history and possible threats to this poorly known species.

GENERAL DISTRIBUTION:
Native: Cameroon; Congo, Democratic Republic of the; Ethiopia (Lavrenchenko *et al.*, 2004b: 141); Kenya; Malawi; Mozambique (Monadjem *et al.*, 2010c: 384 as *S. hindei/albigula*); Nigeria; Somalia; Sudan; Tanzania; Zambia.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
See Taylor *et al.* (2005).

MOLECULAR BIOLOGY:
Karyotype
Nagorsen *et al.* (1976: 9) reported 2*n* = 30, FN = 50, BA = 22, a subtelocentric X chromosome and a submetacentric Y chromosome.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 90 minutes, and the digestibility rate about 78.3 %.

POPULATION:
Structure and Density
It is very rarely recorded, and there is little information available on the population abundance or size of this species (Jacobs *et al.*, 2008af; IUCN, 2009).

Trend
2008: Unknown (Jacobs *et al.*, 2008af; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In Malawi, the births take place early in the wet season (Happold and Happold, 1990b: 567).

PARASITES:
PROTOZOA
Babyesiza *et al.* (2025: 4) found *Trypanosoma vespertilionis* in four out of the five *Scotoecus hindei* bats they examined.

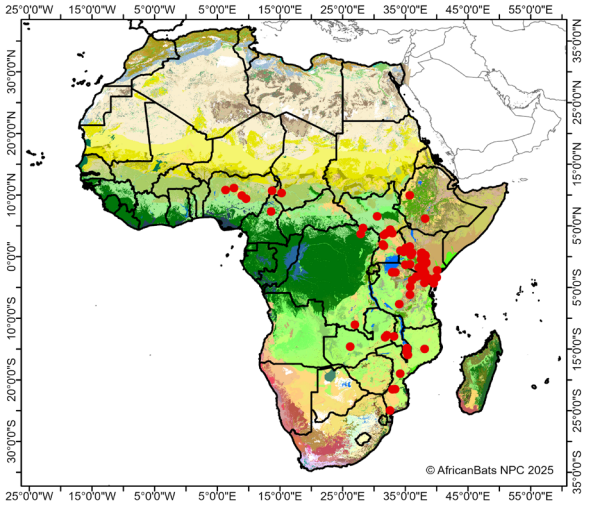

Figure 342. Distribution of *Scotoecus hindei*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Cameroon, Congo (Democratic Republic of the), Ethiopia, Kenya, Malawi, Mozambique, Nigeria, South Sudan, Tanzania, Uganda, Zambia.

Scotoecus hirundo (de Winton, 1899)

*1899. *Scotophilus hirundo* de Winton, Ann. Mag. nat. Hist., ser 7, 4 (23): 355. Publication date: 1 November 1899. Type locality: Ghana: Gambaga [10 32 N 00 26 W]. [Goto Description]. Holotype: NHMUK 1899.6.15.8. - Etymology: From the feminine Latin noun, in apposition, *hirùndo*, meaning "swallow", referring to the species' appearance (see Lanza *et al.*, 2015: 471).

1923. *Scotoecus artinii* de Beaux, Atti Soc. ital. Sci. nat., 62: 98. Publication date: July 1923. Type locality: Kenya: Northern Guaso Nyiro: Archer's Post [00 39 N 37 41 E, 2 000 ft]. [Goto Description]. Holotype: MSNM 1443: ad ♀, skin and skull. Collected by: L. Franchetti and L. Tonker; collection date: 26 December 1919. 2 paratypes: see De Beaux (1923: 98). Paratype: MSNG 45844: alcoholic (skull not removed). Collected by: L. Franchetti and L. Tonker; collection date: 26 December 1919. See Gippoliti (2024: 3). - Etymology: In honour of prof. E. Artini, director of the Museo Civico di Storia Naturale di Milano (see De Beaux, 1923: 98).

2013. *Scotoecus cf. hirundo:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) showed that the karyotype from Senegal (2*n*=30, FN=50, aFN=46) had a reduced number of arms than reported previously from the Ivory Coast (2n=30, FN=54, Fna=50 Volleth *et al.* (2006)), and suggested that this may represent a distinct species. Further investigations are needed to compare other related species of *Scotecus*, as both the cytogenetics only compared the specimens from Sengal with that of Ivory Coast. (Name Combination).

? *Scotoecus hirundo artinii:* (Name Combination).

? *Scotoecus hirundo:* - Comments: . (Name Combination, Current Combination).

TAXONOMY:

Koopman (1993a: 226) included *hindei*; see Hayman and Hill (1971: 36) and Robbins (1980: 84); but see also Hill (1974b).

COMMON NAMES:

Chinese: 暗翼宽吻蝠. Czech: netopýr vlaštovčí. English: Dark-winged Lesser House Bat, Swallow Lesser House Bat. French: Scotoèque hirundine, Scotophile à ailes noires. German: Schwarzflügel-Hausfledermaus. Italian: Scotoèco róndine. Malawian: Liputiputi, Ndemiya, Namzeze.

CONSERVATION STATUS:

Global Justification

Although this species is known mainly from isolated records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008af; IUCN, 2009; Cotterill *et al.*, 2017).

Assessment History

Global

2016: LC ver 3.1 (2001) [includes *S. albigula* and *S. hindei*] (Cotterill *et al.*, 2017). 2008: LC ver 3.1 (2001) [includes *S. albigula* and *S. hindei*] (Jacobs *et al.*, 2008af; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs, 2004g; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

While the threats to this species are not well known, it is presumed not to have any major threats in view of the species wide distribution in habitats that are not rapidly declining throughout much of its recorded range (Jacobs *et al.*, 2008af; IUCN, 2009; Cotterill *et al.*, 2017).

CONSERVATION ACTIONS:

There appear to be no direct conservation measures in place. It has been recorded from the Zinave National Park in Mozambique (Cotterill, 2001d), and from the Mole National Park in Ghana (Grubb *et al.*, 1998), and in view of its wide range, is presumably present in additional protected areas. Further studies are needed into the natural history and possible threats to this poorly known species (Jacobs *et al.*, 2008af; IUCN, 2009; Cotterill *et al.*, 2017).

GENERAL DISTRIBUTION:

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 555,102 km^2.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 626); Cameroon; Côte d'Ivoire (Volleth *et al.*, 2006); Ethiopia; Ghana; Guinea-Bissau (Rainho and Ranco, 2001: 59); Senegal; Tanzania; Uganda (Kityo and Kerbis, 1996: 63).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

Scott *et al.* (2012: 2943) report that the mandibular symphysis is completely fused in this species.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
Two FM/QCF calls from Maroua (Cameroon) were reported by Manga Mongombe (2012: 79) having the following parameters: F_{max}: 58.4 (57.2 - 59.6) kHz, F_{min}: 54.5 (54.2 - 54.8) kHz, F_{mean}: 56.6 (55.9 - 57.2) kHz, F_{knee}: 58.2 (57.2 - 59.2) kHZ, F_{char}: 54.7 (54.5 - 54.8) kHz, and duration: 0.87 (0.82 - 0.91) ms.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2006) reported 2*n* = 30, FN = 50, BA = 22, and a subtelocentric X chromosome for a female from Ivory Coast.

Koubínová *et al.* (2013: 3) report the following karyotype for 1 ♂ from Senegal: 2*n* = 30, Fna = 46, FN = 50, X = metacentric, and Y = dot-like (probably acrocentric). They also found that the Senegalese specimen differed for 1.6 % in its *rag2* gene when compared with a specimen from Tanzania, which is more than in other non-cryptic species. As such they assign their specimen to *S.* cf. *hirundo*.

Genetics
See Hoofer and Van Den Bussche (2003) from Tanzania.

HABITAT:
In southern Africa, this species inhabits Savanna habitats (84 %; Cooper-Bohannon *et al.*, 2016: Table S2).

DIET:
Feacal pellets of 2 bats from Cameroon examined by Waghiiwimbom *et al.* (2019a: 156), contained the following volume (± SD) and frequency percentages: Lepidoptera (44.4 ± 5.8; 95), Diptera (39.7 ± 9.2; 98.3), Coleoptera (13.5 ± 4.1; 70.4), Hymenoptera (2.3 ± 1.5; 26.4), Nauroptera (1.4 ± 1.4; 3.3), Trichoptera (0.2 ± 0.2; 3.3).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 85 minutes, and the digestibility rate about 78.9 %.

POPULATION:
Structure and Density
It is very rarely recorded, and there is little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008af; IUCN, 2009; Cotterill *et al.*, 2017).

Trend
2016: Unknown (Cotterill *et al.*, 2017). 2008: Unknown (Jacobs *et al.*, 2008af; IUCN, 2009).

PARASITES:
HEMIPTERA
Cimicidae
Szentiványi *et al.* (2022: 12) reported *Cacodmus vicinus* Horváth, 1934 from Senegal.

DIPTERA
Nycteribiidae
Dick *et al.* (2023: 73) found *Basilia (Basilia) ansifera* Theodor, 1956 has been found on *Scotoecus hirundo* from the Samburu National Game Reserve (Kenya).

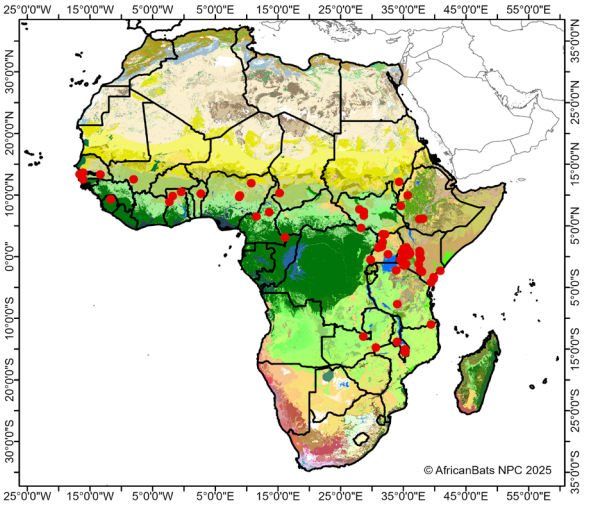

Figure 343. Distribution of *Scotoecus hirundo*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Cameroon, Central African Republic, Côte d'Ivoire, Ethiopia, Ghana, Kenya, Malawi, Mali, Nigeria, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, The Gambia, Uganda, Zambia.

†*Scotoecus olduvensis* Gunnell, Butler, Greenwood and Simmons, 2015

*2015. *Scotoecus olduvensis* Gunnell, Butler, Greenwood and Simmons, Am. Mus. Novit., 3846: 1, 10, figs 6B, 7. Publication date: 16 December 2015. Type locality: Tanzania: Arusha province: Olduvai Gorge: Bed I, FLK NI, Layer 3. - Etymology: Named for Olduvai Gorge, Tanzania (Gunnell *et al.*, 2015a: 10).

SIMILAR SPECIES:
The teeth of *S. olduvensis* are on average 12 % larger than those of its congeners (Gunnell *et al.*, 2015a: 10)..

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Timeframe:
Pleistocene (Brown *et al.*, 2019: Suppl.).

Genus ***Vansonia*** Roberts, 1946

1946. *Vansonia* Roberts, Ann. Transv. Mus., 20 (4): 304 [Goto Description]. - Comments: Type species: *Pipistrellus vernayi* Roberts, 1932 (=*Vespertilio rüppellii* Fischer, 1829), by original designation. Not *Vansonia* Schein, 1956 (Insecta, Coleoptera, Scarabaeidae) (see Jackson and Groves, 2015: 275). - Etymology: The name *Vansonia* refers to George van Son, entomologist of the Transvaal Museum (see Lanza *et al.*, 2015: 382). .

Vansonia rueppellii (J.B. Fischer, 1829)

1826. *Vespertilio temminckii* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 17: pl 6. Type locality: Sudan: Northern province: Dongola [19 10 N 30 27 E]. [Goto Description]. Lectotype: SMF 4308: ad ♂, skin only. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1824. Old catalog: II.N.11.b: see Mertens (1925: 22).
Lectotype of both *Vespertilio temminckii* and *V[espertilio] Rüppelii*. - Comments: Preoccupied by *temmincki* Horsfield, 1824 (a *Scotophilus*): see Allen (1939a: 95), Meester *et al.* (1986: 51), Simmons (2005). The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831".

*1829. *V[espertilio] Rüppelii* J.B. Fischer, Synopsis Mamm, 109. Publication date: 1829. Type locality: Sudan: Northern province: Dongola [19 10 N 30 27 E]. [Goto Description]. Paralectotype: RMNH MAM.35913: ad ♀, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1824. Paralectotype: RMNH MAM.35914: ad ♂, mounted skin (skull not removed). Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1824. - Comments: Mertens (1925: 22) mentions that the specimen designated as lectotype for *temminckii* is also the lectotype for *rüppellii*. - Etymology: The type (*Vespertilio temminckii*) was described in Rüppell's (1827) *Atlas zu der Reise im Nordlichen Afrika* and renamed by Fischer (1829) after Rüppell (*V. rüppellii*) (see Taylor, 2005).

1838. *Scotophilus Temminckii:* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 497.
1855. *V[espertilio] rüppelli:* Giebel, Die Säugethiere, 945. (Name Combination).
1855. *Vespertilio (Vesperugo) Rüppellii:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 745. (Name Combination).
1860. *Panugo rüppelii:* Kolenati, Monographie der Europäischen Chiroptern, 10. (Name Combination, Alternate Spelling).
1868. *Vespertilio (Alobus) Temminckii:* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 707 (for 1867).
1877. *V[esperugo] Temminckii:* Heuglin, Reise in Nordost Afrika, 2: 32.
1877. *Vesperugo Rüppellii:* Heuglin, Reise in Nordost Afrika, 2: 32. (Name Combination).
1878. *Vesperugo (Vesperugo) temminckii:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 233. Publication date: 15 June 1878.
1880. *Vesperugo temminckii:* Dobson, Report on accessions to our knowledge of the chiroptera during the past two years (1878 - 1880), 186.
1891. *Vesperugo temmincki:* Noack, Jb. Hamb. Wiss. Anst., 9: 140.
1901. *Pipistrellus Temminckii:* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (46): 274.
1902. *Pipistrellus rueppelli:* Anderson and de Winton, Zoology of Egypt: Mammalia, 127. (Name Combination).
1917. *Scotozous rüppelii:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 409. (Name Combination).
1918. *Pipistrellus rüppelii:* Hollister, Bull. U.S. natl. Mus., 99: 93. (Alternate Spelling).
1919. *P[ipistrellus] rüppelli:* Thomas, J. Bomb. nat. Hist. Soc., 26: 747. (Alternate Spelling).
1920. *Pipistrellus rüppelli:* Schwarz, Fledermäuse aus West- und Zentralafrika, ???. (Alternate Spelling).
1925. *Pipistrellus rüppellii:* Mertens, Senckenb. biol., 7 (1/2): 22. (Alternate Spelling).
1925. *V[espertilio] Rüppellii:* Mertens, Senckenb. biol., 7 (1/2): 22. (Name Combination).
1928. *Scotozous rüppellii:* Gyldenstolpe, Ark. Zool. Stockholm, 20A (4): 71. (Alternate Spelling).
1935. *Scotozous trüppellii:* Monard, Arq. Mus. Bocage, 6: 31. - Comments: Lapsus (see Kock, 1969a: 174; Meester *et al.*, 1986: 51). (Lapsus).
1938. *[Scotozous] rüppeli:* Frechkop, Exploration du Parc National Albert, 52. (Lapsus, Alternate Spelling).
1953. *Pipistrellus (Scotozous) rueppelli:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1956. *Pipistrellus ruppelli:* Harrison, Proc. zool. Soc. Lond., 127: ???. (Alternate Spelling).
1957. *[Pipistrellus] rueppeli:* Aellen, Rev. suisse Zool., 64 (6): 204. (Lapsus).
1962. *Scotozous rüppelli:* Wassif, Proc. zool. Soc. Lond., 811. (Alternate Spelling).
1964. *Scotozous temmincki:* Lehmann, in: Niethammer, Alexander Koenigs Reisen am Nil, 72.
1969. *Vespertilio temmincki:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 174. (Alternate Spelling).
1980. *Pipistrellus rueppellii:* Swanepoel, Smithers and Rautenbach, Ann. Transv. Mus., 32 (7): 171. (Name Combination).
1981. *Pipistrellus (Pipistrellus) rueppellii:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination).
1983. *Pipistrellus (Scotozous) rueppellii:* Smithers, Mammals Southern African subreg, 97. (Name Combination).

† Scotoecus olduvensis

1985. *Pipistrellus ruepellii:* Rautenbach, Fenton and Braack, Koedoe, 28: 74. (Lapsus).
1986. *Pipistrellus (Vansonia) rueppellii:* Meester, Rautenbach, Dippenaar and Baker, Transv. Mus. Monogr., 5: 50. (Name Combination).
1990. *Pipistrellus ruppellii:* Yom-Tov, Cohen and Wollberg, Mammalia, 54 (2): 281. (Name Combination).
1995. *P[ipistrellus (?Hypsugo)] rueppelli:* Pavlinov, Borissenko, Kruskop and Jahonton, Arch. Zool. Mus., Moscow State Univ., 133: 107. (Name Combination).
1995. *P[ipistrellus (Pipistrellus)] ruepelli:* Nowak, Walker's Bats of the World, 94. (Lapsus).
1996. *Eptesicus rueppellii:* Kityo and Kerbis, J. East Afr. Nat. Hist., 85: 53. (Name Combination).
2013. *Neoromicia rueppellii:* McCulloch, Barcoding of South African bat species and evaluation of their natural exposure to lyssaviruses, 145. Publication date: July 2013. (Name Combination).
2014. *Vansonia rueppellii:* Benda, Lučan, Shohdi, Porteš and Horáček, Vespertilio, 17: 45. (Current Combination).
2020. *Vansonia cf. rueppellii:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1122. Publication date: 10 September 2020. (Name Combination).
? *Pipistrellus rueppellii vernayi:* (Name Combination).
? *Scotozous rueppellii:* (Name Combination).
? *Vansonia cf. rueppellii Rwanda*
? *Vansonia cf. rueppellii TD-2020*
? *Vesperugo hesperida:*

Taxonomy:



Figure 344. *Vansonia rueppellii* (ECJS-126/2009) caught in the Okavango, Botswana.

Renaming of *V. temminckii* Cretzschmar, 1826 (see Allen, 1939a: 95). Mentioned in the subgenus *Vansonia* by Koopman (1994: 116). Mentioned in the subgenus *Hypsugo* inc. sedis by Pavlinov *et al.* (1995: 107).

Meester *et al.* (1986) state that Ellerman *et al.* (1953: 79) do not recognize *Vansonia*, and instead place *Pipistrellus rueppellii* in the subgenus *Scotozous*, as do later authors (Rosevear, 1965; Hayman and Hill, 1971: 41; Smithers, 1983). Corbet and Hill (1980: 68), however, retain *Scotozous* as a full genus for the Indian *S. dormeri* Dobson, 1875, and both J.E. Hill (in litt.) and K.F. Koopman (in litt.) agree that it is incorrect to use this name for *rueppellii*. *Vansonia* is therefore the prior subgeneric name for this species. Benda *et al.* (2014c: 81; 2016b: 322) place *rueppellii* in the genus *Vansonia*.

Helbig *et al.* (2010: 168) suggest that *rueppellii* needs to be transferred to a genus that needs to be newly created or resurrected from the current synonymy. Also Koubínová *et al.* (2013: 8) found evidence in the cyt *b* gene to support the transfer of *rueppellii* to a distinct genus, but they indicate that further investigations on material from the type countries of *P. rueppellii* [=Sudan] and the type locality of *P. vernayi* (the type species of *Vansonia* [Maun, Ngamiland, Botswana] are needed to confirm the relationship with *Vansonia*.

Although no material from Sudan nor Botswana was included in the cyt *b* sequence analyses performed by Monadjem *et al.* (2020a: 1122), their results indicate that *rueppellii* is quite different from the other African *Pipistrellus* species, and supports the views held by other authors (e.g., Benda *et al.*, 2014b: 51); 2014c: 81; Dietz and Kiefer, 2016: 351).

The original name was spelled as *Rüppelii*, so the present spelling should probably be *rueppelii*. However, this spelling was only found one single time in all of the literature data: as a misspelling in Koopman (1975). There are a number of earlier authors which use *rueppelli* (e.g., Anderson and de Winton, 1902). Older literature data are: Wagner (1855) as *Vespertilio (Vesperugo) rüppelli*, Kolenati (1860) as *Panugo rüppelii*, and Heuglin (1877) as *Vesperugo rüppellii*. So the earliest record we were able to find was Wagner (1855), who already used the double "ll" (and double "ii"), but still used "ü", as did Heuglin (1877). Only Kolenati (1860) used a single "l". So if we consider Wagner to be the first reviewer, the name should be spelled as "*rueppellii*" with double "ll" and double "ii" and with "ue" since diacritics are no longer allowed in scientific names.

Common Names:

Afrikaans: Rüppell se vlermuis, Rüppell-vlermuis. Arabian: Khaffash. Chinese: 吕氏伏翼. Czech: netopýr Rüppellův, netopýr dvoubarvý. Dutch: Rüppells dwergvleermuis. English: Rüppell's Bat, Ruppell's Pipistrelle, Rüppel's Pipistrelle Bat, Rüppel's Pipistrelle. French: Pipistrelle de Rueppel, Pipistrelle de Rüppell. German: Rüppells Zwergfledermaus, Rüppells Pipistrelle,

Dongola-Dämmerungsfledermaus. Hebrew: Atalfon Rippel. Italian: Pipistrèllo di Rùppell.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
Butler and Greenwood (1965) found in the early Pleistocene at Olduvai material which they referred to as "cf *Pipistrellus* (*Scotozous*) *rueppelli* (Fischer)" (see Butler, 1978).

CONSERVATION STATUS:
Global Justification
A widespread species with no known major threats, hence is assessed as Least Concern (LC ver 3.1 (2001)) (Jacobs *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as "*Pipistrellus rueppellii*" (Monadjem *et al.*, 2017c). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004ag; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016q). 2004 - considered a vagrant not assessed, only one locality in SA (Augrabies Falls) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:
Use of pesticides against locusts is a threat (Jacobs *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017c).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008a) [in IUCN (2009)] and Monadjem *et al.* (2017c) report that no specific measures are known. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
Vansonia rueppellii has been recorded throughout Africa, with scattered records from southwest Asia. North African records include a disjunct distribution being recorded from a small part of eastern Morocco into western Algeria, Tunisia, a single record from eastern Libya (on the border with Egypt; Benda *et al.*, 2004a) and then in a broad strip in Egypt including all of the Nile River valley and delta and extending to the Red Sea (but not in the south) and the westernmost part of the Sinai. West African records are from the Senegal coast and the Senegal/Mauritania border. The largest contiguous range consists of a strip stretching from northern Sudan down to northern Zimbabwe, which at its widest point ranges from western Zambia to western Mozambique. Occurs up to 1,100 m in Morocco.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 477,914 km^2.

Bates *et al.* (2013: 339) reject the occurrence of *V. rueppellii* in the Republic of Congo as Malbrant and Maclatchy (1949) only suggested that it 'likely' occurs in that country.

Native: Algeria; Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 572); Benin; Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 572); Burkina Faso; Burundi; Cameroon; Central African Republic (Benda *et al.*, 2004a: 91); Chad; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 572); Egypt (Sinai); Equatorial Guinea; Ethiopia; Gabon; Gambia; Ghana; Guinea; Guinea-Bissau; Iraq; Israel; Kenya; Liberia; Libyan Arab Jamahiriya (Benda *et al.*, 2004a: 91); Madagascar (Goodman *et al.*, 2022: 1898); Malawi (Ansell and Dowsett, 1988: 40; Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 572); Mali; Mauritania (Padial and Ibáñez, 2005: 240); Morocco (Benda *et al.*, 2004d; 2010a; El Ibrahimi and Rguibi Idrissi, 2015: 362; Dbiba *et al.*, 2025: 7); Mozambique; Namibia (Monadjem *et al.*, 2010d: 572); Nigeria (Benda *et al.*, 2004a: 91); Rwanda; Senegal; Sierra Leone; Somalia; South Africa (Monadjem *et al.*, 2010d: 572); Sudan; Tanzania (including Unguja [O'Brien, 2011: 290]); Togo; Tunisia; Uganda (Kityo and Kerbis, 1996: 62); Yemen; Zambia (Monadjem *et al.*, 2010d: 572); Zimbabwe (Monadjem *et al.*, 2010d: 572).

Presence uncertain: Kuwait.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.8 Pa, aspect ratio 6.3 for a wingspan of 25 cm and a wing area of 101 cm^2 and a body mass of 7 g.

ECHOLOCATION:
See Jacobs (1996), Taylor (1999b) and Taylor *et al.* (2005).

Disca *et al.* (2014: 226) indicate that the type of call is FM-QFC. They also provide two different sets of parameters: A - long) F_{start}: 93.0 ± 8.9 kHz,

F_{end}: 51.7 ± 0.7 kHz, F_{peak}: 53.6 ± 1.3 kHz, bandwidth: 41.3 ± 8.6 kHz, duration: 6.1 ± 1.2 ms; B - short) F_{start}: 68.2 ± 6.1 kHz, F_{end}: 52.8 ± 1.7 kHz, F_{peak}: 55.8 ± 2.0 kHz, bandwidth: 15.4 ± 6.7 kHz, duration: 2.4 ± 0.5 ms. The "B" type has not been reported from *Pipistrellus* before, and the peak frequencies of both types differ from those observed in Kenya (37.3 ± 0.8 kHz) and Zimbabwe (45 kHz).

84 calls from Israeli bats were reported by Hackett *et al.* (2016: 223): F_{start}: 62.24 ± 3.75 (55.5 - 72.0) kHz, F_{end}: 51.94 ± 0.88 (50.0 - 54.7) kHz, F_{peak}: 52.19 ± 0.97 (50.0 - 55.0) kHz, pulse duration: 4.22 ± 0.39 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 52.19 kHz, F_{start}: 62.24 kHz, F_{end}: 51.94 kHz, Band width: 10.3 kHz, and duration: 4.22 ms.

In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 8 calls: Interpulse interval: 80.8 ± 36.7 (55.5 - 168.9) ms; F_{max}: 49.9 ± 2.2 (46.5 - 53.7) kHz; Start slope: -23.1 ± 4.0 (-19.0 - -28.2) kHz/ms; End slope: -7.4 ± 5.1 (-10.7 - 0.4) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.4 - 0.5) ms. They also indicate that the F_{max} value is 10 kHz higher than the one reported by Monadjem *et al.* (2020f, and that the interpulse interval is much lower than the value reported by Kearney *et al.* (2010): 80.8 ms versus 131.7 ms.

Molecular Biology:

Karyotype

Rautenbach *et al.* (1993) reported 2*n* = 36, FN = 54, BA = 20, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa.

Protein / allozyme

Based on the analysis of eight mitochondrial and nuclear genes, Koubínová (2013: 7) found that "*P. rueppellii*" was basal to the whole *Pipistrellus* / *Nyctalus* clade, and possibly might be placed in a genus of its own.

Genetics

See Mayer *et al.* (2007).

Habitat:

In southern Africa, this species occurs primarily in Savanna (82 %) and Afromontane (11 %) habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

In Madagascar, it is found in disturbed marshland dominated by *Bismarckia* palms.

Diet:

Benda *et al.* (2014c: 86) analysed the content of the digestive tract of the single specimen they captured and found it contained 50 % by the volume of brachyceran Diptera, 30% of Lepidoptera and 20% of nematoceran Diptera.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 74 minutes, and the digestibility rate about 80.4 %.

Predators:

Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Population:

Structure and Density

Unknown, because it is primarily known only from mist net captures (Jacobs *et al.*, 2008a; IUCN, 2009; Monadjem *et al.*, 2017c).

Trend

2016: Unknown (Monadjem *et al.*, 2017c). 2008: Unknown (Jacobs *et al.*, 2008a; IUCN, 2009).

Reproduction and ontogeny:

Happold and Happold (1990b: 567) mention juveniles in November and December in western Zambia, and very young subadults in late December in Malawi.

Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

Parasites:

SIPHONAPTERA

Ischnopsyllidae

Ischnopsyllus emminus Jordan and Rothschild, 1921 was reported from Malawi by Beaucournu and Kock (1996).

IXOIDIDA

Hornok *et al.* (2017b: 3) collected a larva of *Argas vespertilionis* (Latreille, 1796) from a *P.* cf. *rueppellii* from South Horr, Kenya. Hornok *et al.* (2019: 2) probably refer to the same bat and tick and mentioned that the tick itself was infected by *Rickettsia* sp. Bacteria.

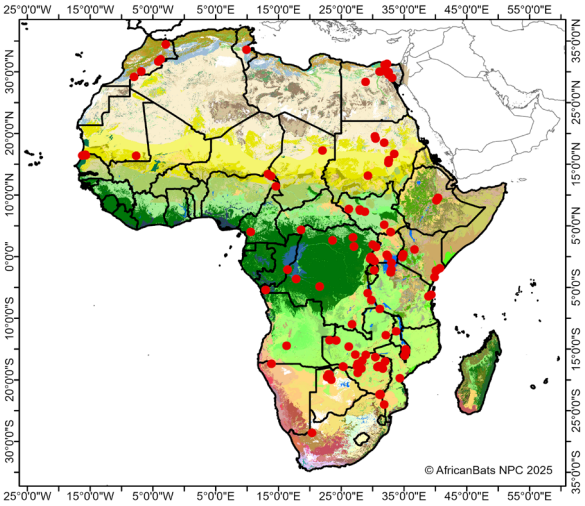

Figure 345. Distribution of *Vansonia rueppellii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Egypt, Ethiopia, Kenya, Malawi, Mauritania, Morocco, Mozambique, Namibia, Nigeria, Rwanda, Senegal, South Africa, South Sudan, Sudan, Tanzania, Togo, Tunisia, Uganda, Zambia, Zimbabwe.

Vansonia rueppellii fuscipes (Thomas, 1913)

*1913. *Pipistrellus fuscipes* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 315. Publication date: 1 March 1913. Type locality: Uganda: Entebbe, 60 mi (90 km) W [00 04 N 32 20 E, 3 700 ft]. [Goto Description]. Holotype: NHMUK 1906.7.1.5: ad ♂, skin and cranium only (no mandibula). Collected by: R.E. Dent and The Ruwenzori Expedition; collection date: 29 November 1905; original number: 1. See Thomas (1913b: 315).
1939. *Pipistrellus rüppellii fuscipes:* G.M. Allen, Bull. Mus. comp. Zool., 83: 96. (Name Combination).
1951. *Pipistrellus (Scotozous) ruppellii fuscipes:* Swynnerton and Hayman, J. East Afr. Nat. Hist. Soc., 20 (6-7) (90): 293 (for 1950). (Name Combination).
1960. *Pipistrellus ruppelli fuscipes:* Harrison, J. East Afr. Nat. Hist. Soc., 23 (7)(104): 294. Publication date: December 1860. (Name Combination, Alternate Spelling).
1966. *Pipistrellus (Scotozous) rüppelli fuscipes:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 55. (Name Combination).
1975. *P[ipistrellus] r[ueppelli] fuscipes:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 404. (Name Combination).
1984. *Pipistrellus (Scotozous) rueppelli fuscipes:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1994. *P[ipistrellus (Vansonia)] r[ueppelli] fuscipes:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116. (Name Combination).
? *Pipistrellus (Pipistrellus) rueppellii fuscipes:* (Name Combination).
? *Pipistrellus (Vansonia) rueppellii fuscipes:* (Name Combination).
? *Pipistrellus rueppellii fuscipes:* (Name Combination).
? *Vansonia rueppellii fuscipes:* (Current Combination).

GENERAL DISTRIBUTION:
Ethiopia to northern Angola.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
South Sudan, Tanzania, Uganda.

Vansonia rueppellii pulcher (Dobson, 1875)

*1875. *Vesperugo pulcher* Dobson, Proc. zool. Soc. Lond., 1875, III: 471. Publication date: October 1875. Type locality: Tanzania: Zanzibar [ca. 06 10 S 39 12 E]. [Goto Description]. Holotype: NHMUK 1868.12.22.3: ad ♂, alcoholic (skull not removed). Presented/Donated by: Dr. Kirk.
1878. *Vesperugo (Vesperugo) pulcher:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 233. Publication date: 15 June 1878. (Name Combination).
1902. *P[ipistrellus] pulcher:* Anderson and de Winton, Zoology of Egypt: Mammalia, 129. (Name Combination).
1910. *Pipistrellus pulcher:* Thomas and Wroughton, Trans. Linn. Soc. Lond., 19 (5) (63): 489. (Name Combination).
1984. *Pipistrellus (Scotozous) rueppelli pulcher:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1994. *P[ipistrellus (Vansonia)] r[ueppelli] pulcher:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116. (Name Combination).
? *Pipistrellus (Pipistrellus) rueppellii pulcher:* (Name Combination).
? *Pipistrellus rueppellii pulcher:* (Name Combination).
? *Vansonia rueppellii pulcher:* (Current Combination).

GENERAL DISTRIBUTION:
Northeastern Tanzania and Zanzibar.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Tanzania.

Vansonia rueppellii rueppellii (J.B. Fischer, 1829)

1827. *Vespertilio temminckii* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 17: pl 6. Type locality: Sudan: Northern province: Dongola [19 10 N 30 27 E]. Lectotype: SMF 4308: ad ♂, skin only. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1824. Old catalog: II.N.11.b: see Mertens (1925: 22).
Lectotype of both *Vespertilio temminckii* and *V[espertilio] Rüppelii*. - Comments: Preoccupied by *temmincki* Horsfield, 1824 (a *Scotophilus*): see Allen (1939a: 95), Meester *et al.* (1986: 51), Simmons (2005). The publication date of Cretzschmar's work is sometimes indicated as "1826" (as mentioned on the title page), but also as "1827", "1828", "1830-1831".
*1829. *Vespertilio ruppellii* J.B. Fischer, Synopsis Mamm, 109. Publication date: 1829. Type locality: Sudan: Northern province: Dongola [19 10 N 30 27 E].
1866. *Vesperugo hypoleucus* Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 546. Publication date: 1866. Type locality: Sudan: between Kéréri, Halfaye & Surerát on the Nile: Sennaar, near Khartoum, [ca. 15 35 N 33 38 E]. [Goto Description]. Holotype: NMW 24574: ad, skin and skull. Collection date: August 1853. - Comments: Meester *et al.* (1986: 51) assigned it to Fitzinger only.
1866. *Vesperugo sennaariensis* Heuglin and Fitzinger, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 546. Publication date: 1866. Type locality: Sudan: Khartoum [15 40 N 32 35 E, 380 m]. [Goto Description]. - Comments: Nomen nudum (see Allen, 1939a: 95; Meester *et al.*, 1986: 51).
1877. *Vesperugo senarensis* Heuglin, Reise in Nordost Afrika, 2: 32. Publication date: 1877 [Goto Description]. - Comments: Nomen nudum (see Allen, 1939a: 95; Meester *et al.*, 1986: 51).
1939. *Pipistrellus rüppellii rüppellii:* G.M. Allen, Bull. Mus. comp. Zool., 83: 95. (Name Combination).
1955. *Pipistrellus ruppelli ruppelli:* Sanborn and Hoogstraal, J. Egypt. Publ. Health Ass., 30 (4): xxx.
1958. *Pipistrellus (Scotozous) rueppelli rueppeli:* Anciaux de Faveaux, Bull. IFAN, (A) 20 (1): 273. (Name Combination, Alternate Spelling).
1962. *Pipistrellus ruppelii ruppelii:* Heyneman and Macy, J. Egypt. Publ. Health Ass., 37 (4): 123. (Alternate Spelling).
1964. *Scotozous r[üppelli] rüppelli:* Niethammer, Alexander Koenigs Reisen am Nil, 72. (Name Combination).
1966. *Pipistrellus (Scotozous) rüppelli rüppelli:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 172. (Name Combination).
1974. *Pipistrellus rueppelli rueppelli:* Largen, Kock and Yalden, Mon. Zool. ital., (NS) 16 (Suppl 5): 222, 245.
1978. *Pipistrellus rüppelli rüppelli:* Madkour, Zool. Anz., 201 (5/6): 387. (Alternate Spelling).
1983. *P[ipistrellus (Vansonia)] r[ueppellii] rueppellii:* Smithers, Mammals Southern African subreg, 97. (Name Combination).
1984. *Pipistrellus rueppellii rueppellii:* Rautenbach, Schlitter and Braack, Koedoe, 27: ???. (Name Combination).
1988. *Pipistrellus (Pipistrellus) rueppellii rueppellii:* Ansell and Dowsett, Mammals of Malawi, 39. (Name Combination).
1994. *P[ipistrellus (Vansonia)] r[ueppelli] rueppelli:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116. (Alternate Spelling).
2014. *V[ansonia] r[ueppellii] rueppellii:* Benda, Spitzenberger, Hanák, Andreas, Reiter, Ševčík, Šmíd and Uhrin, Acta Soc. Zool. Bohem., 78: 85. Publication date: 22 December 2014. (Current Combination).

MAJOR THREATS:
Sherwin *et al.* (2012: 174) consider water stress and the aerial hawking feeding style to be risk factors related with climatic change.

GENERAL DISTRIBUTION:
Egypt to Nigeria and Central Sudan.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Egypt, Ethiopia, South Sudan, Sudan, Tanzania.

Vansonia rueppellii senegalensis (Dorst, 1960)

*1960. *Pipistrellus Rüppelli senegalensis* Dorst, Bull. Mus. natn. Hist. nat., Paris, sér 2, 31: 473 (for 1959). Type locality: Senegal: Richard Toll [16 48 N 15 42 W]. [Goto Description]. Holotype: MNHN ZM-MO-1960-81: ad ♀, skull and alcoholic. Collected by: Francis Roux; collection date: September 1958.
1965. *Pipistrellus (Scotozous) rueppelli senegalensis:* Rosevear, Bats of West Africa, 272. (Name Combination).
1972. *P[ipistrellus] ruepelli senegalensis:* Adam and Hubert, Mammalia, 36 (1): 59. (Lapsus).
1972. *Pipistrellus rueppeli senegalensis:* Adam and Hubert, Mammalia, 36 (1): 64. (Name Combination).
1972. *Pipistrellus rueppelli senegalis:* Adam and Hubert, Mammalia, 36 (1): 59. (Lapsus).
1982. *Pipistrellus ruppelli senegalensis:* Verschuren, Mém. IFAN, 92: 307. (Alternate Spelling).
1994. *P[ipistrellus (Vansonia)] r[ueppelli] senegalensis:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116. (Name Combination).
1998. *P[ipistrellus (Pipistrellus)] r[ueppellii] senegalensis:* Grubb, Jones, Davies, Edberg, Starin and Hill, Mammals of Ghana, Sierra Leone and The Gambia, 84.
2014. *V[ansonia] r[ueppellii] senegalensis:* Benda, Spitzenberger, Hanák, Andreas, Reiter, Ševčík, Šmíd and Uhrin, Acta Soc. Zool. Bohem., 78: 85. Publication date: 22 December 2014. (Current Combination).
? *Pipistrellus (Pipistrellus) rueppellii senegalensis:* (Name Combination).
? *Pipistrellus rueppellii senegalensis:* (Name Combination).

GENERAL DISTRIBUTION:
Algeria to Senegal.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Senegal.

Vansonia rueppellii vernayi (Roberts, 1932)

*1932. *Pipistrellus vernayi* Roberts, Ann. Transv. Mus., 15 (1): 16. Publication date: 1 October 1932. Type locality: Botswana: Ngamiland: Maun [19 59 S 23 25 E]. [Goto Description]. Holotype: TM 6546: ad ♂. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 29 May 1930; original number: 648.
1933. *Pipistrellus leucomelas* Monard, Bull. Soc. Neuchât. Sci. nat., 57: 47 (for 1932?). Publication date: 1933. Type locality: Angola: South-Central Angola: Vila da Ponte [14 25 S 16 15 E].
1939. *Pipistrellus rüppellii vernayi:* G.M. Allen, Bull. Mus. comp. Zool., 83: 96. (Name Combination).
1946. *[Vansonia] vernayi:* Roberts, Ann. Transv. Mus., 20 (4): 304. (Name Combination).
1951. *Vansonia vernayi:* Roberts, Mammals of South Africa, 82. (Name Combination).
1953. *Pipistrellus (Scotozous) rueppelli vernayi:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1978. *Pipistrellus rueppelli vernayi:* Ansell, Mammals of Zambia, 24. (Name Combination).
1983. *P[ipistrellus (Scotozous)] r[ueppellii] vernayi:* Smithers, Mammals Southern African subreg, 97. (Name Combination).
1984. *Pipistrellus (Scotozous) rueppelli leucomelas:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., 244: 49.
1986. *Pipistrellus (Vansonia) rueppellii vernayi:* Meester, Rautenbach, Dippenaar and Baker, Transv. Mus. Monogr., 5: 51. (Name Combination).
1994. *P[ipistrellus (Vansonia)] r[ueppelli] leucomelas:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 116.
? *Pipistrellus (Pipistrellus) rueppellii vernayi:* (Name Combination).
? *Pipistrellus (Vansonia) rueppellii leucomelas:*
? *Pipistrellus rueppellii leucomelas:* (Name Combination).
? *Pipistrellus rueppellii vernayi:* (Current Spelling).
? *Vansonia rueppellii vernayi:* (Current Combination).

TAXONOMY:
If *vernayi* and *leucomelas* indeed represent the same form, then it might become important to check the actual publication date of *leucomelas*. This name was published in the 1932 issue of the "Bulletin de la Société Neuchâteloise de Sciences Naturelles", but the issue seemed to have appeared in 1933. Otherwise, this name might have priority over *Pipistrellus vernayi* which was published on 1 October 1932.

At present, we synonymize both names and consider *vernayi* to be the oldest name.

Kock (1969a: 174) points out that *leucomelas* might be a homonym of *Vespertilio leucomela* Cretzschmar, 1830.

GENERAL DISTRIBUTION:
Malawi to Transvaal and Southern Angola.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, South Africa, Zambia.

TRIBE Plecotini J. E. Gray, 1866

*1866. *Plecotini* J. E. Gray, Ann. Mag. nat. Hist., ser 3, 17 (98): 90. Publication date: 1 February 1866.
1897. *Plecotinæ* Miller, N. Am. Fauna, 13: 41, 46. Publication date: 16 October 1897. - Comments: Type genus: *Plecotus* E. Geoffroy, 1818. Originally included the genera *Euderma* H. Allen, 1891 and *Plecotus* E. Geoffroy, 1818 (see Jackson and Groves, 2015: 270).
2025. *Plectoini:* Guan, Huang, Huang, Zhou, Yang, Yu, Guo, Feng, Wu, Hu and Wei, Sci. China Life Sci., xxx: 3. Publication date: 18 July 2025. (Lapsus).

Genus ***Barbastella*** J. E. Gray, 1821

*1821. *Barbastella* J. E. Gray, London Med. Repos., 15 (1): 300. Publication date: 1 April 1821. - Comments: Type species: *Vespertilio barbastellus* Schreber, 1774. - Etymology: From Latin "*barba*" meaning bearded and "*stella*" meaning star (see Rydell and Bogdanowicz, 1997: 5). (Current Combination).
1825. *Barbastellus* J. E. Gray, Ann. Philos., 10 (5): 243. Publication date: November 1825. (Alternate Spelling).
1839. *Synotus* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 305. Publication date: 1839. - Comments: Type species: *Vespertilio barbastellus* Schreber, 1774. - Etymology: From the Greek "*σύν*", meaning together and "*οὖς*" or "*ὠτός*", meaning ear (see Palmer, 1904: 657).

TAXONOMY:
See Simmons (2005), Kruskop *et al.* (2019).

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Barbastella*: ***barbastellus*** (Schreber, 1774); *beijingensis* Zhang, Han, Jones, Lin, Zhang, Zhu, Huang and Zhang, 2007 – China; *caspica* Satunin, 1908 – Caucasus, Transcaucasia; *darjelingensis* Hodgson, 1855 – Afghanistan, Iran; India, Nepal, and W China, Japan, perhaps Indo-China (Laos, Vietnam), Taiwan; ***leucomelas*** (Cretzschmar, 1826); *pacifica* Kruskop, Kawai and Tiunov, 2019 – Japan.

COMMON NAMES:
Czech: ďasíci, strostlouchové, saukušanové, širokouší ušanové, netopýři širokouší. English: Barbastelle Bats, Barbastelles. French: Barbastelles. German: Mopsfledermäuse. Широковух (= Shyrokovukh).

Barbastella barbastellus (Schreber, 1774)

*1774.	*Vespertilio barbastellus* Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, 1 (8): pl 55 + 1 (9): 168. Publication date: 1774. Type locality: France: Burgundy. - Etymology: From Latin "*barba*" meaning bearded and "*stella*" meaning star (see Rydell and Bogdanowicz, 1997: 5).
1838.	*Barbastellus communis* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 495. Publication date: 1 February 1838. Type locality: : Burgundy and Germany. - Comments: Renaming of *V. barbastellus* Schreber, 1774.
1985.	*Vespertilio barbestellus:* Qumsiyeh, Spec. Publ. Mus. Texas Tech. Univ., 23: 63. (Lapsus).
2002.	*Barbastella barbastellus guanchae* Trujillo, Ibáñez and Juste, Rev. suisse Zool., 109 (3): 544, , figs 1- 2. Publication date: September 2002. Type locality: Canary Islands (Spain): Tenerife island: La Guancha: "Barranco de La Cantera". [Goto Description]. Holotype: MNH 109: ad ♂. Collected by: Domingo Trujillo; collection date: 1 September 1987. Paratype: EBD 16024M: Collected by: Domingo Trujillo, Carlos J. Ibáñez Uargui and E. Barone; collection date: 15 - 20 September 1987. Agulo, La Gomera Island. Paratype: EBD 16028M: Collected by: Domingo Trujillo, Carlos J. Ibáñez Uargui and E. Barone; collection date: 15 - 20 September 1987. Agulo, La Gomera Island. Paratype: MNH 110: Collected by: Domingo Trujillo, Carlos J. Ibáñez Uargui and E. Barone; collection date: 15 - 20 September 1987. Agulo, La Gomera island. Paratype: MNH 111: Collected by: Domingo Trujillo, Carlos J. Ibáñez Uargui and E. Barone; collection date: 15 - 20 September 1987. Agulo, La Gomera island. - Comments: MNH = Museo de La Naturaleza e El Hombre, Santa Cruz de Tenerife, Spain. Trujillo *et al.* (2002) mention 4 paratypes, EBD 16024M, 16028M, MNH 111, 110; 3 ♀♀ + 1 ♂ from Agulo, La Gomera Island, collector Domingo Trujillo, Carlos Ibáñez & E. Barone, 15-20 September 1987). (Name Combination).
?	*Barbastella barbastellus:* (Current Combination).

TAXONOMY:
Does not include *leucomelas*, see Rydell and Bogdanowicz (1997: 1, Mammalian Species, 557); but see Qumsiyeh (1985) and Horáček *et al.* (2000: 133), although the latter authors still consider *leucomelas* to be a valid species.

The population from the Canary Islands is at present regarded as an endemic subspecies *B. b. guanchae* (Trujillo *et al.*, 2002). Western Mediterranean and Canary Island forms reviewed by Juste *et al.* (2003).

COMMON NAMES:
Albanian: Barbastela e zakonshme. Armenian: Եվրոպական լայնականջ չղջիկ. Azerbaijani: Avropa enliqulağı. Basque: Baso-saguzar, Baso-saguzar arrunt. Belarusian: Шыракавух еўрапейскі. Bosnian: Širokouhi šišmiš. Breton: Barbastell Europa. Bulgarian: Широкоух прилеп. Castilian (Spain): Barbastela, Murciélago de bosque. Catalan (Spain): Ratpenat de bosc, Rat penat de bosc. Croatian: Širokouhi mračnjak, Širokouhi šišmiš. Czech: Netopýr černý, Ušan širokouchý, Srostlouch, netopýr černý, Netopýr mopsličí, saukušan. Danish: Vestlig bredøret flagermus, Bredøret flagermus. Dutch: Westelijke mopsvleermuis, Mopsvleermuis, Dwarsoorvleermuis. English: Western Barbastelle Bat, Barbastelle, Western Barbastelle, Common Barbastelle, Barbastelle bat. Estonian: Euroopa laikõrv. Finnish: Mopsilepakko. French: Barbastelle, Barbastelle d'Europe, Barbastelle commune, Barbastelle occidentale. Frisian: Westlike breedearflearmûs. Galician (Spain): Morcego das fragas. Georgian: ევროპული მაჩქათელა. German: Mopsfledermaus, Kurzmaulige Fledermaus. Greek: Μπαρμπαστέλλος. Hungarian: Nyugati piszedenevér, Pisze denevér, Piszedenevér, Nycteris i mikromolossos. Irish Gaelic: Ialtóg bharbastail Iartharach. Italian: Barbastello. Latvian: Eiropas platausis. Lithuanian: Europinis plačiaausis. Luxembourgish: Europäesch Mopsfliedermaus. Macedonian: Широкоушест лилјак. Maltese: Barbastell. Montenegrin: širokouhi slijepi miš. Norwegian: Bredøre. Polish: Mopek zachodni, Mopek. Portuguese: Morcego-negro. Rhaeto-Romance: Barbastel, Barbastel ureglio lada. Romanian: Liliacul cârn, Liliac-cârn. Russian: Широкоушка европейская. Serbian: Европски широкоушан [= Evropski širokoušan], Европейская широкоушка [= Evropejskaya shirokoushka]. Scottish Gaelic:

Ialtag bharbastail iarach. Slovak: Uchaňa čierna. Slovenian: Širokouhi netopir. Swedish: Barbastell. Turkish: Basıkburunlu Yarasa. Ukrainian: Широковух європейський [= Shyrokovukh yevropeys'kyy]. Welsh: Ystlum du.

CONSERVATION STATUS:

Global Justification

Although this species has a large range, it is generally rare, occurring in low density and numbers. It is mainly sedentary. The population is fragmented and linked to particular kinds of old forest habitats, which are declining. The species does not easily colonise new areas. Declines are widely reported in most of its range with a few exceptions in recent years. The status of this species is linked to forestry practices and the decline in the number of old trees (one colony may use up to 30 old trees with holes each summer season). Has specific habitat and diet requirements (Hutson *et al.*, 2008b; IUCN, 2009). Listed as Near Threatened (approaching A4c), as it is suspected that population declines will approach 30% over a 15 year period including both the past and the future (Hutson *et al.*, 2008b; IUCN, 2009; Piraccini, 2016c).

Assessment History

Global

2016: NT ver 3.1 (2001) (Piraccini, 2016c). 2008: NT ver 3.1 (2001) (Hutson *et al.*, 2008b; IUCN, 2009). 1996: VU A2c ver 2.3 (1994).

Legal Status

It is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention where these apply. It is included in Annex II (and IV) of EU Habitats and Species Directive, and hence requires special measures for conservation including designation of Special Areas for Conservation. Some habitat protection through Natura 2000.

MAJOR THREATS:

Loss of old mature woodland and ancient trees with loose bark or wood crevices (reforested areas are not suitable for this species); disturbance and loss of underground habitats, disturbance and loss of roost sites in older buildings (Hutson *et al.*, 2008b; IUCN, 2009). In Germany, habitat loss and fragmentation (caused by inter alia infrastructure development, forestry, and the renovation or demolition of old buildings used as roost sites), and disturbance (e.g., from cave tourism) are major threats (Schulenberg, 2005); accidental mortality (roadkill) is also a problem (Rudolph *et al.*, 2003).

CONSERVATION ACTIONS:

Hutson *et al.* (2008b) [in IUCN (2009)] indicate that research is underway to establish conservation requirements for this species. Recommendations include adopting forestry practices that maintain old trees in sufficient numbers.

GENERAL DISTRIBUTION:

Barbastella barbastellus is largely restricted to central and southern Europe, although its range extends into the Caucasus, Anatolia, Morocco (North Africa) and the Canary Islands (La Gomera and Tenerife only). It has recently been recorded from Iran on the Arabian Peninsula. It occurs to 1,800 m in the Alps (Spitzenberger, 2002), 1,900 m in the Caucasus and 2,260 m in the Pyrenees (Mitchell-Jones *et al.*, 1999).

Native: Andorra; Armenia; Austria; Azerbaijan; Belarus; Bosnia and Herzegovina; Bulgaria; Croatia; Czech Republic; Denmark; France; Georgia; Germany; Greece; Holy See [Vatican City State]; Hungary; Iran (Benda *et al.*, 2008b) [in Karami *et al.*, 2009: 69]); Ireland; Italy (Sardinia, Sicily); Latvia; Liechtenstein; Lithuania; Luxembourg; Macedonia, the former Yugoslav Republic of; Moldova; Monaco; Montenegro; Morocco (Benda *et al.*, 2010a: 158; Rebelo *et al.*, 2012: 2763; El Ibrahimi and Rguibi Idrissi, 2015: 364; Dbiba *et al.*, 2025: 7); Netherlands; Poland; Portugal; Romania; Russian Federation; San Marino; Serbia; Slovakia; Slovenia; Spain [Baleares, Canary Is.]; Sweden; Switzerland; Ukraine; United Kingdom.

Presence uncertain: Norway; Senegal; Turkey.

FUNCTIONAL MORPHOLOGY:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 9.1 Pa, aspect ratio 6.0 and tip shape index of 2.33 for a wingspan of 26 cm and a wing area of 111 cm^2 and a body mass of 10 g.

ECHOLOCATION:

Walters *et al.* (2012: suppl.) report the following figures for 28 calls from bats from France, Slovenia, Switzerland and the UK: duration: 3.57 ± 1.84 ms, F_{max}: 43.23 ± 8.31 kHz, F_{min}: 28.87 ± 3.18 kHz, bandwidth: 14.36 ± 8.29 kHz, F_{peak}: 35.48 ± 4.32 kHz.

Barataud (2011: 95) indicates that Barbastelles alter their echolocation signals to mislead their prey, which primilary consists of tympanic moths. He reports (p. 96) two sets of data from France: A) F_{start}: 37.5 ± 1.8 kHz, F_{end}: 27.6 ± 1.1 kHz, F_{peak}: 34.5 ± 1.5 kHz, bandwidth: 9.8 ± 2.0 kHz, duration: 3.2 ± 0.9 ms, interpulse interval: 82.6 ±

40.2 ms (based on 18 calls); B) F_{start}: 45.5 ± 2.1 kHz, F_{end}: 34.2 ± 4.0 kHz, F_{peak}: 43.1 ± 2.3 kHz, bandwidth: 11.3 ± 3.8 kHz, duration: 5.9 ± 2.5 ms, interpulse interval: 58.5 ± 8.4 ms (based on 17 calls). These calls are alternately emitted. The interval between type A and type B calls was 58.5 ± 8.4 ms, and between type B and type A 82.6 ± 40.2 ms.

Luo *et al.* (2019a: Supp.) reported the following data (from two calls): F_{peak}: 38.9, 33.2 kHz, F_{start}: 43.9, 39.4 kHz, F_{end}: 28.9, 28 kHz, Band width: 15, 11.4 kHz, and duration: 4.3, 3.4 ms.

Molecular Biology:

Karyotype

Capanna (1968: 624) reported 2*n* = 32. Rushton (1970: 463) reported 2 *n* = 32, FN = 50, X = metacentric, Y = minute. Arslan and Zima (2014: 14) mention 2*n* = 32, FNa = 50, FN = 54, a metacentric X and an acrocentric Y.

Genetics

See García-Mudarra *et al.* (2009).

Roost:

In Hungary, Görföl *et al.* (2018: 184) found that *B. barbastellus* almost always roosted behind loose bark of native tree species (oak, maple and elm), and frequently switched roosts. The roosts were generally found in dead trees or in dead branches of old trees.

Migration:

Movements up to 290 km in Austria (Kepka, 1960).

Diet:

Andreas *et al.* (2012: 81) indicate that, in the Czech Republic, this bat's main food source are larger species of moths. At the end of Autumn (November) the bats switched to smaller preys (e.g., *Operophtera brumata*, wingspan <= 30 mm) as the larger species were no longer flying around. These findings confirmed that *B. barbastellus* is primarily an aerial hawking species.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 79 minutes, and the digestibility rate about 79.7 %.

Population:

Structure

See Piraccini (2016c) and Hutson *et al.* (2008b) and IUCN (2009) for information on European populations.

Density

See Piraccini (2016c) and Hutson *et al.* (2008b) and IUCN (2009) for information on European populations.

Trend

2016: Decreasing (Piraccini, 2016c). 2008: Decreasing (Hutson *et al.*, 2008b; IUCN, 2009). In Africa, population size and trends are unknown (Hutson *et al.*, 2008b; IUCN, 2009; Piraccini, 2016c).

Viruses:

Despite sampling and testing of 35 individuals of this species, no evidence of influenza A-like viruses (Orthomyxoviridae) were obtained (Fereidouni *et al.*, 2015).

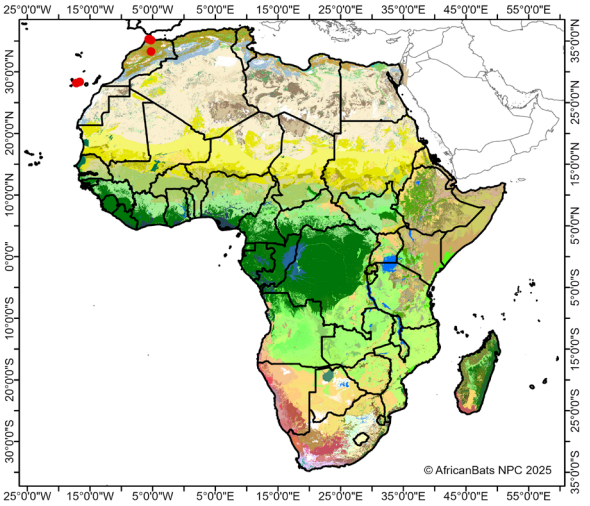

Figure 346. Distribution of *Barbastella barbastellus*.

Distribution based on voucher specimens:

Canary Islands (Spain), Morocco.

Barbastella leucomelas (Cretzschmar, 1826)

*1826. *Vespertilio leucomelas* Cretzschmar, in: Rüppell, Atlas Reise Nördlichen Afrika, Zoologie Säugethiere, 1: 73, pl 28b [Goto Description]. Lectotype: SMF 4373: mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1860; original number: II.M.1.a. See Mertens (1925: 21). Paralectotype: RMNH MAM.35738: ad, mounted skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1826. Paralectotype: RMNH MAM.35739: ad, mounted skin (skull not removed). Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1826. - Comments: For an extensive discussion on the type locality see Benda *et al.* (2008f: 50 - 54), who conclude: "From the Rüppell's (1829) descriptions and according to his traveling schedule, it is fully clear, that in his concept the 'Arabia Petraea' represent 'the area of the Sinaitic peninsula to the south of the connecting line between the towns of Suez and Aqaba', as pointed out above, see also Fig. 52. Since it seems to be appropriate to consider localities given by Cretzschmar to be in

accordance with those given by the collector, with the above 'area' is most convenient to associate the type locality of the species Vespertilio leucomelas Cretzschmar, 1830 = Barbastella leucomelas (Cretzschmar, 1830). In this area the type series lectotype: SMF II.M.1.a = SMF 4343; paralectotype: SMF II.M.1.b = SMF 12393; Mertens (1925), Kock (1969a) was collected in 1822 and/or 1826."
Benda and Mlíkovský (2008: 36) mention "Several authors believed that the name *Vespertilio leucomelas* was published in 1826, i.e. in the year when "Rüppell's Atlas" (see Cretzschmar, 1826) begun to be issued. According to Mertens (1925: 19), the sheets 18-19 associated with Tables 27-30 of Cretzschmar (1826-1830), containing also the description of *V. leucomelas* (sheet 18 and Table 28, respectively), were published in 1830 (see also Kock, 1969a, Corbet and Hill, 1992, Bates and Harrison, 1997, and/or Rydell and Bogdanowicz, 1997).". - Etymology: From the Greek "leucos" and "melas".

? *Barbastella barbastellus leucomelas:* (Name Combination).

? *Barbastella leucomelas:* (Current Combination).

TAXONOMY:

Included in *barbastellus* by Kock (1969a: 176). Horáček *et al.* (2000: 133 - 134) indicate that western *leucomelas* might be conspecific with *barbastellus*, but retain it as a valid species. If both are conspecific, the correct name for the eastern Barbastelle would be *Barbastella darjelingensis* Hodgson, in Horsfield, 1855. Zhang (2007: 1393) indicate that *leucomelas* from Sichuan, Taiwan, and Japan is different from the Egyptian one, and should therefore not be considered conspecific with *darjelingensis*.

.

Benda *et al.* (2008f: 49) confirmed that *leucomelas* represents a separate species.

COMMON NAMES:

Arabian: Khaffash. Czech: ďasík arabský (netopýr skalní). Dutch: Arabische mopsvleermuis. English: Eastern Barbastelle, Eastern Barbastelle Bat, Arabian barbastelle, Sinai Barbestelle, Asiatic Barbastelle, Asian Barbastelle. French: Barbastelle orientale. German: Östliche Mopsfledermaus. Hebrew: בלומף שחור, Blumaf Shahor. Russian: Азиатская широкоушка [= Aeiatskaya shirokouchka].

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)), although it seems to be rare, it is very widespread and is unlikely to be declining fast enough to qualify for listing in a more threatened category (Benda *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017cz).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017cz). 2008: LC ver 3.1 (2001) (Benda *et al.*, 2008b; IUCN, 2009). 1996: Lower Risk/least concern.

Regional

None known.

Legal Status

It is included in Eurobats (Bonn Convention) and so should be protected in party range states (e.g., Georgia).

MAJOR THREATS:

More information is needed regarding threats to this species throughout its range. In South Asia (India, Nepal, and Pakistan) deforestation has decreased the area and quality of the species' habitat. Activities associated with war may be a threat to this species in all parts of its western Palaearctic range (damage and disturbance to caves and old buildings, disruption to habitat) (Benda *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017cz).

CONSERVATION ACTIONS:

Further surveys and monitoring are needed for this species to determine the current population status, range and major threats (Benda *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017cz).
It probably occurs in several protected areas throughout its range (Benda *et al.*, 2008b; IUCN, 2009; Monadjem *et al.*, 2017cz).

GENERAL DISTRIBUTION:

Barbastella leucomelas was considered to be a very widespread species, with a distribution reaching from the Caucasus eastwards to Iran, Afghanistan and India, and onwards to China and Japan. These populations were, however, reassigned to *B. darjelingensis*. In the western part of the distribution area, there were isolated populations known from Sinai (Egypt) and the southern tip of Israel, as well as Eritrea in North Africa (Benda *et al.*, 2008b). It occurs up to 2,500 m asl.

Native: Eritrea, Egypt (Sinai); Israel, Jordan (Benda *et al.*, 2010b: 185; Kruskop *et al.*, 2019: 463), and Saudi Arabia.

ECHOLOCATION:

In Jordan, Benda *et al.* (2010b: 204) recorded three different types of calls, which they called A, A2, and B. These calls had the following parameters: A: Start frequency: 37.1 ± 1.3 (34.9 - 40.3) kHz, End frequency: 29.2 ± 1.1 (27.7 - 31.8)

kHz, Peak frequency: 33.8 ± 1.0 (32.7 - 36.0) kHz, Pulse duration: 2.9 ± 0.4 (1.9 - 3.5) ms, and Inter-pulse duration: 76.8 ± 39.3 (50.5 - 146.0) ms. A2: Inter-pulse duration: 125.8 ± 30.5 (94.0 - 201.0) ms. B: Start frequency: 44.1 ± 0.5 (43.0 - 45.0) kHz, End frequency: 34.3 ± 2.9 (29.8 - 38.5) kHz, Peak frequency: 42.7 ± 1.3 (40.0 - 44.2) kHz, Pulse duration: 13.0 ± 4.2 (6.9 - 17.6) ms, and Inter-pulse duration: 52.6 ± 6.4 (43.0 - 65.0) ms.

In Israel, *B. leucomelas* alternates between two call types (Hackett *et al.*, 2016: 223, 225): type I (8 calls): Pulse duration: 1.81 ± 0.11 ms, F_{start}: 35.85 ± 0.71 kHz, F_{end}: 29.70 ± 0.53 kHz, F_{peak}: 33.20 ± 0 kHz. Type II (6 calls): Pulse duration: 4.62 ± 0.40 ms, F_{start}: 43.90 ± 0 (43.8 - 44.0) kHz, F_{end}: 32.33 ± 2.67 (29.1 - 35.2) kHz, F_{peak}: 39.83 ± 0.75 (38.9 - 41.1) kHz.

ROOST:
It roosts in caves, tunnels, crevices, old buildings, mines, tree hollows, and can be found beneath bark (Benda *et al.*, 2008b).

POPULATION:
Structure
It is a sedentary insectivore, with 3 - 8 females in nursery colonies, with females normally living separately to males (Benda *et al.*, 2008b).

Density
Considering its wide range there seems to be little information available about the population of this species. Within its range in Africa the population size and trends are currently unknown. In Southwest Asia, it is considered to be rare and is poorly known. In 2005, the species was found in Sinai (Egypt) in surveys for the first time in 180 years (D. Kock *pers. comm.,* in Benda *et al.*, 2008b). For the former Soviet Union, the species is listed in the second edition of the Red Book of the USSR (1984) as Rare but was considered to be "least concern" (K. Tsytsulina *pers. comm.,* in Benda *et al.*, 2008b). In Japan, it has been observed only rarely except in Hokkaido. In the past 30 years there have also been records from the prefectures of Iwate, Saitama, Gifu and Ehime (Abe *et al.*, 2005).

Trend
2016: Unknown (Monadjem *et al.*, 2017cz). 2008: Unknown (Benda *et al.*, 2008b; IUCN, 2009).

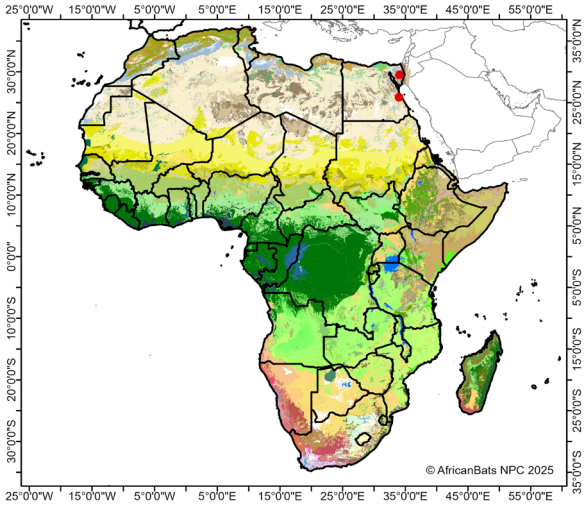

Figure 347. Distribution of *Barbastella leucomelas*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Egypt.

Genus ***Otonycteris*** Peters, 1859

*1859. *Otonycteris* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 223. Publication date: 1859 [Goto Description]. - Comments: Type species: *Otonycteris hemprichi* Peters, 1859. This publication covers a meeting held on 28 February 1859. - Etymology: From the Greek "*οὖς*" or "*ὠτός*", meaning ear and "*νυκτερις*", meaning bat (see Palmer, 1904: 489; Gharaibeh and Qumsiyeh, 1995: 3). (Current Combination).

TAXONOMY:
Koopman (1993a) and McKenna and Bell (1997) placed it in the tribe Nycticeini, but recent phylogentic analysis have grouped this taxon within the tribe Plecontini (Bogdanowicz *et al.*, 1998; Qumsiyeh and Bickham, 1993; Simmons, 2005: 481). Pine *et al.* (1971) and Hoofer and Van Den Bussche (2001) who suggest a close relationship between *Otonycteris* and *Antrozous* which presently is within the subfamily Antrozoinae (Simmons, 2005). Simmons (2005: 498) places the subfamily Antrozoinae within the Vespertilionidae based on recent molecular studies based on DNA sequence data (Hoofer and Van Den Bussche, 2001), a placement in line with more traditional classifications (Miller, 1897; Hill and Smith, 1984; Koopman, 1993a, 1994; McKenna and Bell, 1997). But, Simmons (1998) who raised this group to family level also moved it to the family Molossidae. Simmons (2005: 498) retained Antrozoinae as a subfamily level within the Vespertilionidae, but its placement is unclear and further studies are needed to clarify it.

Miller (1907) suggested *Otonycteris* shares relationships with *Eptesicus*, *Scoetocus* and *Scotomanes*. Hill and Harrison (1987) included *Otonycteris* in the Plecotini but included

Rhogeessa, *Baedon*, and *Nycticeius*. While Koopman (1993a) suggested that the genus *Otonycteris* is a distinct genus with no relationship to other vespertilionidae species.

Earlier systematics recognised six species, which Ellerman and Morrison-Scott (1951) synonymised all recognised forms within a single species *O. hemprichii*. Benda and Gvoždík (2010: 97) showed using morphological and molecular data, that a second species should be recognised *O. leucophaea* (Severcov, 1873) from central Asia.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Otonycteris*: ***hemprichii*** Peters, 1859; *leucophaea* (Severtzov, 1873) - Turkmenistan, Uzbekistan, Kirghizia, Tadzhikistan, Afghanistan, Iran, Pakistan and Kashmir.

COMMON NAMES:
Czech: pustinní ušani. English: Desert Bats, Desert Long-eared Bats, Long-eared Desert Bats, Desert Big-eared Bats. French: Oreillards du désert. German: Wüsten-Großohren.

GEOGRAPHIC VARIATION:
Benda and Gvoždík (2010: 87) using morphological comparison across the entire genus range supports the existence of three morphotypes which correspond to their geographic origin:

O. h. hemprichii Peters, 1859 - small and medium-sized bats from North Africa and the Levant with relatively wide and short rostra, wide braincases, large tympanic bullae and high coronoid processes of the mandible and rather small and robust bacula.

O. h. cinerea Satunin, 1909 and *O. h. jin* Cheesman and Hinton, 1924 - large bats from Iran and Saudi Arabia with relatively narrow and short rostra, narrow braincases, large tympanic bullae and high coronoid processes of the mandible and rather small, robust bacula.

O. leucophaea (Severcov, 1873) - medium-sized bats from Central Asia with relatively wide and long rostra, medium-wide braincase, small tympanic bullae, and low coronoid process of the mandible and rather large and narrow bacula.

Otonycteris hemprichii Peters, 1859

*1859. *Otonycteris Hemprichii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 223. Publication date: 1859. Type locality: Egypt: Nile Valley S of Assuan (Egypt) & Chondek (Sudan). [Goto Description]. Syntype: ZMB 441: skull in skin. Collected by: Friedrich Wilhelm Hemprich and Christian Gottfried Ehrenberg; collection date: September 1821 - 21 July 1822. See Qumsiyeh (1985: 59); Turni and Kock (2008). Syntype: ZMB 442: skull in skin. Collected by: Friedrich Wilhelm Hemprich and Christian Gottfried Ehrenberg; collection date: September 1821 - 21 July 1822. See Qumsiyeh (1985: 59); Turni and Kock (2008). - Comments: This publication covers a meeting held on 28 February 1859. Type locality restricted by Kock (1969a: 183 - 184), since originally no locality was given. - Etymology: In honour of Friedrich Wilhelm Hemprich (1796 - 1825) (see Kozhurina, 2002: 15). (Current Combination).

1866. *Plecotus ustus* Fitzinger and Heuglin, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 546. Publication date: 1866. Type locality: Sudan: Northern province: Wadi Halfa [21 55 N 31 20 E]. Holotype: NMW 8604: skull only. Collected by: Theodor Von Heuglin. See Benda and Gvoždík (2010: 101). - Comments: *Nomen nudum*: see Anderson and de Winton (1902: 118), Ellerman and Morrison-Scott (1951: 180), Allen (1939a: 93), Kock (1969a: 183), Qumsiyeh (1985: 59), Gharaibeh and Qumsiyeh (1995: 1).

1902. *Otonycteris petersi* Anderson, Zoology of Egypt: Mammalia. Revised and completed by W.E. de Winton, F.Z.S. Hugh Ress, Ltd., London, 120. Type locality: Iraq: Fao: Persian Gulf. - Comments: Extralimital.

1909. *Otonycteris cinereus* Satunin, Materials on the knowledge of mammals of Caucasus and Transcaspian Regions, XII-XVI. Izvestiya Kavkazskago Muzyeya (Tiflis). [in Russian, with German summary], 4: 281. Type locality: : "Nukendzag, Ge country, Persian Beluchestan". - Comments: Nevertheless, Ognev (1928: 579) restricted the type locality to "Zirkuh country, near Bamrud, Khorasan" (= Zarakkuh country, near Bamrud, Khorassan, E Iran) and this change was accepted by subsequent authors (Etemad, 1967, 1969; DeBlase, 1980; Baranova et al., 1981; Gharaibeth and Qumsiyeh, 1995).
Extralimital.

1924. *Otonycteris jin* Cheesman and Hinton, Ann. Mag. nat. Hist., Series 9, 14: 549. Type locality: Saudi Arabia: Hasa: Hufuf. - Comments: Extralimital.

1936. *Plecotus auritus saharae* Laurent, Bull. Soc. Hist. nat. Afr. Nord, 27: 408, fig. Publication date: December 1936. Type locality: Algeria: El Goléa [30 35 N 02 53 E].

? *Otonycteris hemprichi hemprichi:* (Alternate Spelling).

? *Otonycteris hemprichi:* (Alternate Spelling).

? *Otonycteris hemprichii cinerea:* (Name Combination).

? *Otonycteris hemprichii hemprichii:* (Name Combination).

? *Otonycteris hemprichii jin:* (Name Combination).

? *Otonycteris hemprichii:* (Current Spelling).

TAXONOMY:
Reviewed by Harrison and Bates (1991), Horáček (1991), Bates and Harrison (1997) and Benda and Gvoždík (2010).

Most of the forms currently attributed to the species rank of *O. hemprichii* (Simmons, 2005: 481), were originally described as separate species: *O. petersi* Anderson, 1902 (Anderson and de Winton, 1902; Kinnear, 1916; Bianchi, 1917; Cheesman and Hinton, 1924; Ognev, 1928); *O. cinerea* Satunin, 1909 (Bobrinskoy, 1925; Noack, 1887; Kuzyakin, 1950, 1965; Strelkov, 1963; Strelkov *et al.*, 1978). Ellerman and Morrison-Scott (1951) synonymised all recognised forms within *Otonycteris* into a single species *O. hemprichii*, with tree subspecies (*hemprichii, cinerea, jin*), but marked this combination with a question mark. Kock (1969a: 183) did not recognise any subspecies within *O. hemprichii*. Although Corbet (1978: 59) recognised five valid subspecies (*hemprichii, jin, petersi, leucophaeus, cinerea*, he noted that "it seems likely that variation will prove to be continuous throughout the range". While Nader and Kock (1983c) stated that pelage coloration was inadequate for subspecies definition, Horáček (1991) and Horáček *et al.* (2000: 133) carried out a partial analysis of geographic variation where they found that the differences in pelage coloration and size was clinal, and did not support the recognition of separate subspecies. Benda *et al.* (2006) performed a simple comparison of a set of *Otonycteris* specimens from North Africa and the Middle East, which showed clear morphotypes that confirmed categorial variation recognising two subspecies (*hemprichii, cinerea*). In the past, five subspecies have been recognized (Atallah, 1977; Ellerman and Morrison-Scott, 1951; Harrison and Bates, 1991; Gharaibeh and Qumsiyeh, 1995; Koopman, 1993a) - the nominotypical form *O. h. hemprichii* Peters, 1859, *O. h. leucophaeus* (Severcov, 1873); *O. h. cinerea* Satunin, 1909; *O. h. petersi* Anderson, 1902; and *O. h. jin* Cheesman and Hinton, 1924.

Benda and Gvoždík (2010), examining both morphological and molecular data, concluded that one of the previously recognized subspecies, *O. h. leucophaeus* (Severcov, 1873), should be elevated to full species rank *O. leucophaea* (Severcov, 1873), from central Asia. In *Otonycteris hemprichii*, they recognized three distinct subspecies: *O. h. hemprichii* Peters, 1859 from North Africa, Levant and Mesopotamia; *O. h. cinerea* Satunin, 1909, from the mountainous areas of eastern Arabia and Iran; and *O. h. jin* Cheesman and Hinton, 1924, from the lowland deserts of eastern Arabia and southeasternmost Iran.

COMMON NAMES:
Albanian: Lakuriq nate veshgjatë i Hemprich-it. Arabian: Khafash abiad, Khaffash. Armenian: Սպիտակպոչ սրականջ. Azerbaijani: Ağqarın oxqulaq yarasa. Basque: Hemprich belarrihandi. Belarusian: Стрэлавух Хемрыха. Bosnian: Hemprihov dugouhi šišmiš. Breton: Skouarnegell Hemprich. Bulgarian: Пустинен дългоух прилеп. Castilian (Spain): Orejudo de Hemprich. Catalan (Spain): Orellut d'Hemprich. Croatian: Hemprichov dugouhi šišmiš. Czech: Netopýr pustinný, ušan pustinný. Danish: Storøret flagermus. Dutch: Woestijngrootoorvleermuis. English: Hemprich's Long-eared Bat, Hemprich's Desert Bat, Hemprich's Desert Long-eared Bat, Hemprich's Long-eared Desert Bat, Long-eared Desert Bat, Desert Long-eared bat, Hemprich's Arrow-headed Bat, Hemprich's Big-eared Bat, Hemprich´s arrow-eared bat. Estonian: Suur-teravkõrv. Finnish: Aavikkolepakko. French: Chauve-souris à oreilles pointues de Hemprich, Oreillard d'Hemprich. Frisian: Woastyngrutearflearmûs. Galician (Spain): Orelludo de Hemprich. Georgian: ჰემპრიხის ისარყურა. German: Wüsten-Großohr, Hemprichs Wüstengroßohr, Hemprichs Großohrfledermaus. Greek: Ωτονυχτερίδα της ερήμου. Hebrew: אודן, Udnan. Hungarian: Sivatagi hosszúfülű-denevér. Irish Gaelic: Ialtóg fhadchluasach Hemprich. Italian: Orecchione di Hemprich. Latvian: Hempriha sikspārnis. Lithuanian: Strėliaausis lygianosis. Luxembourgish: Wüstegroussouer. Macedonian: Хемпричиев долгоушест лилјак. Maltese: Farfett il-Lejl Widnejħ Twal tad-Dežert. Montenegrin: Pustinjski škorpiojed. Norwegian: Ørkenlangøre. Polish: Uszorek pustynny. Portuguese: Morcego de Hemprich. Rhaeto-Romance: Ureglia lunga da Hemprich. Romanian: Liliacul urecheat de desert. Russian: Стрелоух белобрюхий. Serbian: Пустињски дугоушан [= Pustinjski dugoušan]. Scottish Gaelic: Ialtag fhad-chluasach Hemprich. Slovak: Večernica šípouchá. Slovenian: Škorpjonojedi pušcavež. Swedish: Okenlångöra. Turkish: Uzunkulaklı Çöl Yarasası. Ukrainian: Стріловух білочеревий. Welsh: Ystlum hirglust Hemprich.

CONSERVATION STATUS:
Global Justification
This is a relatively common species in desert and sub-desert habitats of the SW Palaearctic. It has a presumed large population, but the current trend is unknown. However, if it is in decline, it is unlikely to be at a rate which would qualify it for inclusion in the threatened categories. There are no major threats to the species, although it may

be affected by pesticides in some parts of its range. Therefore, it is listed as Least Concern (LC ver 3.1 (2001)) (Benda *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017b). 2008: LC ver 3.1 (2001) (Benda *et al.*, 2008c; IUCN, 2009). 1996: LR/lc [as *Otonycteris hemprichi*].

Regional
None known.

MAJOR THREATS:
Although not a major threat this species is affected by pesticides (Benda *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017b). Sherwin *et al.* (2012: 174), furthermore, list the small distribution range, water stress and the aerial hawking feeding style to be the risk factors related to climatic change. Bilgin *et al.* (2012: 434) predict that climatic change will result in a major range contraction for *O. hemprichii*.

CONSERVATION ACTIONS:
Benda *et al.* (2008c) [in IUCN (2009)] and Monadjem *et al.* (2017b) report that the species presumably occurs in some protected areas across its range. No other specific measures are known, although it will be protected under national legislation in some of the range states. A study on the impacts of pesticides is required, especially ways in which the impact might be minimised.

GENERAL DISTRIBUTION:
Otonycteris hemprichii occurs in the southern desert and sub-desert belt of Western and Central Palaearctic from Morocco and Niger as far east as north-west India. It is possibly present in the whole of the desert area in the north of Africa where there is suitable habitat. In the Mediterranean region it is recorded from Morocco, Algeria, Tunisia, Libya, Niger, northern Sudan and Egypt. In the Middle East it is found in Israel, Palestine, Jordan, Lebanon, Syria and a single locality from southeastern Turkey. It has an area of occupancy of >20,000 km^2 and occupies an altitude of up to 2,400 m (in Pakistan).

Albayrak and Aşan (1999: 65) mention one specimen from a locality in southern Turkey.

Benda and Gvoždík (2010: 95) allocate specimens previously referred to *O. hemprichii* from Central Asian should be rather referred to *Otonycteris leucophaea* (Severcov, 1873).

Native: Afghanistan; Algeria; Egypt; Iran, Islamic Republic of; Israel; Jordan; Kazakhstan; Libyan Arab Jamahiriya; Morocco (Benda *et al.*, 2010a: 158; El Ibrahimi and Rguibi Idrissi, 2015: 363; Dbiba *et al.*, 2025: 7); Niger; Oman; Qatar; Saudi Arabia; Sudan; Syrian Arab Republic; Tajikistan; Tunisia (Dalhoumi *et al.*, 2016b: 867; 2023: 4); Turkey; Turkmenistan; United Arab Emirates (Anonymus, 2008: 38); Uzbekistan.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
In their study on the reversibility of the mandibular symphyseal fusion, Scott *et al.* (2012: 2943) mention that this symphysis is fully fused in *O. hemprichii*.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987), and Benda and Gvoždík (2010: 93). Benda and Gvoždík (2010: 87) found that the bacula from different parts of the distribution range were very similar in shape. The bones are simple, dorso-ventrally flattened, crescent-shaped sticks. The baculum length were 2.47 - 3.31 mm long. Slightly differing specimens, originating in northeastern Iran and Kirghizstan, possessed larger bacula (length= 3.02 - 3.31 mm), relatively narrower and in most cases also slightly less curved than bacula from other parts of the range (baculum length = 2.47 - 2.96 mm) (Benda and Gvoždík, 2010: 87).

FUNCTIONAL MORPHOLOGY:
In Israel, Marom *et al.* (2006: 954) found that the physiological responses of *O. hemprichii* to a range of ambient temperatures (both by night and by day) are characteristic of a mammal adapted to arid environments.

SEXUAL DIMORPHISM:
Bogdanowicz and Owen (1996: 494) found that females are approximately 4.4 % larger than males.

ECHOLOCATION:
Holderied *et al.* (2010: 425) indicate that *Otonycteris hemprichii* is a whispering bat (approx. 80 dB peSPL), with short, multiharmonic calls. The two dominant harmonics sweep from 39 to 22 kHz, and from 77 to 43 kHz, with average peak frequencies respectively 29.96 ± 5.3 kHz and 54.45 ± 5.5 kHz. The pulse duration is 2.46 ± 1.1 ms, the pulse interval 131.6 ± 82.0 ms.

In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for 66 calls: F_{start}: 46.8 ± 8.6 (34.2 - 68.3) kHz, F_{end}: 20.4 ± 3.0 (15.0 - 25.6)

kHz, F_{peak}: 26.8 ± 3.2 (19.4 - 31.8) kHz, duration: 7.2 ± 2.4 (2.9 - 11.9) ms, and interpulse interval: 142.7 ± 52.9 (72.0 - 302.0) ms.

For Iran, Benda *et al.* (2012a: 183) provide two series of data: **1**: F_{start}: 38.8 ± 2.1 (28.6 - 32.8) kHz, F_{end}: 22.1 ± 0.2 (21.9 - 22.3) kHz, F_{peak}: 22.9 ± 6.1 (16.9 - 29.9) kHz, duration: 3.7 ± 0.3 (3.4 - 4.1) ms, interpulse interval: 157.9 ± 22.1 (143.0 - 190.1) ms; **2** (hand released in a close room): F_{start}: 35.0 ± 2.2 (30.5 - 38.6) kHz, F_{end}: 20.1 ± 0.7 (19.0 - 21.2) kHz, F_{peak}: 26.2 ± 2.6 (23.5 - 32.3) kHz, duration: 2.6 ± 0.5 (1.7 - 3.6) ms, interpulse interval: 44.4 ± 19.3 (26.8 - 80.5) ms.

From Israel, the following values were obtained by Hackett *et al.* (2016: 223) from 68 calls: Pulse duration: 5.19 ± 3.52 ms, F_{start}: 36.86 ± 2.95 (25.3 - 46.3) kHz, F_{end}: 20.94 ± 2.16 (18 - 25.3) kHz, F_{peak}: 24.45 ± 2.73 (20.5 - 34.1) kHz.

Disca *et al.* (2014: 226) indicate that the type of call is FM multi H for specimens from Morocco, with the following parameters: F_{start}: 42.4 ± 1.6 kHz, F_{end}: 17.0 ± 0.6 kHz, F_{peak}: 25.3 ± 1.0 kHz, $F_{max\ first\ harmonic}$: 45.3 ± 1.7 kHz, bandwidth: 25.3 ± 1.9 kHz, duration: 5.2 ± 0.3 ms.

Tunisian bats were reported to have F_{start}: 46.68 ± 6.35 (30.7 - 55.9) kHz, F_{end}: 17.72 ± 1.40 (15.7 - 18.9) kHz, F_{max}: 22.97 ± 2.80 (18.9 - 27.7) kHz, duration: 6.49 ± 1.54 (4.0 - 8.4) ms and Interpulse interval: 200.92 ± 61.65 (112.2 - 313.9) ms (Dalhoumi *et al.*, 2023: 5).

Luo *et al.* (2019a: Supp.) reported the following data (Free flying bats): F_{peak}: 24.45 kHz, F_{start}: 36.86 kHz, F_{end}: 20.94 kHz, Band width: 15.92 kHz, and duration: 5.19 ms.

In the United Arab Emirates, Davis (2007: 7) reports the ending frequency to be around 18 kHz.

Holderied *et al.* (2010: 425) also suggest that this bat is probably a passive gleaner, listening to noises generated by their prey. In a test environment, moving scorpions were found within 5 to 58 seconds, whereas non-moving or dead scorpions were not found at all.

Hackett *et al.* (2014: 3028), however, found that *O. hemprichii* switches between being a passive gleaner and an aerial hawker. Aerial hawking seems to occur when their usual prey becomes scarcer (e.g., desert scorpions - *Scorpio maurus palmatus* - at the end of a hot, dry summer) or less active (e.g., common yellow scorpions - *Buthus occitanus israelis* (Hackett *et al.*, 2014: 3031). The bats also switch from low-amplitude echolocation calls during ground gleaning to high-call amplitude when flying in the open, suggesting that the cost of the shorter detection distance of low-amplitude calls is too high during aerial hawking. (de Framond *et al.*, 2023: 1).

Molecular Biology:

Karyotype

Arslan and Zima (2014: 14) mention 2*n* = 28, FNa = 46, FN = 50, and a medium-sized submetacentric X. No data were available for the Y chromosome. The autosomal complement contains seven large metacentrics, two large submetacentrics, one small metacentric and three acrocentric pairs (of which one is dot-like). They also indicate that the karyotype with 2*n* = 30, FN = 48, BA = 20, a submetacentric X chromosome and a dot-like Y chromosome for specimens reported by Zima *et al.* (1992b) from Kyrgystan is actually for *O. leucophaea*.

Genetics

See Hoofer and Van Den Bussche (2003), Mayer *et al.* (2007), and Benda and Gvoždík (2010: 88).

Habits:

Horáček (1991) reported that *O. hemprichii* foraged in two different ways; very close to the ground (40 - 80 cm) or at a height of some 4 - 8 meters above the ground. Holderied *et al.* (2010: 429) reported a flight height of 2.19 ± 1.0 m above the ground while searching for prey at Park Sapir, Israel, and a flight speed of 3.52 ± 1.3 m/s.

Hackett *et al.* (2014: 3030) found that *O. hemprichii* specimens flew slower during aerial hawking than during their passive gleaning foraging flights.

Roost:

Daniel *et al.* (2010: 295) found that during pregnancy, female bats roosted either alone, or in small groups of two to five individuals. While during lactation, female bats roosted without males in groups of two to five individuals. Korine *et al.* (2013: 131) reported that, in Israel, female bats roosted primarily in cracks during reproduction, and most of these were facing the morning sun. They also indicated that during pregnancy horizontal cracks were used, whereas vertical cracks were used by lactating females. Some of these roosts were used year after year.

Diet:

Studies from different parts of its range indicate that its prey includes mainly large ground arthropods (Coleoptera, Blattodae, Othoptera, Solpugida, Heteroptera, Hymenoptera, and Scorpionidae) (Horáček, 1991; Whitaker *et al.*, 1994: 75; Arlettaz *et al.*, 1995; Fenton *et al.*,

1999; Benda *et al.*, 2001, 2006, 2010: 83, 2012a: 469; Conenna and Korine, 2024: 115).

Andreas (2010: 265) mentions that it is suggested that *O. hemprichii* is a potential carnivore. However, there is no proof for this. Furthermore, no perch feeding was observed for this species and this type of tactics is generally used when consuming relatively larger preys.

Holderied *et al.* (2010: 425) indicate that 70 % of the droppings can contain scorpion fragments. They also observed that while capturing the scorpions, the bats were frequently stung, even in their faces, without any indication of poisoning, and the scorpions' poison glands and stinger were eaten too. Page and Bernal (2019: "3") indicated that the toxicity of the scorpions did not influence their selection as prey.

Benda *et al.* (2014c: 100) analysed 14 faecal pellets from one individual and found robust crickets (Ensifera; 97.1 % by volume), complemented by a small proportion of moth remnants (Lepidoptera; 2.9 %).

POPULATION:
Structure and Density
Mostly solitary animals, female colonies up to 18 individuals (Benda *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2017b).

Trend
2016: Unknown (Monadjem *et al.*, 2017b). 2008: Unknown (Benda *et al.*, 2008c; IUCN, 2009). *O. hemprichii* populations within the Asia Minor and Levant region are unknown population trend, under predictive climate change scenarios (Bilgin *et al.*, 2012: 433).

ACTIVITY AND BEHAVIOUR:
Daniel *et al.* (2010: 296) showed that *O. hemprichii* delayed their foraging emergence time as gestation progressed from the first to the second trimester, while during nursing the bats' emergence time to forage did not change. Emergence time of female bats from their roosts during pregnancy was delayed from an average of 18h33 (about 40 min after sunset) in the first trimester of pregnancy (late March and beginning of April) to an average of 20h00 (about 1 h and 50 min after sunset) during the second trimester of pregnancy (Daniel *et al.*, 2010: 295). Contrary to the situation during pregnancy, emergence time of bats from their day roosts during nursing did not change with the sunset times, and was almost always between 20h00 and 21h00 (Daniel *et al.*, 2010: 295). Pregnant bats did not emerge to forage more than four times per night; the average was two bouts per night, whereas lactating bats made up to six foraging bouts per night (Daniel *et al.*, 2010: 296).

Daniel *et al.* (2010: 297) observed that female bats often used both deep and shallow daily torpor during the first two trimesters of pregnancy, with skin temperature frequently dropping as low as 15° C, while pregnant females used only shallow torpor during the last trimester of pregnancy and nursing.

Korine *et al.* (2015: 5) point out that the activity of *O. hemprichii* could be underestimated because of the whispering nature of their echolocation calls.

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

Daniel *et al.* (2010: 295) estimated that pregnancy began by the end of March, and that parturition took place around the first week in June. Body mass of pregnant bats increased by over 50% from the beginning to the end of pregnancy (22 - 35 g).

In the United Arab Emirates, Davis (2007: 7) thinks the females are pregnant in May-June.

PARASITES:
The tick *Argas vespertilionis* (Latreille, 1802) was reported from Jordan by Benda *et al.* (2010b: 294), who also indicate that the only two other ectoparasites found in the Middle East are *Argas hermanni* Audouin, 1827 in Egypt, and the flea *Araeopsylla wassifi* Traub, 1954 in Turkey.

Sándor *et al.* (2021a: 4) reported the presence of the argasid ticks *Chiropterargas boueti* (Roubaud and Colas-Belcour, 1933) and *Chiropterargas confusus* (Hoogstraal, 1955).

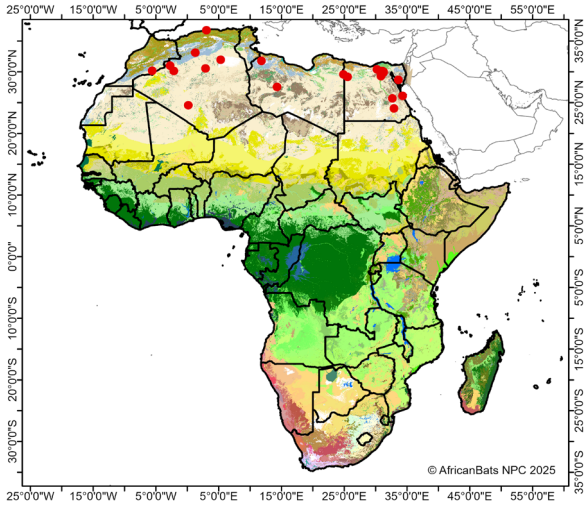

Figure 348. Distribution of *Otonycteris hemprichii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Algeria, Egypt, Libya, Morocco, Niger, Sudan.

Genus ***Plecotus*** E. Geoffroy St.-Hilaire, 1818

1816. *Macrotus* Leach, Cat. Mamm. Birds B.M, p 5. - Comments: Type species: *Macrotus europaeus* Leach, 1816 [= *Vespertilio auritus* Linnaeus, 1758]. Preoccupied by *Macropus* Gray, 1842, *Nomen nudum* by Pavlinov *et al.* (1995: 103).. - Etymology: From the Greek "*μακρός*", meaning large and "*ούς*" or "*ώτός*", meaning ear, referring to very large ears (see Palmer, 1904: 395).

*1818. *Plecotus* E. Geoffroy Saint-Hilaire, Description des Mammifères qui se trouve en Egypte, 2: 112, pl 2, No 3. Publication date: 1818. - Comments: Type species: *Vespertilio auritus* Linnaeus, 1758. - Etymology: From the Greek "*pleko*" meaning folded or twisted and "*otis*" meaning ear (see Jones, 1977a: 3; Álvarez-Castañeda and Álvarez Solórzano, 1996: 43). Gardner (2005: 184) considers this to be masculine (*Plec* = twisted + *ot* = ear(ed) + *us* (Latin second declension ending)). (Current Combination).

1829. *Plecautus:* F. Cuvier. - Comments: Lapsus: see Cabrera (1914). (Lapsus).

? *Plecotus sp.:*

TAXONOMY:
A key to the genus was published by Jones (1977a: 1). Mediterranean and Atlantic islands forms reviewed by Juste *et al.* (2004a).

Benda *et al.* (2006) indicated that Benda *et al.* (2004c) and Spitzenberger *et al.* (2006) performed combined genetic and morphological analyses of Mediterranean plecotine bats with very similar results but with a slightly different interpretation. The difference is in the taxonomic evaluation of the *kolombatovici* clade of the *austriacus* group (in the sense of Juste *et al.* (2004a). This clade consists of a mosaic of morphotypes with a relatively very shallow genetic divergence. Benda *et al.* (2004c) coidentified this group with one species *P. teneriffae*, containing three to four more or less distinct forms living in allopatry (*teneriffae*, *kolombatovici*, *gaisleri*, and a possible fourth form in the Maghreb, but preliminary included into *gaisleri*). Spitzenberger *et al.* (2006) distinguished two species in the clade, the monotypic *P. teneriffae* and *P. kolombatovici* with three forms, *kolombatovici*, *gaisleri*, and the unnamed Maghrebian form. A third possible interpretation, considering three species within the clade (which well confirm with the morphological evidence) was recently suggested by Mayer *et al.* (2007). Since all three analyses used almost the same types of character sets, their interpretations are alternatives arising from almost identical results. Thus, contrary to Benda *et al.* (2006) who suggest to follow the 'intermediate' designation *P.* (*teneriffae*) *gaisleri* for the populations of the Maghreb and Cyrenaica, the IUCN evaluated *P. kolombatovici* including these North African populations. Spitzenberger (2021: 19) mentioned that *P. kolombatovici* occurs in the Maghreb (Morocco, Algeria, Tunisia), Tripolitania and Cyrenaica (Libya) in the south, and Anatolia, Greece, Albania, Croatia, and Italy in the north of the Mediterranean region, but she also indicates that the systematics of *P. kolombatovici* should still be subjected to a thorough study using nuclear markers, especially to assess its relation to P. teneriffae.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Plecotus*: *auritus* (Linnaeus, 1758) – Norway, Ireland and Spain to Sakhalin Isl (Russia), Korea, Japan, northern China, Nepal, India (Simmons, 2005: 482); *austriacus* (J.B. Fischer, 1829) – England and Spain to Mongolia and western China (Simmons,

2005: 482); ***balensis*** Kruskop and Lavrenchenko, 2000; ***christii*** Gray, 1838; *gobiensis* Dolch, Stubbe, Gärtner, Thiele, Ariunbold, Batsaikhan, Lkhagvasuren, Stubbe and Steinhauser, 2021 – Mongolia; *homochrous* Hodgson, 1847 – Nepal, Pakistan, India; *kolombatovici* Dulic, 1980 – Croatia and nearby islands in the Adriatic Sea (Simmons, 2005: 483); ***koslovi*** Bobrinskii, 1926 – S Mongolia, N China; *macrobullaris* Kusjakin, 1965 – from the Caucasus and Asia Minor (Russia, Georgia, Armenia, Azerbaijan, Iran, Turkey), the Alps (France, Switzerland, Liechtenstein, Austria) and the Balkans (Croatia, Serbia, Albania, Montenegro, Macedonia, Greece), the Pyrenees (Andorra, France, Spain), Crete, Syria; *ognevi* Kishida, 1927 – Taiga and southern Siberian mountains, Sakhalin, Kurilles, N Mongolia, Korea, China, Kazakhstan, Mongolia, Russia; *sacrimontis* G.M. Allen, 1908 – Asia from Altai Mts through C Siberia and Tranbaicalia to Far East and Japan; *sardus* Mucedda, Kiefer, Pidinchedda and Veith, 2002; *strelkovi* Spitzenberger, 2006 – Afghanistan, China, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Tadjikistan; *taivanus* Yoshiyuki, 1991 – Taiwan (Simmons, 2005: 483); ***teneriffae*** Barrett-Hamilton, 1907; *turkmenicus* Strelkov, 1988 – Turkmenistan, Usturt, Mangyashlak, Kazakhstan (possibly Iran), Mongolia; *wardi* Thomas, 1911 – Caucasus, Transcaucasia, Pamiro-Altain, Tian-Shan, Kazakhstan, Tarbatatai, Karakorum, Hindukush, Himalaya, ? Iran, ? Turkey, Pakistan, India, and Nepal.

COMMON NAMES:
Czech: praví ušani, ušanové, srostlouchové, pletušanové, vrásničové. English: Long-eared bats, Old World Big-eared Bats, Big-eared Bats, Old World Long-eared Bats. French: Oreillards, Chauves-souris à grandes oreilles. German: Langohrfledermäuse, Langohren. Ukrainian: Вухань [= Vukhan'].

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
González-Dionis *et al.* (2021: 12) indicate that the genus *Plecotus* was split up into the "*austriacus*" group (Europe and north Africa) and the "*auritus*" group (Middle East and Europe), which occurred during the Miocene/Pleistocene boundary at about 5 mya.

GENERAL DISTRIBUTION:
Dorst and de Naurois (1966: 292) report on *Plecotus austriacus* specimens collected on the Cape Verdian islands of Maio and Santiago. Borloti *et al.* (2020: 3), however, indicate that it is still unknown whether the Cape Verdian bats belong to *P. austriacus (sensus strictu)* or *P. teneriffae/P. kolombatovici*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Canary Islands (Spain), Cape Verde.

Plecotus balensis Kruskop & Lavrenchenko, 2000

*2000. *Plecotus balensis* Kruskop and Lavrenchenko, Myotis, 38: 6, figs 1, 5, 6, 7. Publication date: December 2000. Type locality: Ethiopia: Southern Ethiopia, Bale Mountains National Park: Harenna Forest [06 45 N 39 44 E, 2 760 m]. [Goto Description]. Holotype: ZMMU S-164904: ad ♂, skin and skull. Collected by: Sergey V. Kruskop; collection date: 29 December 1995. - Etymology: In reference to the Bale mountains, the area from where the type specimen originated (see Kruskop and Lavrenchenko, 2000: 8). (Current Combination).

TAXONOMY:
See Simmons (2005).

COMMON NAMES:
Czech: ušan habešský. English: Bale Big-eared Bat, Bale Long-eared Bat, Ethiopian Big-eared Bat, Ethiopian Long-eared Bat. French: Oreillard d'Ethiopie. German: Bale-Langohr.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status. The species has only been recently described, and there remains very little information on the distribution of the species. While it is currently known from fewer than five locations, it seems plausible that the species ranges more widely than this and does not therefore qualify for a threatened category (Lavrenchenko *et al.*, 2008; IUCN, 2009; Lavrenchenko *et al.*, 2019).

Using machine learning techniques, Wieringa (2022: 535) predicted this species to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) (Lavrenchenko *et al.*, 2019). 2008: DD ver 3.1 (2001) (Lavrenchenko *et al.*, 2008; IUCN, 2009). 2004: VU D2 ver 3.1 (2001) (Lavrenchenko *et al.*, 2004a; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
This species is threatened by the rapid destruction of montane forest, presumably through extraction of timber and firewood, and the conversion of land to agricultural use (Lavrenchenko *et al.*, 2008; IUCN, 2009; Lavrenchenko *et al.*, 2019, Razgour *et al.*, 2020).

CONSERVATION ACTIONS:
Lavrenchenko *et al.* (2008) [in IUCN (2009)] and Lavrenchenko *et al.* (2019) report that this species has been recorded within the Bale Mountains National Park. Additional management of the area is needed to prevent further deforestation of the Harenna Forest. There is a need for further field surveys to better determine the range of this species.

GENERAL DISTRIBUTION:
Plecotus balensis is endemic to the Ethiopian highlands were it is currently known only with certainty from the upper belts of the Harenna Forest in the Bale Mountains National Park and from Abune Yosef (Kruskop and Lavrenchenko, 2000; Juste *et al.*, 2004a; Benda *et al.*, 2004c). There is an early record from "Shoa" (= Shewa), which probably came from the uplands north or northwest of Addis Ababa (Kruskop and Lavrenchenko, 2000). It is possible that the species occurs in similar areas of montane forest, but it has not been recorded during surveys in either the Beletta Forest or the Sheko Forest (Kruskop and Lavrenchenko, 2000). The species is found at elevations of 2,500 to 3,000 m asl, which is confirmed by new records reported by Ahmed *et al.* (2024: 179).

There are a number of poorly documented museum specimens that may have come from additional sites within Ethiopia, or possibly from adjacent Eritrea (although this may refer to a specimen of *Plecotus christii*) (Kruskop and Lavrenchenko, 2000).

Benda *et al.* (2011b: 44) tentatively assign *Plecotus* specimens from Yemen to this taxon as *Plecotus* cf. *balensis*.

Native: Ethiopia (Kruskop and Lavrenchenko, 2000; Juste *et al.*, 2004a; Benda *et al.*, 2004c).

Presence uncertain: Eritrea (Kruskop and Lavrenchenko, 2000).

DETAILED MORPHOLOGY:
Baculum
See Kruskop and Lavrenchenko (2000), Benda *et al.* (2004c).

MOLECULAR BIOLOGY:
Genetics
See Benda *et al.* (2004c), Juste *et al.* (2004c).

HABITAT:
All of the females and subadults caught by Razgour *et al.* (2020: 798) were found in *Juniperus procera* or *Erica arborea* forests, whereas they only caught adult males at the higher altitude Afroalpine moorlands.

Chakravarty *et al.* (2024: 7) assigned this species to the group of "highland dwelling species."

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 76 minutes, and the digestibility rate about 80.1 %.

POPULATION:
Structure and Density
Kruskop and Lavrenchenko (2000) mention that this bat appears to be relatively common within its limited distribution.

Trend
2018: Unknown (Lavrenchenko *et al.*, 2019).
2008: Unknown (Lavrenchenko *et al.*, 2008; IUCN, 2009).

PARASITES:
ARACHNIDAE
Argasidae
Ševčík *et al.* (2024: 6) reported *Secretargas transgariepinus* from *Plecotus balensis* in Ethiopia.

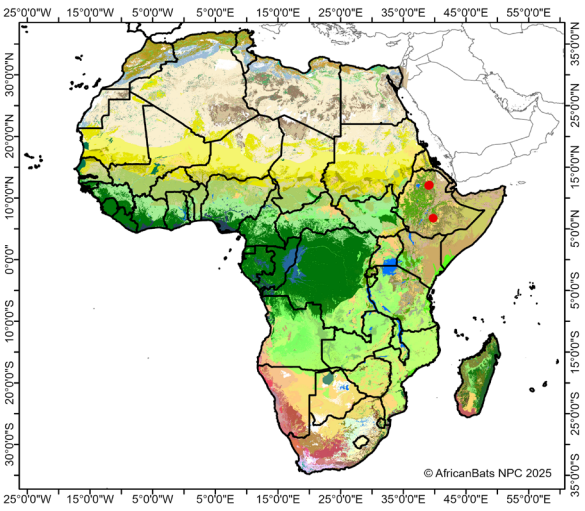

Figure 349. Distribution of *Plecotus balensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia.

Plecotus christii J. E. Gray, 1838

1829. *[Vespertilio auritus] ß aegyptius* J.B. Fischer, Synopsis Mamm, 117. Publication date: 1829 [Goto Description]. - Comments: Junior homonym of *Vespertilio pipistrellus var aegyptius*: see Qumsiyeh (1985: 65). Allen (1939a: 96) mentioned this form to be based on the description by E. Geoffroy, 1818: Description de l'Egypte, 2: 119.

*1838. *Plecotus christii* J. E. Gray, Mag. Zool. Bot., Edinburgh, 2 (12): 495. Publication date: 1 February 1838. Type locality: Egypt: southern Egypt: Nile valley between Qena and Aswan. Lectotype: NHMUK 1866.a: skin only. Collected by: Major (Dr.) Turnbell Christie. Skin in poor condition. Sometimes also mentioned as "NHMUK GMC M66a". - Comments: Type locality originally North Africa but restricted by Qumsiyeh (1985: 65, 67) to southern Egypt, Nile valley between Qena and Aswan. Between 16° 10' N, 32° 43' E and 24° 05' N, 32° 53' E: see Benda *et al.* (2008f: 70). - Etymology: In honour of Dr. Turnbull Christie, the collector of the type specimen (see Gray, 1838: 495).

1866. *Plecotus æthiopicus* Heuglin, in: Fitzinger and Heuglin, Sber. k. Akad. Wiss. Wien, math. naturw. Kl., 54 (1) 10: 546. Publication date: 1866. Type locality: Sudan: Bahr-el-Abiad [ca. 14 00 N 33 00 E]. - Comments: Nomen nudum. Mentioned by Allen (1939a: 96) as a synonym of *Plecotus auritus aegyptiacus* Geoffroy.

1878. *Plecotus ægyptiacus* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, p 178. Publication date: 15 June 1878. Type locality: Egypt. Topotype: MCZ 32976: ♂, alcoholic (skull not removed). Collected by: Dr. John Anderson. - Comments: Allen (1939a: 96) mentioned "I. Geoffroy, Mag. de Zool., 2: cl. 1, p. 2 of description of pl. 2-3, 1832, who repeats characters given by E. Geoffroy, in Description de l'Egypte, 2: 119, 1818. Egypt". Kock (1969a: 179) also mentions "I. Geoffr.", buf refers to Fitzinger (in Heuglin and Fitzinger, 1866: 545) as first reference, who reported it from Egypt, Abyssinia and Shoa. Pavlinov *et al.* (1995) mentioned Dobson, 1878 as author.

1911. *Plecotus christiei:* Thomas, Proc. zool. Soc. Lond., 1911, I: 160. - Comments: Unjustified emendation (Benda *et al.*, 2006). (Emendation).

1964. *Plecotus austriacus christiei:* - Comments: Unjustified emendation (see Thomas, 1911; Benda *et al.*, 2006). (Name Combination, Lapsus).

2002. *Plecotus cristiei:* Kiefer and Veith, Myotis, 39: 12. (Lapsus).

2008. *Plecotus christii petraeus* Benda, in: Benda, Dietz, Andreas, Hotový, Lučan, Maltby, Meakin, Truscott and Vallo, Acta Soc. Zool. Bohem., 72: 1, 71, fig 68. Type locality: Egypt: Sinai: Janub Sina Governate: Wadi Feiran: western edge of Feiran Oasis [28 43 N 33 37 E, 595 m]. Holotype: NMP 90496: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 8 September 2005; original number: pb2858. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NHMUK 1903.12.8.5: ad ♀, skull and alcoholic. Collected by: Dr. John Anderson. Tor [= El Tur], Sinai [Egypt]. Paratype: NMP 90497: sad ♀, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 9 September 2005; original number: pb2859. El Milga, Sinai, Egypt. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NMP 90499: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 10 September 2005; original number: pb2861. Feiran, Sinai, Egypt. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NMP 90518: ad ♀, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 10 September 2005; original number: pb2880. El Tur, Hammam Musa, Sinai, Egypt. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NMP 90519: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 10 September 2005; original number: pb2881. El Tur, Hammam Musa, Sinai, Egypt. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NMP 90523: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 15 September 2005; original number: pb2885. Ain Hudra, Sinai, Egypt. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: NMP 90533: ad ♀, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Josef Hotový and Radek K. Lučan; collection date: 18 September 2005; original number: pb2895. Ain Sudr, Sinai. See Benda in Mlíkovský *et al.* (2011: 138). Paratype: TAU M.7160: ad ♂, skin and skull. Collection date: 01 December 1977. Hashiba [= Umm Khisheib], Sinai [Egypt]. See Benda *et al.* (2008f: 71).

? *Plecotus auritus aegyptiacus:*

? *Plecotus austriacus christei:* (Lapsus).

? *Plecotus austriacus christii:* (Name Combination).

TAXONOMY:
Generally considered to be a subspecies of *austriacus* but see Benda *et al.* (2004c: 23), who raised it to species rank.

Since *Plecotus austriacus* is a strictly European species (Juste *et al.*, 2004a; Mayer *et al.*, 2007). Therefore, this species is removed from the list of African species. All the African records of *P. austriacus* in fact belong to *P. christii*, *P.* (*teneriffae*) *gaisleri* or to *P. balensis*.

COMMON NAMES:
Arabian: Khaffash. Czech: ušan egyptský. Dutch: Egyptische grootoorvleermuis. English: Christie's Long-eared Bat. French: Oreillard d'Egypte. German: Christis Graues Langohr. Hebrew: אוזן, Oznan.

CONSERVATION STATUS:
Global Justification
Probably a small population, suitable habitat might be fragmented, but needs more research to be properly assessed (Aulagnier and Benda, 2008; IUCN, 2009; Aulagnier and Benda, 2019).

Assessment History
Global
2018: DD ver 3.1 (2001) (Aulagnier and Benda, 2019). 2008: DD ver 3.1 (2001) (Aulagnier and Benda, 2008; IUCN, 2009). 2006: DD ver 3.1 (2001) (Aulagnier and Benda, 2004b; IUCN,

2006). 2004: DD ver 3.1 (2001) [assessed as *Plecotus christiei*] (Aulagnier and Benda, 2004b; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
Affected by human disturbance (Aulagnier and Benda, 2008; IUCN, 2009; Aulagnier and Benda, 2019).

CONSERVATION ACTIONS:
Aulagnier and Benda (2008) [in IUCN (2009)] and Aulagnier and Benda (2019) report that no conservation measures are in place. Further research on population is needed in order to make an assessment.

GENERAL DISTRIBUTION:
Plecotus christii is known only from a few localities in NE Africa, including eastern Libya (S. Aulagnier *pers. comm.*, 2007 in Aulagnier and Benda, 2008 [in IUCN, 2009]), Egypt including Sinai and Sudan. Benda *et al.* (2004c: 26) restricted its confirmed distribution to the north-eastern African desert region, Mayer *et al.* (2007) suggested its occurrence also in the Jordan desert.

A specimen from Eritrea may belong to this species or to *P. balensis* (Kruskop and Lavrenchenko, 2000).

Native: Egypt [Sinai] (Horáček *et al.*, 2000: 135); Libyan Arab Jamahiriya (Horáček *et al.*, 2000: 135); Saudi Arabia; Sudan (Horáček *et al.*, 2000: 135).

Presence uncertain: Eritrea.

DETAILED MORPHOLOGY:
Baculum
See Benda *et al.* (2004c).

ECHOLOCATION:
In Jordan, Benda *et al.* (2010b: 204) recorded the following parameters for 42 calls: Start frequency: 44.2 ± 2.8 (34.5 - 49.0) kHz, End frequency: 25.0 ± 1.0 (22.6 - 26.7) kHz, Peak frequency: 30.5 ± 1.7 (28.6 - 34.2) kHz, Pulse duration: 2.3 ± 0.5 (1.4 - 3.5) ms, and Inter-pulse duration: 57.6 ± 18.9 (18.0 - 89.0) ms.

Hackett *et al.* (2016: 223) reported on 25 calls from Israel: Pulse duration: 3.05 ± 0.98 ms, F_{start}: 37.22 ± 3.43 kHz, F_{end}: 23.85 ± 2.45 kHz, F_{peak}: 28.47 ± 2.74 kHz.

MOLECULAR BIOLOGY:
Genetics
See Benda *et al.* (2004c), Juste *et al.* (2004c), Spitzenberger *et al.* (2006, Mayer *et al.* (2007).

POPULATION:
Structure and Density
Probably very small population, only scattered and isolated records (Aulagnier and Benda, 2008; IUCN, 2009; Aulagnier and Benda, 2019).

Trend
2018: Unknown (Aulagnier and Benda, 2019).
2008: Unknown (Aulagnier and Benda, 2008; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
Korine *et al.* (2015: 5) indicate that the activity of *P. christii* could be underestimated because of the whispering nature of their echolocation calls.

PARASITES:
Argasidae
Sándor *et al.* (2021a: 4) reported the presence of *Secretargas transgariepinus* (White, 1846) and *Carios vespertilionis* Latreille, 1802. In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following tick: Argasidae: *Carios vespertilionis* Latreille, 1802.

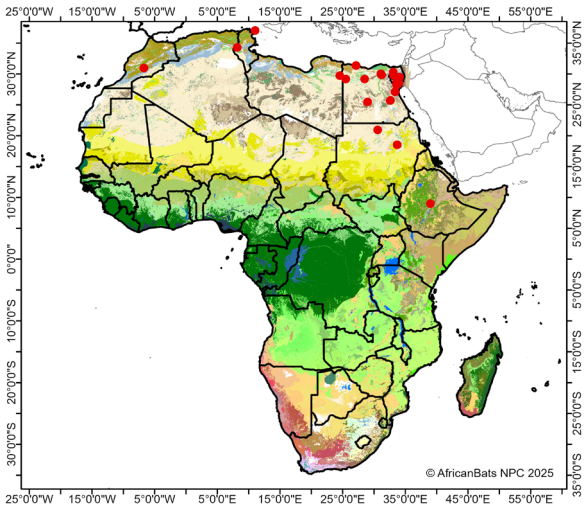

Figure 350. Distribution of *Plecotus christii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Egypt, Ethiopia, Libya, Morocco, Sudan, Tunisia.

Plecotus gaisleri Benda, Kiefer, Hanak & Veith, 2004

*2004. *Plecotus teneriffae gaisleri* Benda, Kiefer, Hanák and Veith, Folia Zool., 53 (Monogr 1): 28. Type locality: Libya: Cyrenaica: Al Jabal Al Akhdar district: 8 km SW Massah,: Wadi al Kuf (Jabal Akhdar Mts) [32 42 N 21 35

E, ca. 330 m]. [Goto Description]. Holotype: NMP 49911: ad ♀, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002. Paratypes: 4 MM + 2 FF; see Benda *et al.* (2004c: 29). Paratype: NMP 49905: ad ♂, skull and alcoholic. Collected by: Michal Andreas, Petr Benda, Vladimír Hanák, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2153. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). Paratype: NMP 49906: ad ♂, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2154. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). Paratype: NMP 49907: ad ♂, skull and alcoholic. Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2155. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). Paratype: NMP 49908: ad ♂, alcoholic (skull not removed). Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2156. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). Paratype: NMP 49909: ad ♀, alcoholic (skull not removed). Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2157. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). Paratype: NMP 49910: ad ♀, alcoholic (skull not removed). Collected by: Petr Benda, Vladimír Hanák, Michal Andreas, Antonin Reiter and Marcel Uhrin; collection date: 20 May 2002; original number: pb2158. See Benda *et al.* (2004c: 29), Benda in Mlíkovský *et al.* (2011: 137). - Comments: Considered a valid species by Mayer *et al.* (2007: Additional file 1) based on mitochondrial DNA analyses. - Etymology: In honour of professor Jiri Gaisler (Brno, Czech Republic) who significantly contributed to the knowledge of the North Afrian bat fauna (see Benda *et al.*, 2004c: 29).

2006. *P. kolombatovici gaisleri:* Spitzenberger, Strelkov, Winkler and Haring, Zool. Scr., 35 (3): 221. (Name Combination).

2020. *Plecotus cf. gaisleri* Ancillotto, Bosso, Smeraldo, Mori, Mazza, Herkt, Galimberti, Ramazzotti and Russo, Ecol. Evol., 10 (12): 5791. Publication date: 29 April 2020.

? *Plecotus gaisleri:* (Name Combination, Current Combination).

Taxonomy:

See under *Plecotus* above. Formerly considered as *P. auritus* or *P. austriacus*, for details see Benda *et al.* (2004c). Spitzenberger *et al.* (2006) include it in *P. kolombatovici*.

See Mayer *et al.* (2007) and Mayer *et al.* (2007: Additional material).

Ancillotto *et al.* (2020: 9) indicate that Maghrebian bats from Morocco show molecular and morphological differences and identified these tentatively as "*Plecotus* cf. *gaisleri*", although they might represent a yet undescribed species (p. 12).

Common Names:

Czech: ušan berberský. Dutch: Gaislers grootoorvleermuis. English: Gaisler's Long-eared Bat, The North African long-eared bat. French: Oreillard du Gaisler, Oreillard du Maghreb. German: Gaislers Langohrfledermaus, Libysches Langohr. Italian: Orecchione di Gaisler.

Conservation status:

Assessment History

Global

VU (Baillie and Groombridge, 1996); DD ver 3.1 (2001) (IUCN, 2004; Juste *et al.*, 2004a) as *P. teneriffae*.

General distribution:

Northern Cyrenaica (Libya); north-west Africa [Maghreb: Morocco (Benda *et al.*, 2010a: 158; El Ibrahimi and Rguibi Idrissi, 2015: 364 [as "*Plecotus teneriffae = (P. austriacus, P. gaisleri)*"]; Dbiba *et al.*, 2025: 7), Algeria, Tunisia (Dalhoumi *et al.*, 2014: 53; 2016b: 867; 2019b: 26; 2023: 4); Pantelleria island (Italy) and Malta (Batsleer *et al.*, 2019: 172; Ancillotto *et al.*, 2020: 1). In Lybia it is found in two areas, Tripolitania in the northwest and Cyrenaica in the northeast (Razgour, 2023: 658).

Echolocation:

Benda *et al.* (2010a: 163) are the first to provide echolocation data for this species, based on 58 Moroccan specimens. They report a F_{start}: 41.7 ± 1.7 (37.2 - 44.5) kHz, F_{max}: 31.9 ± 2.0 (28.3 - 37.0) kHz, F_{end}: 21.7 ± 2.3 (16.1 - 26.5), with a duration of 1.4 ± 0.3 (0.9 - 1.9) ms, and an inter-pulse interval of 40.9 ± 23.5 (12.9 - 95.7) ms.

Also from Morocco, Disca *et al.* (2014: 226) report the following: call type FM multi H, F_{start}: 51.4 ± 1.1 kHz, F_{end}: 22.0 ± 0.7 kHz, $F_{max\ all\ harmonics}$: 29.7 ± 1.0 kHz, bandwidth: 29.3 ± 1.0 kHz, duration: 2.6 ± 0.2 ms.

From Tunisia, Dalhoumi *et al.* (2023: 5) reported F_{start}: 43.00 ± 4.27 (38.1 - 48.3) kHz, F_{end}: 20.06 ± 3.46 (15.7 - 24.3) kHz, F_{max}: 28.10 ± 1.20 (26.4 - 29.7) kHz, duration: 3.44 ± 0.66 (2.3 - 4.0) ms and Interpulse interval: 135.30 ± 42.12 (85.6 - 186.2) ms.

Habitat:

Plecotus gaisleri is found in Mediterranean woodland habitats and sub-Mediterranean dry steppes, but also in desert habitats up to a few hundred kilometers from the coast (Razgour, 2020: 24). In Morocco, it occurs in the Atlas mountains up to an elevation of 2,630 m, whereas in Tunisian open pine forests, it occurs up to 950 m, where it was found flying over river beds and wadis (Razgour, 2023: 660). In Lybia, it

has been caught in oases, large caves, lakes surrounded by dense riparian vegetation, quarries, fortress ruins, under bridges, and in wadis with open shrubby vegetation (Benda *et al.*, 2014c: 104).

ROOST:
Benda *et al.* (2014c: 103) found a roost (probably the remainder of a maternity colony) in deep holes and crevices of the ceiling of an ancient ruin covered by carob trees. Further specimens were also recovered from ruins, indicating that *P. gaisleri* is probably a petrophilous species, which seems to select its roosts solely in underground spaces rather open to daylight and in rock fissures

Razgour (2020: 25) [referring to Benda and Aulagnier (2013b) and Benda *et al.* (2014b)] mentions summer roosts in rock crevices, caves, mosque towers, ancient ruins, caverns, old houses, cistern, and an underground aqueduct, whereas winter roosts include caves, mines, attics, wells and tree holes.

DIET:
Benda *et al.* (2014c: 108) examined eight sample sets of the diet and found large amounts of moths (Lepidoptera), most with wingspans between 30 and 35 mm. From other areas in Libya, orthopterans (Ensifera) or cockroaches (Blattoidea) formed the major part of the diet.

Based on three fecal samples, Gonçalves *et al.* (2024: 4) reported the diet for "*Pipistrellus austriacus*" on Madeira to consist mainly of Lepidoptera (80 %), followed by Coleoptera (20 %). In the Lepidoptera, the Noctuidae were the most common family (70 %), followed by Cerambycidae (20 %), and Geometridae (10 %). At species level, *Arhopalus ferus* (Mulsant, 1839) (Cerambycidae) and *Mythimna unipuncta* (Haworth, 1809) (Noctuidae) were the most common items (both 20 %). Of the 6 prey species, at least 50% referred to known agriculture pests.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

REPRODUCTION AND ONTOGENY:
Two pregnant females, both with one foetus, were collected in the central part of Wadi Al Kuf (Libya) on 19 May, whereas lactating females were found between 9 May and 4 August (Benda *et al.*, 2014c: 105).

PARASITES:
Benda *et al.* (2014c: 109) reported one egg with praelarvae of a mite belonging to the superorder Acariformes.

From Algeria, Bendjeddou *et al.* (2017: 15) and Khelfaoui *et al.* (2018: 67) reported the following ectoparasites: Nycteribiidae: *Nycteribia (Nycteribia) latreillii* (Leach, 1817) and Arachnida: *Spinturnix myoti* (Kolenati, 1856), *Eyndhovenia euryalis* (Canestrini, 1884) and *Argas vespertilionis* (Latreille, 1802).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Carios vespertilionis* Latreille, 1802; Ischnopsyllidae: *Rhinolophopsylla unipectinata arabs* Jordan and Rothschild, 1921; Nycteribiidae: *Nycteribia schmidlii schmidlii* Schiner, 1853; and Spinturnicidae: *Eyndhovenia euryalis euryalis* (Canestrini, 1884), *Spinturnix plecotinus* (Koch, 1839).

Razgour (2020: 25) also mentioned the mite *Eyndhovenia euryalis* (Canestrini, 1884), the flea *Nycteridopsylla pentactena* (Kolenati, 1856) and the tick *Carios boueti* Roubaud and Colas-Belcour, 1933.

VIRUSES:
Coronaviridae
Zeghbib *et al.* (2025: 22) mention that the first Coronavirus that was described from Algerian bats was more related to *Rhinolophus* viruses from Kenya and Guinea than Algeria.

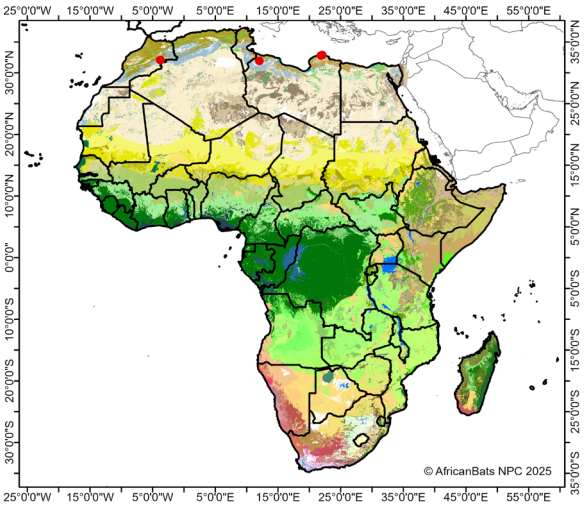

Figure 351. Distribution of *Plecotus gaisleri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Libya, Morocco.

Plecotus kolombatovici Dulic, 1980

*1980. *Plecotus austriacus kolombatovici* Dulic, 5th Internat. Bat Res. Conf., (D.E. Wilson and A.L. Gardner, eds), Texas Tech Press, 159. Type locality: Croatia: Dalmatia: 2.5 km NW Zrnovo: Korčula Isl [42??N 17??E, 276m]. Holotype: UZ 3007: ad ♀, skin and skull. Collected by: B. Dulic and O. Seple; collection date: 21 July 1969. See Spitzenberger *et al.* (2002: 3), Spitzenberger *et al.* (2006: 220). - Etymology: Dedicated to Juraj Kolombatovič, the investigator of the vertebrate fauna of Dalmatia.

2001. *Plecotus kolombatovici:* Spitzenberger, Strelkov and Haring, 50 (3): 162. - Comments: This species rank was errouneously attributed to a genetic clade that subsequently emerged to pertain to *P. macrobullaris* (Spitzenberger *et al.*, 2003).

TAXONOMY:
Synonymized with *P. austriacus* by Corbet (1978); but Mayer and von Helversen (2001) reported a high sequence divergence between a specimen from Germany and individuals caught in Croatia and Greece that could represent two separate species. This status was supported by Spitzenberger *et al.* (2001) and subsequent studies. Juste *et al.* (2004c: 10) suggest *teneriffae* is closely related with *kolombatovici*.

Fukui *et al.* (2020: 73) consider *P. kolombatovici* to be a valid species occurring in Morocco and Libya.

COMMON NAMES:
Croatian: Kolombatovićev dugoušan. Czech: ušan balkánský. Dutch: Balkangrootoorvleermuis. English: Kolombatovic's Big-eared Bat, Balkan long-eared bat, Kolombatovic's Long-eared Bat, Mediterranean Long-eared Bat. French: Oreillard Des Balkans. German: Balkan-Langohr. Italian: Orecchione di Kolombatovic.

CONSERVATION STATUS:
Global Justification
Assessed as Least Concern (LC ver 3.1 (2001)), as this species range is wide and uses a variety of habitats. Population trend has not been quantified, but it does not appear to be declining at a fast rate in North Africa (Hutson *et al.*, 2008d; IUCN, 2009).

Assessment History
Global
2008: LC ver 3.1 (2001) (Hutson *et al.*, 2008d; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
Pesticides and roost disturbance have a negative impact on the species but are not thought to be causing significant population declines at the global level. However, in Europe, where this species is largely restricted to coastal areas, disturbance of roost sites by tourists may be a major threat (Hutson *et al.*, 2008d; IUCN, 2009).

The small distribution range and the aerial hawking feeding style are identified by Sherwin *et al.* (2012: 174) as the risk factors linked with climatic change

CONSERVATION ACTIONS:
Hutson *et al.* (2008d) [in IUCN (2009)] report that it is protected by national legislation in most range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in those parts of the range where these apply. It is included in Annex IV of EU Habitats and Species Directive, and there is some habitat protection through Natura 2000. Recommended actions include monitoring population trends and minimising or preventing disturbance to roost sites in Europe.

GENERAL DISTRIBUTION:
Plecotus kolombatovici is a Mediterranean endemic with its distribution fragmented into three parts: southern regions of the Balkans and Asia Minor (Cyprus, Turkey, Syria, Lebanon and probably into Israel, Palestine and Jordan), northeast Libya (Cyrenaica) and northwest Africa from Morocco to northwest Libya, it was found in Malta and Pantellaria (Spitzenberger *et al.*, 2006). It occurs from sea level to higher altitudes in the Rif and Atlas mountains.

Native: Albania; Algeria; Croatia; Cyprus; Greece [Kriti]; Italy; Lebanon; Libyan Arab Jamahiriya Fukui *et al.*, 2020: 73); Malta; Morocco (Fukui *et al.*, 2020: 73); Serbia; Tunisia; Turkey.

Presence uncertain: Bosnia and Herzegovina; Israel; Montenegro; Palestinian Territory, Occupied; Syrian Arab Republic.

DETAILED MORPHOLOGY:
Baculum
See Đulić (1980), Benda *et al.* (2004c).

MOLECULAR BIOLOGY:
Karyotype
Đulić (1980) reported 2n = 32, X = metacentric, Y = acrocentric, differing from *P. austriacus* by biarmed small autosomes of pair 14.

Genetics
See Mayer and von Helversen (2001), Benda *et al.* (2004c), Juste *et al.* (2004c), Spitzenberger *et al.* (2006), Mayer *et al.* (2007).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 76 minutes, and the digestibility rate about 80.1 %.

POPULATION:
Structure and Density
Little is known about population size and trends in this species, although it is regarded as relatively common in North Africa. In Europe, the total population is estimated at fewer than 10,000 mature individuals, and it is suspected that the population may be declining. Summer colonies usually number 10 - 30 females, although a breeding colony of 120 females was found in a building in Croatia (F. Spitzenberger *pers. comm.,* 2006). Winter clusters are smaller (10 individuals), and the species is often solitary at this time of year (S. Aulagnier *pers. comm.,* 2007). It was thought that European, African and southwest Asian populations were isolated from each other, but range extensions as a result of recent records indicate that they might not be as isolated as was previously thought (Hutson *et al.*, 2008d; IUCN, 2009).

Trend
Decreasing (Hutson *et al.*, 2008d; IUCN, 2009).

Plecotus teneriffae Barrett-Hamilton, 1907

*1907. *Plecotus teneriffae* Barrett-Hamilton, Ann. Mag. nat. Hist., ser 7, 20 (120): 520. Publication date: 1 December 1907. Type locality: Canary Islands (Spain): Tenerife island: Orotava [28 23 N 16 31 W]. [Goto Description]. Holotype: NHMUK 1887.4.18.1: ad, skin and skull. Collected by: Ramon Gómez; collection date: 3 April 1887. See Benda *et al.* (2004c: 39). - Comments: Barrett-Hamilton (1907: 520) mentions that the type specimen has no skull. - Etymology: Referring to the island where the type specimen was collected. (Current Combination).
1939. *Plecotus auritus teneriffae:* G.M. Allen, Bull. Mus. comp. Zool., 83: 96. Publication date: February 1939. (Name Combination).
1971. *Plecotus austriacus teneriffae:* Hayman and Hill, Order Chiroptera. In Meester, J. & H.W. Setzer [Eds]: The mammals of Africa. An Identification manual. Part 2, 35. (Name Combination).
1978. *Plecotus austriacus austriacus:* Corbet, The mammals of the Palaearctic region: a taxonomic review, 61. - Comments: Not of J.B. Fischer, 1829. (Name Combination).
2021. *P[lecotus]. cf. teneriffae:* Kruskop, Artyushin, Yuzefovich, Undrakhbayar, Speranskya, Lisenkova, Bannikova and Lebedev, Acta Chiropt., 22 (2): Suppl. Publication date: 4 March 2021. (Name Combination).
? *Plecotus austriacus:* (Name Combination).

TAXONOMY:
Synonymized with *P. austriacus* by Corbet (1978); but see Ibáñez and Fernández (1985b). Genetic studies clearly show that *teneriffae* is more closely related with *kolombatovici*, while Pestano *et al.* (2003a: 306) suggested the North African to be the closest relative.

COMMON NAMES:
Albanian: Lakuriq nate veshgjatë i Teneriffae-ve. Armenian: Կանարյան կամ Տենեռիֆյան ականջեղ. Azerbaijani: Kanar palazqulağı. Basque: Belarrihandi kanariar. Belarusian: Вушан канарскі. Bosnian: Kanarski dugouhi šišmiš. Breton: Skouarnegell Tenerife. Bulgarian: Канарски дългоух прилеп. Castilian (Spain): Orejudo canario, Murciélago orejudo canario. Catalan (Spain): Orellut canari, Rat penat orellut canari. Croatian: Kanarski dugoušan. Czech: Netopýr kanárský, Ušan kanárský. Danish: Kanarielangøre. Dutch: Canarische grootoorvleermuis. English: Canary Long-eared Bat, Canary big-eared bat. Estonian: Kanaari suurkõrv. Finnish: Kanariankorvayökkö. French: Oreillard de Ténérife. Frisian: Kanaryske grutearflearmûs. Galician (Spain): Orelludo canario. Georgian: კანარიელი ყურა. German: Kanaren-Langohr, Kanaren-Langohrfledermaus, Teneriffa-Langohr. Greek: Ωτονυχτερίδα της Τενερίφης. Hungarian: Kanári-szigeteki hosszúfülű-denevér. Irish Gaelic: Ialtóg fhadchluasach Chanárach. Italian: Orecchione di Tenerife. Latvian: Tenerifes garausis. Lithuanian: Kanarinis ausylis. Luxembourgish: Kanaren-Laangouer. Macedonian: Тенерифов ушест лилјак. Maltese: Farfett il-Lejl Widnejħ Twal tal-GŻejjer Kanarji. Montenegrin: Kanarski slijepi miš. Norwegian: Kanarilangøre. Polish: Gacek kanaryjski. Portuguese: Morcego-orelhudo-canarino. Rhaeto-Romance: Ureglia gronda da Teneriffa. Romanian: Liliacul urecheat din Tenerife. Russian: Ушан канарский. Serbian: Канарски сиви дугоушан. Serbian Latin: Kanarski sivi dugoušan. Scottish Gaelic: Ialtag fhad-chluasach Chanaireach. Slovak: Ucháč kanársky. Slovenian: Kanarski uhatež.

Swedish: Kanarielångöra. Turkish: Kanaryarlar Uzunkulaklı Yarasası. Ukrainian: Вухань канарський. Welsh: Ystlum hirglust yr Ynysoedd Dedwydd.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:
González-Dionis *et al.* (2021: 13) reported on fossil remains of *P. teneriffae* on El Hierro and found these to differ from other European and north African species, specifically in the height of the paracone and metacone of M3 and in the cingulid of p4 and the lower molars.

CONSERVATION STATUS:
Global Justification
Juste and Alcaldé (2016b) justification for the global listing as Vulnerable (VU B1ab(iii,v)) due to this species has an EOO of < 20,000 km^2 and it is found on three, or possibly four, of the Canary Islands, which are each considered to be a single location based on the threat of habitat decline. It is linked to forest habitats that are shrinking, and recent declines have been recorded in the largest known breeding colony.

Assessment History
Global
2016: Vulnerable B1ab(iii,v) ver 3.1 (2001) (Juste and Alcaldé, 2016b). 2004: DD ver 3.1 (2001) (IUCN, 2004; Juste *et al.*, 2004a). 1996: VU (Baillie and Groombridge, 1996).

Legal Status
It is protected by national legislation in Spain. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention. It is included in Annex IV of EU Habitats & Species Directive.

MAJOR THREATS:
The population declined in the 1950s after aerial fumigation for pest control. Current threats include disturbance of colonies in their roosts, use of pesticides on agricultural land near to the forests, loss of woodland habitat, restoration of buildings and the destruction of roost sites (Trujillo, 2002). The recent decline of the La Palma maternity colony has been attributed to disturbance, and it is known that at least one individual from this colony has been taken by private collectors (Trujillo, 2002).

Sagot and Chaverri (2015: 1670) mention roost loss or disturbance, and habitat degradation or loss as major threats for this species.

CONSERVATION ACTIONS:
A bat protection programme aimed at protecting caves used as roost sites from human disturbance was instigated in 1993 (Benzal and Fajardo 1999). Protection of the species' woodland foraging habitat is also recommended (Trujillo 2002).

GENERAL DISTRIBUTION:
Plecotus teneriffae is endemic to the Canary Islands (Tenerife, La Palma, El Hiero) (Spain) (Benda *et al.*, 2004c: 28; Razgour, 2023: 661), where it occurs on altitudes between 100 and 2,300 m.

DETAILED MORPHOLOGY:
Baculum
See Ibáñez and Fernández (1985b), Benda *et al.* (2004c).

MOLECULAR BIOLOGY:
Genetics
See Pestano *et al.* (2003a), Benda *et al.* (2004c), Juste *et al.* (2004a), Spitzenberger *et al.* (2006), Mayer *et al.* (2007).

HABITAT:
On Madeira, Ferreira *et al.* (2022a: 1) reported that the activity of "*Plecotus austriacus*" was negatively influenced by cropland cover and that also altitude had a negative effect on its activity.

Ibáñez and Fernández (1985b: 148) report it to be primarily associated with *Pinus canariensis* forests and the transition zones with laurel forests.

ROOST:
Plecotus teneriffae is a crevice dwelling bat that mainly roosts in volcanic tubes, caves, water mines, and abandoned buildings (Razgour, 2020: 28, 2020: 663). In caves, these bats roost individually or in small clusters.

MIGRATION:
Razgour (2020: 28) mention that this species is very sedentary, not moving more that 10 km between roosts.

DIET:
Trujillo (1992: 80 - 83) report that the diet of *Plecotus teneriffae* mainly consists of Lepidoptera, and to a lesser extent Coleoptera. Within the Lepidoptera, the majority of the species belonged to the Noctuidae and the Geometridae.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 80 minutes, and the digestibility rate about 79.5 %.

POPULATION:
Structure and Density
Juste and Alcaldé (2016b) report that summer colonies usually consist of 10-30 females (the maximum number recorded is 61). Winter clusters are usually small (c.10 animals), and the species often roosts solitarily at this time of year. There are only two known breeding colonies (on La Palma and Tenerife respectively). The larger of these two (the La Palma colony) has declined in number in recent years (Trujillo, 2002).

Trend
2016: Decreasing (Juste and Alcaldé, 2016b).

REPRODUCTION AND ONTOGENY:
Razgour (2020: 28) mention that young are born in July, and lactating females were found between mid-July and the end of August/begin.of September.

PARASITES:
Estrada-Peña and Sanchez (1988: 309) described the mite *Steatonyssus (Steatonyssus) teidae* from a *P. teneriffae* specimen from La Caldera, Tenerife, Canary Islands.

Trujillo (1992: 83) and Razgour (2020: 28) mention the presence of *Steatonyssus (Steatonyssus) balcellsi* Estrada-Pena and Sanchez, 1988, *Steatonyssus (Steatonyssus) teidae* Estrada-Pena and Sanchez, 1988 and *Spinturnix plecotinus* (Koch, 1839).

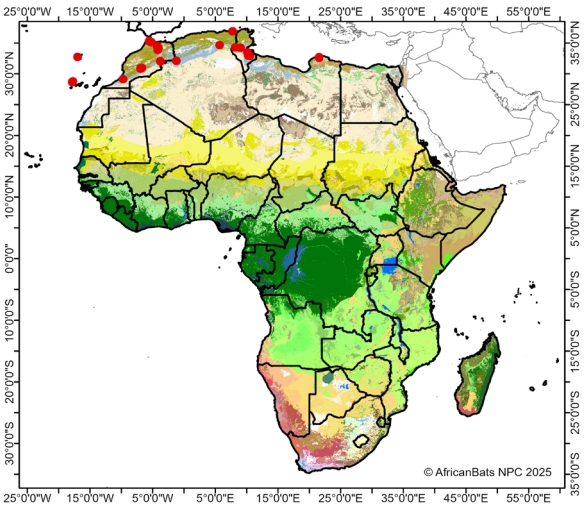

Figure 352. Distribution of *Plecotus teneriffae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Canary Islands (Spain), Libya, Madeira (Portugal), Malta, Morocco, Tunisia.

TRIBE Vespertilionini J. E. Gray, 1821

*1821. *Vespertilionini* J. E. Gray, London Med. Repos., 15 (1): 299. Publication date: 1 April 1821.

GENERAL COMMENTS:
Based on karyological data (the presence of three derived Robertsonian fusion chromosomes, 7/11, 8/9, and 10/12,), Volleth *et al.* (2023c: 35) created a new subtribe - Laephotina - containing the genera *Laephotis, Neoromicia, Afronycteris*, and *Pseudoromicia*. The close relationship of these genera is also supported by their penis and bacular morphology. Within the Laephotina, *Laephotis* and *Neoromicia* are the closest relatives, but Volleth *et al.* (2023c: 46)'s data were unable to support a close relationship between *Afronycteris* and *Pseudoromicia*.

TAXONOMY:
Baird *et al.* (2025: 6) state that the relationship between *Afronycteris+Pseudoromicia* and *Neoromica* and *Laephotis* is still not well resolved. However, based on four independent nuclear introns, Demos *et al.* (2025: 143) found strong support for the subtribe Laephotina, containing the genera *Afronycteris, Laephotis, Neoromicia* and *Pseudoromicia*. They also found a sister relation between *Laephotis* and *Neoromicia*, but the relation between *Afronycteris* and *Pseudoromicia* remains unclear. *Nycticeinops* + *Afropipistrellus* are considered to be sister to the Laephotina, and the differences between the two in nuclear introns, dentition and bacula support their recognition as separate genera.

Genus ***Afronycteris*** Monadjem, Patterson and Demos, 2020

1852. *Vespertilio:* Peters, Reise nach Mossambique, 61.
1860. *Hypsugo:* Kolenati, Monographie der Europäischen Chiroptern, 20. - Comments: In part. Not of Kolenati, 1856 (see Monadjem *et al.*, 2020a: 1127, 1138).
1878. *Vesperugo:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 183. Publication date: 15 June 1878. - Comments: In part. Not of Keyserling and Blasius, 1839 (see Monadjem *et al.*, 2020a: 1127, 1138).

1900. *Pipistrellus:* Miller, Proc. Wash. Acad. Sci., 2: 647. Publication date: 28 December 1900. - Comments: In part. Not of Kaup, 1829 (see Monadjem *et al.*, 2020a: 1138).
1907. *Myotis:* Matschie, Liste der von Herrn V.B. Schillings gesammelten Säugetier-Arten, 534. - Comments: In part. Not of Kaup, 1829 (see Monadjem *et al.*, 2020a: 1138).
1934. *Neoromicia:* Shortridge, The mammals of South West Africa, 59. - Comments: In part. Not of Kaup, 1829 (see Monadjem *et al.*, 2020a: 1138).
1951. *Eptesicops:* Roberts, The mammals of South Africa, 84. - Comments: In part. Not of Roberts, 1926 (see Monadjem *et al.*, 2020a: 1138).
*2020. *Afronycteris* Monadjem, Patterson and Demos, in: Monadjem et al., Zool. J. Linn. Soc., 191 (4): 1120, 1138. Publication date: 10 September 2020. - Etymology: From the Greek word νυχτερίδα, meaning bat, and the prefix Afro- referring to the African continent (see Monadjem *et al.*, 2020a: 1138).

TAXONOMY:
Currently (Simmons and Cirranello, 2024a) recognized species in the genus *Afronycteris*: ***helios*** (Heller, 1912); ***nanus*** (Peters, 1852).

Afronycteris helios (Heller, 1912)

*1912. *Pipistrellus helios* Heller, Smiths. Misc. Coll., 60 (12): 3. Publication date: 4 November 1912. Type locality: Kenya: 30 mi (48 km) S Mount Marsabit: Merelle Water [01 23 S 37 44 E]. [Goto Description]. Holotype: USNM 181813: ad ♂, skin and skull. Collected by: Edmund Heller; collection date: 22 July 1911; original number: 3065. - Etymology: From the masculine Greek substantive "*ἥλιος*" (hèlios), meaning "sun", referring to the ochraceous-buff colour of the dorsal fur (see Lanza *et al.*, 2015: 407).
1951. *Pipiestrellus helios:* Watson, Uganda J., 15 (1): xx. - Comments: Lapsus. . (Lapsus).
1968. *Pipistrellus nanus helios:* Funaioli and Lanza, Mon. Zool. ital., (NS) 2 (Suppl): 199. (Name Combination).
1987. *Pipistrellus (Hypsugo) helios:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination).
1994. *P[ipistrellus (Pipistrellus)] a[fricanus] helios:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 113. (Name Combination).
2002. *Hypsugo helios:* Kruskop, Plecotus et al., pars spec: 21. (Name Combination).
2006. *Neoromicia helios:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 134. (Name Combination).
2019. *L[aephotis] helios:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2020. *Afronycteris helios:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1138. Publication date: 10 September 2020. (Name Combination).

TAXONOMY:
Hayman and Hill (1971) indicated that the shape of the baculum supports the separation of *helios* from *Afronycteris nana*, which is confirmed by Kock (pers. Comm.). See discussion in Simmons (2005).

Simmons and Cirranello (2020) included *helios* in the genus *Laephotis*, but Monadjem *et al.* (2020a: 1138) include it (together with nana) in the newly erected genus *Afronycteris*.

COMMON NAMES:
Chinese: 桑布鲁伏. Czech: netopýr slunečný. English: Samburu Pipistrelle Bat, Helios Pipistrelle Bat, Heller's Pipistrelle Bat, Heller's Pipistrelle. French: Pipistrelle soleil. German: Samburu-Zwergfledermaus, Samburu-Pipistrelle. Italian: Pipistrèllo di Hèller.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of sufficient information on its extent of occurrence, natural history, threats and conservation status (Jacobs *et al.*, 2008t; IUCN, 2009; Jacobs *et al.*, 2014b).

Assessment History
Global
2014: DD ver 3.1 (2001) [assessed as "*Neoromicia helios*"] (R). 2008: DD ver 3.1 (2001) [assessed as "*Pipistrellus helios*"] (Jacobs *et al.*, 2008t; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004z; IUCN, 2004).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs *et al.*, 2008t; IUCN, 2009; Jacobs *et al.*, 2014b).

CONSERVATION ACTIONS:
Jacobs *et al.* (2014b) repeats what stated by Jacobs *et al.* (2008t) [in IUCN (2009)] who report that it is not known if the species is present in any protected area. There is a need for studies into the distribution, abundance, natural history and possible threats to this species.

GENERAL DISTRIBUTION:
Afronycteris helios is an East African species, which has been recorded from Djibouti, southern Somalia, southern Sudan, northeastern Uganda, Kenya and northern Tanzania. It may be more widely distributed (Peterson, 1987; Simmons, 2005).

Native: Djibouti; Kenya; Somalia; Sudan; Tanzania; Uganda.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

HABITS:
Keeley and Keeley (2004: 116) [referring to O'Shea (1980) and Happold and Happold (1996)] mention that male "*Pipistrellus nanus*" roosting in palm-thatched roofs show territoriality and aggressive competition for spacious roosts, whereas males in populations roosting in banana leaves appear not to defend territories aggressively, and indicate that this difference might be based on the availability of preferred roosts. However, the more likely explanation being that these differences are due to these two groups belonging to different species, as the thatched roof inhabiting form is most likely *A. helios*.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 52 minutes, and the digestibility rate about 84.4 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species (Jacobs *et al.*, 2008t; IUCN, 2009; Jacobs *et al.*, 2014b).

Trend
2014: Unknown (Jacobs *et al.*, 2014b). 2008: Unknown (Jacobs *et al.*, 2008t; IUCN, 2009).

PARASITES:
DIPTERA
Nycteribiidae
Basilia ansifera Theodor, 1956 - mainly a West African species reaching Lake Victoria in the east and Lake Nyasa in the south - nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110; Dick *et al.*, 2023: 73).

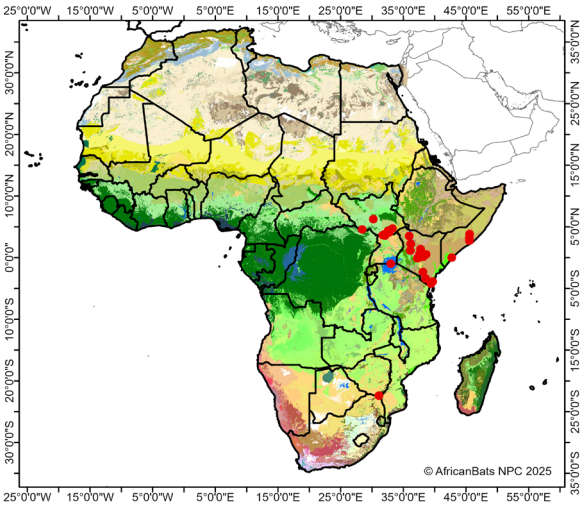

Figure 353. Distribution of *Afronycteris helios*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya, Somalia, South Africa, South Sudan, Tanzania, Uganda.

Afronycteris nanus (Peters, 1852)

1842. *Vespertilio Pipistrellus varietas africana* Rüppell, Mus. Senckenberg., 3 (2): 156. Type locality: Ethiopia: Shoa province: Shoa province [ca. 09 00 N 39 00 E]. [Goto Description]. Lectotype: SMF 4306: ad ♀, skin and skull. Collected by: Wilhem Peter Edward Simon Rüppell; collection date: 1842. Old number II.N.9*.a. (Name Combination).

*1852. *Vespertilio nanus* Peters, Naturwissenschaftliche Reise nach Mossambique, Zoologie, Säugethiere, 63, pl 16, fig 2. Publication date: 1852. Type locality: Mozambique: Inhambane [24 00 S 35 28 E]. [Goto Description]. Syntype: NHMUK 1907.1.1.421: ad, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters. See Turni and Kock (2008). Syntype: NHMUK 1907.1.1.422: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters. Syntype: NHMUK 1907.1.4.421: ad, skin and skull. Collected by: Prof. Wilhelm Carl Hartwig Peters. Syntype: NHMUK 1907.1.4.422: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters. Syntype: NMW 19644: ad ♂, alcoholic (skull not removed). Collected by: Prof. Wilhelm Carl Hartwig Peters. See Turni and Kock (2008). Syntype: ZMB 588a: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 588b: ad ♀, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). Syntype: ZMB 588c: ad ♂, skull and alcoholic. Collected by: Prof. Wilhelm Carl Hartwig Peters; collection date: between 1843 and 1847. See Turni and Kock (2008). - Etymology: From the Latin "*nanus*" meaning dwarf (see Lausen and Barclay, 2005: 5).

1855. *Vespertilio (Vesperugo) nanus:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 746. (Name Combination).

1860. *Hypsugo nanus:* Kolenati, Monographie der Europäischen Chiroptern, 18. (Name Combination).

1870. *Vesperugo pusillulus* Peters, J. Sci. mat. phys. nat., ser 1, 3 (10): 124. Publication date: December 1870. Type locality: Angola: Cabinda: Loango [ca. 04 52 S 12 52 E]. [Goto Description]. Syntype: ZMB 3975: ♂, alcoholic (skull missing). Collected by: José Vicente Barboza du Bocage. See Turni and Kock (2008). - Comments: The type locality (Loango) was originally located in Angola, but see Kock et al. (in prep).
1875. *Vesperugo nanus:* Dobson, Proc. zool. Soc. Lond., 1875, III: 472. (Name Combination).
1878. *Vesperugo (Vesperugo) nanus:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 237. Publication date: 15 June 1878. (Name Combination).
1888. *Vesperugo stampflii* Jentink, Notes Leyden Mus., 10: 54 (for 1887). Publication date: April 1888. Type locality: Liberia: Farmington River [06 08 N 10 22 W]. [Goto Description]. Holotype: RMNH MAM.17836: ad ♂, skull and alcoholic. Collected by: F.X. Stampfli; collection date: 1 July 1887. The RMNH catalog mentions two numbers: 17836.a (skull + loose bones) and 17836.b (wet specimen).
1889. *Vesperugo pagenstecheri* Noack, Zool. Jb. Syst., 4: 220, pl 2, fig 3, pl 5, fig 64 - 65. Publication date: 28 February 1889. Type locality: Congo (Democratic Republic of the): Bas Congo province: near mouth of Congo river, Banana Creek: Netonna [05 58 S 12 27 E]. [Goto Description]. Lectotype: SMF 2524: ad ♀, skull only. Collected by: P. Hesse; collection date: 1887. See Mertens (1925: 22). Paralectotype: SMF 2525: ad ♀, skull only. Collected by: P. Hesse. See Mertens (1925: 22). Noack (1889: 220) refers to two female specimens, both in alcohol and collected by P. Hesse.
1889. *Vesperus pusillus* Noack, Zool. Jb. Syst., 4: 216, pl 2, fig 3, pl 5, fig 60, 61. Publication date: 28 February 1889. Type locality: Congo (Democratic Republic of the): Congo River: Boma [05 50 S 13 03 E, 30 m]. [Goto Description]. Holotype: SMF 2523: juv ♂, skull only. Collected by: P. Hesse; collection date: 1887.
1897. *Vesperugo (Vesperugo) Pagenstecheri:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 112.
1900. *Pipistrellus minusculus* Miller, Proc. Wash. Acad. Sci., 2: 647, fig 43. Publication date: 28 December 1900. Type locality: Liberia: Mount Coffee [06 34 N 10 33 W]. [Goto Description]. Holotype: USNM 84500: ad ♀, skull and alcoholic. Collected by: Orator Fuller Cook Jr. Collection date: May 1894. Catalogued: 11 April 1898.
1900. *Pipistrellus stampflii:* Miller, Proc. Wash. Acad. Sci., 2: 647. Publication date: 28 December 1900.
1901. *Vespertilio (Pipistrellus) nanus:* Sclater, Mammals of South Africa, 123, 126. (Name Combination).
1903. *Pipistrellus nanus:* Cabrera, Mem. Soc. espan. Hist. nat., 1: 22. (Name Combination).
1906. *Vespertilio (Vesperugo) stampflii:* Johnston, Liberia, Volume II: 692. (Name Combination).
1907. *Myotis nanus:* Matschie, Liste der von Herrn V.B. Schillings gesammelten Säugetier-Arten, 534. (Name Combination).
1908. *Vespertilio (Glischropus) nanus:* Lönnberg, Sjöstedts Kilimanjaro-Meru Expedition, 2: 11. (Name Combination).
1911. *Pipistrellus culex* Thomas, Ann. Mag. nat. Hist., ser 8, 7 (41): 458. Publication date: 29 April 1911. Type locality: Nigeria: Northern Nigeria, Bauchi plateau: Kabwir [09 24 N 09 34 E, 2 700 ft]. [Goto Description]. Holotype: NHMUK 1911.3.24.4: ad ♀, skin and skull. Collected by: Rév. G.J. Fox; collection date: 15 May 1910; original number: 100.
1913. *Pipistrellus nanus australis* Roberts, Ann. Transv. Mus., 4: 67. Publication date: 20 October 1913. Type locality: South Africa: Transkei, Western Pondoland: Port St. Johns district: "Port St. Johns district" [ca. 31 27 S 29 33 E, 200 ft]. Holotype: TM 1076: ad ♀, skin and skull. Collected by: H.H. Swinny; collection date: 20 April 1908. Holotype for both *Pipistrellus africanus meesteri* and *Pipistrellus nanus australis*. - Comments: Replaced by *P. africanus meesteri* by Kock (2001a: 129). (Name Combination).
1917. *Pipistrellus abaensis* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 442. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Aba [03 53 N 30 17 E]. [Goto Description]. Holotype: AMNH 48979: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 18 December 1910; original number: 1825. Topotype: AMNH 48980: ♀, skin only. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 48981: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition.
1925. *Pipistrellus pagenstecheri:* Mertens, Senckenb. biol., 7 (1/2): 22.
1926. *Pipistrellus fouriei* Thomas, Proc. zool. Soc. Lond., 1926, I: 288. Publication date: 29 April 1926. Type locality: Namibia: NW Ovamboland: 32 mi NW of Rehoboth Mission Station: Ukualukasi [17 32 S 14 37 E, 3 400 ft]. [Goto Description]. Holotype: NHMUK 1925.12.4.20: ad ♀, skin and skull. Collected by: Captain Guy Chester Shortridge; collection date: 7 October 1924; original number: 1390.
1934. *Neoromicia pusilla pusilla:* Shortridge, Mammals of South West Africa, 59.
1939. *Pipistrellus nanus nanus:* G.M. Allen, Bull. Mus. comp. Zool., 83: 95. (Name Combination).
1951. *Eptesicops fouriei:* Roberts, Mammals of South Africa, 84.
1951. *Pipistrellus (Pipistrellus) nanus nanus:* Swynnerton and Hayman, J. East Afr. Nat. Hist. Soc., 20 (6-7) (90): 293 (for 1950). (Name Combination).
1953. *Pipistrellus (Pipistrellus) culex culex:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78.
1953. *Pipistrellus (Pipistrellus) culex fouriei:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78.
1953. *Pipistrellus (Pipistrellus) culex:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78.
1953. *Pipistrellus (Pipistrellus) nanus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1956. *Pipistrellus culex culex:* Eisentraut, Zool. Jb. Syst., 84 (3): 530.
1957. *[Pipistrellus] stampfli:* Aellen, Rev. suisse Zool., 64 (6): 202.
1959. *Pipistrellus nanus stampflii:* Booth, J. West Afr. Sci. Ass., 5 (1): 29. (Name Combination).
1968. *Pipistrellus (Pipistrellus) nanus fouriei:* Smithers, A check list and atlas of the mammals of Botswana (Africa), ???. (Name Combination).
1978. *Pipistrellus nanus fouriei:* Ansell, Mammals of Zambia, 24. (Name Combination).
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? *Neoromicia nanus nanus:* (Name Combination).
? *Neoromicia nanus stampflii:* (Name Combination).
? *Pipistrellus africanus nanus:* (Name Combination).

TAXONOMY:



Figure 354. *Afronycteris nana* caught in the Ubombo Mtns-NR, northern KwaZulu Natal, South Africa.

The oldest name for this species is (possibly) *africana*; see Koopman (1975: 400), but most authors still remained using the name *nana* (or *nanus*), until Koopman (1994: 112) and Simmons (2005), who mention this species under the name *Pipistrellus africanus*. In Opinion 2120 (Anonymus, 2005), however, the ICZN ruled that the name *Pipistrellus nanus* (currently *Afronycteris nana*) should be given precedence over *africana*, whenever the two are considered to be synonyms.

Bronner *et al.* (2003) state that Volleth *et al.* (2001) and Kearney *et al.* (2002) provided karyotypic evidence for the inclusion of the banana bat (*"Pipistrellus" nanus*) in *Neoromicia*.

Ansell and Dowsett (1988) and Koopman (1966) point out that *africanus* Ruppell, 1842 antedates *nanus* (Peters, 1852) as the valid name for this species. However, they continue to use the better-known name *nanus*, as topotypical *africanus* is restricted to Ethiopia (and is thus unlikely to be conspecific with *nanus*) and Happold (2003) has applied to the International Commission on Zoological Nomenclature for conservation of this specific epithet on the grounds of nomenclatural stability.

Grubb *et al.* (1998: 85) include it - as *nanus* - in the subgenus *Hypsugo*. Kearney *et al.* (2002: 68) states that *nanus* belongs to the genus *Neoromicia*.

Hoofer and Van Den Bussche (2003: 38) include this taxon as "*(Hypsugo) nanus*" in a separate, unnamed genus.

The generic alliance of *nanus* is certainly not clear at this stage. Most authors mention this species in the genus *Pipistrellus*, but as pointed out in the previous paragraphs, present taxonomical investigations seem to indicate that it should be included in *Neoromicia*. However, the assignement to *Hypsugo* or even a new genus is not yet excluded. Further research is needed to fix its generic assignment.

Recently, Meri Happold (pers. comm.) reported that unlike all other pipistrelles placed in *Neoromicia* by Simmons (2005) and also unlike all African species placed in *Hypsugo* (ibid.), "*P. nanus*" has nyctalodont lower molars (as have all African species in *Pipistrellus*). The taxonomic implications need further investigation.

Happold (ibid) also reported that the following subspecies of "*P. nanus*" (as "*Pipistrellus africanus*") were recognized by Koopman (1994) and/or Kock (2001a), but their status and geographic ranges are uncertain:
P. n. stampflii. Sierra Leone to Côte d'Ivoire.
P. n. culex. Nigeria, Ghana.
P. n. africanus. Zaire to Ethiopia, mostly in highlands.
P. n. nanus. Zaire, Kenya and Tanzania to South Africa, also Cameroon (Rosevear 1965).
P. n. fouriei. S Angola, W Zambia, N Namibia.
P. n. meesteri. Transkei, South Africa.
P. n. minusculus. Liberia.

Helbig *et al.* (2010: 168) suggest that *nanus* needs to be transferred to a genus that needs to be newly created or resurrected from the current synonymy.

Simmons and Cirranello (2020) included *nanus* in the genus *Laephotis*, but based on analyses of mitochondrial cytochrome b sequences, Monadjem *et al.* (2020a: 1120) concluded that this species (together with *helios*) should be assigned to a separate sister genus: *Afronycteris*.

Common Names:

Afrikaans: Piesangvlermuis. Arabian: Khouchaf al matoussat. Azande (DRC): Fulo. Castilian (Spain): Pipistrelo Enano. Chewa (Malawi): Ndemia. Chinese: 香蕉伏翼. Czech: netopýr banánový, netopýr šplhavý. English: Banana Pipistrelle Bat, Banana Bat, Banana Pipistrelle. French: Pipistrelle naine, Pipistrelle naine aux ailes brunes. German: Bananen Zwergfledermaus, Bananen-Fledermaus, Bananen-Pipistrelle, Mozambique Dämmerungsfledermaus, Zwerg-Hausfledermaus. Italian: Pipistrèllo di Pèters, Pipistrèllo nàno déi banàni. Kiluba (DRC): Kasusu. Kiswahili: Popomgomba. Malawian: Mnalimpsimpsi, Namsinsi, Ndemia. Manganja (Malawi): Chuchu. Misuku (Malawi): Kashusha. Portuguese: Morcego das bananeiras, Morcego-das-bananas. Tshokwe (Angola): Kateta. Yao (Malawi): Liputiputi (applied to all small bats).

Etymology of Common Name:

Characteristically this species roosts during the day in the rolled-up, sprouting terminal leaves of banana plants and has become associated with them in particular (Taylor, 2005).

Conservation Status:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Hutson *et al.*, 2008g; IUCN, 2009; Monadjem *et al.*, 2017bk).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Neoromicia nana*] (Monadjem *et al.*, 2017bk). 2008: LC ver 3.1 (2001) [assessed as *Pipistrellus nanus* (Hutson *et al.*, 2008g; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as "*Neoromicia nanus*"] (Jacobs, 2004d; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016m). 2004: LC ver 3.1 (2001) [assessed as "*Neoromicia nanus*"] (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this widespread and seemingly adaptable species (Hutson *et al.*, 2008g; IUCN, 2009; Monadjem *et al.*, 2017bk), although Aronson *et al.* (2013: 9) report a fatality due to wind turbines in South Africa.

CONSERVATION ACTIONS:
Hutson *et al.* (2008g) [in IUCN (2009)] and Monadjem *et al.* (2017bk) report that in view of the species wide range it is likely that it is present in many protected areas. Further research is needed into the taxonomy of this species.

GENERAL DISTRIBUTION:
Afronycteris nanus is widely distributed throughout most of sub-Saharan Africa. It ranges from Senegal in the west, through West and Central Africa, to Eritrea, Ethiopia and Somalia in the east; from here it is found southwards to southeastern South Africa. The species has been recorded from Madagascar, where it has only been reported from the Kirindy CFPF forest in western Madagascar, and from Zombitse (Rasolozaka, 1994), although Goodman *et al.* (2015a: 1012) reject the occurrence of the species on Madagascar. It has also been recorded from the Tanzanian islands of Pemba, Unguja [= Zanzibar], and Mafia (O'Brien, 2011: 290).

It appears to be absent, or largely absent, from northern Kenya, Namibia, southern Botswana, western Zimbabwe, northern Mozambique, Lesotho and much of South Africa. It is possible that the species ranges more widely in these areas than is currently known, and further field studies are needed to investigate the distribution of the species.

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,165,508 km^2. In South Africa, its distribution is mainly affected by the minimum temperature of the coldest month (Babiker Salata, 2012: 49).

Besides "*N. nana*", Taylor *et al.* (2018b: 63) also mentioned "*Neoromicia* cf. *nana*", whose echolocation calls do not match any known species.

Bates *et al.* (2006) recommend that the identity of the specimens from Madagascar need to be reviewed.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 568; Taylor *et al.*, 2018b: 63); Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Archer, 1975; Monadjem *et al.*, 2010d: 568); Burkina Faso (Kangoyé *et al.*, 2015a: 620); Burundi; Cameroon; Central African Republic; Chad; Congo (Bates *et al.*, 2013: 337); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 568); Côte d'Ivoire; Djibouti (Pearch *et al.*, 2001: 388); Equatorial Guinea; Eritrea; Eswatini (Monadjem *et al.*, 2010d: 569, Monadjem *et al.*, 2021: 5); Ethiopia; Gabon; Gambia (Emms and Barnett, 2005: 50); Ghana (Decher and Fahr, 2007: 18); Guinea (Ziegler *et al.*, 2002: 78; Fahr *et al.*, 2006a: 73); Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001:60); Kenya; Liberia (Monadjem and Fahr, 2007: 50 [as *Neoromicia nanus*]); Malawi (Happold *et al.*, 1988; Ansell and Dowsett, 1988: 41; Monadjem *et al.*, 2010d: 568); Mali; Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 568; Monadjem *et al.*, 2010c: 384); Namibia (Monadjem *et al.*, 2010d: 569); Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; South Africa (De Graaf, 1960; Monadjem *et al.*, 2010d: 569); Sudan; Tanzania (Stanley and Goodman, 2011: 47); Togo; Uganda (Kityo and Kerbis, 1996: 61); Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 569); Zimbabwe (Monadjem *et al.*, 2010d: 569).

Presence uncertain: Lesotho, Madagascar.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) contains a line drawing of the tragus of specimen DNSM 12594 from Mount Nimba, Liberia.

From western Uganda, Monadjem *et al.* (2011: 30) reported the following data for 5 specimens: Fa: 31.60 ± 0.758 mm, mass: 3.6 ± 0.89 g, wing loading: 4.2 ± 0.59 N/m^2, aspect ratio: 6.2 ± 0.14.

DENTAL FORMULA:
Dorst (1949: 47) indicates that the milk dentition of "*Pipistrellus nanus*" is very similar to that of *Pipistrellus kuhlii*. He also indicated that the milk teeth form a clearly separated arcade outside the permanent tooth series.

DETAILED MORPHOLOGY:
Penis
Fasel *et al.* (2020: 1394) indicated that this bat's glans penis is slightly globular and that long hairs covering the prepuce are radiating from it. There is also a light protuberance at the distal extremity of the penis.

Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

Skull
Using CT-microscans, Curtis and Simmons (2018: 1390) investigated the presence of mineralized elements in the rostra of bats, and found these to be present in *A. nanus*. However, the shape and size of these was different in the two specimens they examined. As both specimens were males, the differences are not sex-based.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 8.4 Pa, aspect ratio 7.3 for a wingspan of 21 cm and a wing area of 58 cm^2 and a body mass of 5 g.

ECHOLOCATION:
See Jacobs (1996), Taylor (1999b) and Taylor *et al.* (2005).

Schoeman and Waddington (2011: 291) mention a peak frequency of 67.1 ± 1.9 kHz and duration of 4.0 ± 0.9 ms for specimens from Durban, South Africa. Naidoo *et al.* (2011: 23) report a peak frequency of 68.1 ± 1.0 kHz and a duration of 3.1 ± 0.8 ms from the same area.

At Uzungwa Scarp Forest Reserve, Tanzania, Trentin and Rovero (2011: 57) indicate that the starting frequency is very variable (mean 86.9 kHz). In about 2 ms the call decreases from its maximum to its minimum at 60.7 kHz, after which it increases slightly to 64.5 kHz. The maximum intensity occurs at 66 kHz.

Taylor *et al.* (2013b: 17) recorded the following parameters for 4 calls from Swaziland: F_{max}: 77.2 ± 3.34 (74.4 - 80.9) kHz, F_{min}: 66.2 ± 0.92 (64.9 - 67.0) kHz, F_{knee}: 68.2 ± 1.60 (66.1 - 69.9) kHz, F_{char}: 66.9 ± 0.96 (65.4 - 67.4) kHz, duration: 3.2 ± 0.59 (2.4 - 3.6) ms. Also from Swaziland, Monadjem *et al.* (2017c: 179) reported: F_{min}: 69.7 ± 2.29 (66.8 - 71.8) kHz, F_{knee}: 72.3 ± 2.08 (70.6 - 75.1) kHz, F_c: 70.2 ± 2.25 (67.5 - 72.2) kHz and duration: 2.8 ± 0.32 (2.6 - 3.2) ms. The maximum distance over which they were able to dectect the calls was 10 m (mean: 5.8 ± 1.07 m).

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 68 (66 - 70) kHz. In the Mapungubwe National Park, Parker and Bernard (2018: 57) recorded 20 calls with F_{char}: 68.53 ± 2.10, F_{max}: 85.09 ± 10.70 kHz, F_{min}: 67.61 ± 2.57 kHz, F_{knee}: 72.45 ± 3.38 kHz, duration: 4.24 ± 0.83 ms and 8.15 ± 3.64 calls/sec.

Moir (2020: 30) and Geoffroy Saint-Hilaire (1810a: 371) recorded 1097 calls of 47 bats from southern KwaZulu-Natal and Eastern Cape (RSA): F_{max}: 91.8 ± 11.23 (71.92 - 118.39) kHz, F_{min}: 66.97 ± 2.26 (60.34 - 71.49) kHz, F_{char}: 67.28 ± 2.27 (61.02 - 71.68) kHz, F_{knee}: 71.17 ± 2.89 (65.27 - 77.96) kHz, and duration: 2.09 ± 0.55 (1.21 - 3.63) ms.

From western Uganda, Monadjem *et al.* (2011: 32) reported the following parameters for 5 calls: F_{min}: 71.06 ± 6.019 kHz, F_{max}: 98.94 ± 4.751 kHz, F_{char}: 79.76 ± 8.196 kHz, F_{knee}: 84.89 ± 7.145 kHz, duration: 1.1 ± 0.089 ms.

Eisenring *et al.* (2016: SI 2) reported PF: 66.8 ± 2.0 (63.0 - 69.9), HF: 94.7 ± 17.5 (69.6 - 117.9), LF: 63.7 ± 2.1 (59.8 - 66.9), DT: 0.0 ± 0.0 (0.0 - 0.1), DF: 31.0 ± 16.9 (4.9 - 55.8), IPI: 0.7 ± 0.3 (0.3 - 1.5) for 27 calls from the Aberdares Range in Kenya.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 70 kHz and duration: 4 ms.

For 1 FM/QCF type call from Maroua, Cameroon, Manga Mongombe (2012: 79) reported: F_{max}: 106.4 kHz, F_{min}: 96.6 kHz, F_{mean}: 101.7 kHz, F_{knee}: 106.4 kHZ, F_{char}: 96.9 kHz, and duration: 0.42 ms.

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 12 calls of a single bat: F_{peak}: 77.2 ± 3.3 (72.7 - 80.6) kHz, F_{min}: 63.4 ± 1.2 (59.9 - 64.6) kHz, F_{max}: 115.2 ± 7.6 (112.8 - 117.8) kHz, duration: 2.7 ± 0.7 (2.1 - 3.5) ms.

Two calls recorded by Adams and Kwiecinski (2018: 4) in the Kalahari Desert had the following characteristics: F_{char}: 61.5 ± 8.9 kHz, F_{max}: 74.3 ± 6.2 kHz, F_{min}: 61.1 ± 3.5 kHz, duration: 3.7 ± 0.3 ms.

17 calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 77.85 ± 5.89 kHz, F_{min}: 67.79 ± 0.86 kHz, F_{knee}: 69.93 ± 1.59 kHz, F_{char}: 68.54 ± 1.06 kHz, slope: 22.23 ± 31.88 OPS, duration: 2.66 ± 0.67 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 11 bats: F_{max}: 149.97 ± 85.61 kHz, F_{min}: 77.16 ± 6.86 kHz, F_{knee}: 1 ± 0.48 kHz, F_{char}: 3.17 ± 0.8 kHz, slope: 68.52 ± 2.18 OPS, duration: 301.04 ± 214.6 ms. 15 calls recorded at

the Venatia min by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 2.83 ± 0.28 ms, F_{min}: 66.95 ± 2.48 kHz, F_{max}: 77.73 ± 5.25 kHz, F_{knee}: 69.55 ± 1.86 kHz and F_{char}: 68.20 ± 1.86 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 21 "*Neoromicia nana*" calls from the Kruger Park (RSA): F_{min}: 63.9 ± 2 (60.3 67.2) kHz, Duration: 3.1 ± 0.8 (2.2 4.8) ms, F_{max}: 89.0 ± 16.9 (70.0 118.5) kHz, F_{knee}: 72.8 ± 7.5 (66.1 93.3) kHz, F_{char}: 67.7 ± 3.4 (63.5 78.5) kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype [as "*Neoromicia nana*"].

65 pulses from "*Neoromicia nanas*" (sic) recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 64 - 67 kHz, F_{max}: 74 - 80 kHz, F_{char}: 65 - 67 kHz, F_{knee}: 66 - 70 kHz and duration 3 - 4 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 68.53 ± 2.10 kHz, F_{max}: 85.09 ± 10.70 kHz and F_{min}: 67.61 ± 2.57 kHz.

In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 12 calls: Interpulse interval: 99.2 ± 56.7 (53.8 - 216.0) ms; F_{max}: 70.1 ± 3.1 (65.7 - 76.9) kHz; Start slope: -27.7 ± 5.1 (-19.1 - -37.5) kHz/ms; End slope: -8.2 ± 4.0 (-11.6 - -8.4) kHz/ms; Ledge duration: 0.6 ± 0.1 (0.4 - 0.8) ms.

Fernandes *et al.* (2025: 4) mention two sonotypes for *Afronycteris nana* in Guinea-Bissau: one with a F_{max} of 60 - 75 kHz and one with a F_{max} of 89 - 96 kHz.

Molecular Biology:

Karyotype

Both Peterson and Nagorsen (1975) and Rautenbach *et al.* (1993) reported 2*n* = 36, FN = 50, BA = 16, a metacentric X chromosome, and an acrocentric Y chromosome. GTG-bands identified three Robertsonian fusion chromosomes (7/11, 8/9, 10,12), considered as distinguishing characters for the genus *Neoromicia* Kearney *et al.* (2002).

From Senegal, Koubínová *et al.* (2013: 3) report the following karyotype for 9 ♂♂ and 7 ♀♀: 2*n* = 34, FNa = 50, FN = 54, X = Subtelocentric and Y = dot-like (probably acrocentric). They also found (p. 7) that two pairs of acrocentric autosomes were missing compared to previous findings, but contained an additional metacentric pair, which could be the result of a Robertsonian fusion. Due to these differences, they assigned their specimens to *Neoromicia* cf. *nana*.

The different diploid number of animals from southern Africa (2*n* = 36) and Senegal (2*n* = 34) led Volleth *et al.* (2023c: 50) to the conclustion that the latter animals should better be assigned to *Afronycteris* cf. *nanus*.

Tolera *et al.* (2021: 127) reported 2*n* = 36 and FN = 50 for a female from Ethiopia. The karyotype consisted of seven pairs of large metacentrics, one pair of small sub-metacentrics and 10 pairs of acrocentrics. The X chromosome is the largest acrocentric. This was identical to the configuration they found for "*Pipistrellus pipistrellus*" specimens.

Protein / allozyme

See Morales *et al.* (1991) for results from two specimens from South Africa.

Genetics

See Hoofer and Van Den Bussche (2003) for the results of a specimen from Kenya.

Habitat:

Monadjem *et al.* (2010a) found that there was no difference in use by *A. nanus* between logged and undisturbed forested areas; however, the species exhibited higher levels of activity along the wide tracks running through the two forests than either 30 m off these tracks or along the narrow forest trails. Naidoo *et al.* (2009: 30) showed that the abundance and feeding activity of *A. nanus* at sludge tank sites and at sites downstream of wastewater treatment works (WWTWs) was significantly higher than at sites upstream of these, probably due to insect abundance, specifically pollution tolerant chironomid midges. Naidoo *et al.* (2013b: 108) found that haematocrits were significantly higher in *A. nanus* foraging at WWTWs indicating that *A. nanus* may be compensating for a chronically low oxygen circulation within the body or kidney damage. They also report that hepatosomatic and renalsomatic indices were significantly higher suggesting hypertrophy of the detoxification organs. Additionally, the gonadosomatic index of the testes were also significantly larger at WWTWs, suggesting that reproductive potential of males may be compromised.

Naidoo *et al.* (2013a: 51) found that essential metals (Cu, Zn and Fe) were detected in all tissue samples from *A. nanus* foraging at upstream and wastewater-polluted sites. Non-essential metals

(Cd, Ni and Cr) were detected only in *A. nanus* foraging at wastewater-polluted sites (except one upstream occurrence of Cd). The first set of metals is essential for normal cellular processes and bodily function, the latter are considered harmful to organisms.

Significant differences for essential metals and mineral nutrients (Fe and Zn in liver; Cu and K in kidneys) were also reported by Naidoo *et al.* (2015a: 830).

The effects of WWTWs on energy stores and leptin levels was examined by Mehl *et al.* (2016), whereas Hill *et al.* (2018: 232) investigated the arsenic concentrations and acetylcholinesterase activity.

Naidoo *et al.* (2014) reported that *A. nanus* specimens captured at WWTWs also had higher DNA damage, lower antioxidant capacity, and higher haematocrits than bats from non-polluted sites.

In another study at WWTWs, Hill *et al.* (2016: 92) found that bats rely on iBrAT (interscapular brown adipose tissue) as an energy source, and that opportunistic foraging on abundant, pollutant-tolerant prey may change fatty acid profiles in their tissue, with possible effects on mitochondrial functioning, torpor and energy usage.

LaVal and LaVal (1977) [in Naidoo *et al.* (2014)] indicate that *A. nanus* has a relatively small home range of about 300 m around its roost.

In the Mount Nimba area, Monadjem *et al.* (2016y: 370) recorded this species from forested and forest edge habitats ranging from 450 to 530 m.

HABITS:
Monadjem *et al.* (2010a) found that *A. nanus* was most active in the first 5 hrs after sunset with activity declining rapidly after midnight.

Keeley and Keeley (2004: 116) [referring to O'Shea (1980) and Happold and Happold (1996)] mention that male "*Pipistrellus nanus*" roosting in palm-thatched roofs show territoriality and aggressive competition for spacious roosts, whereas males in populations roosting in banana leaves appear not to defend territories aggressively, and indicate that this difference might be based on the availability of preferred roosts. However, the more likely explanation being that these differences are due to these two groups belonging to different species, as the thatched roof inhabiting form is most likely *A. helios*.

ROOST:
During the day, *A. nanus* usually roost in furled leaves of banana plants, where the entrance diameter is between 7 and 24 cm. This makes the leaves suitable for one to three days, and makes roost-fidelity impossible. However, about half of the males have a fidelity for a small group of banana plants growing close together. This is not the case for females (Happold and Happold, 2023: 157).

DIET:
From the Umbilo River (KwaZulu Natal, RSA), Naidoo *et al.* (2011: 26) reported the following prey volume percentages: during summer: Lepidoptera (2.3 ± 1.4), Hemiptera (34.6 ± 14.1), Diptera (43.6 ± 17.4), and Trichoptera (19.6 ± 6.8); during winter: Coleoptera (36.4 ± 2.5), Coleoptera (3.2 ± 0.9), Hemiptera (19.1 ± 7.5), Diptera (29.5 ± 3.7), and Trichoptera (12 ± 7.2).

Weier *et al.* (2019c: 6) examined droppings from this species in the Levubu region (Limpopo, RSA) and found DNA sequences of: Lepidoptera: *Cryptophlebia peltastica* (Meyrick, 1921) and *Thaumatotibia batrachopa* (Meyrick, 1908); Hemiptera: *Bathycoelia distincta* Distant, 1878 and *Nezara viridula* (Linnaeus, 1758).

Faecal pellets of 33 bats from Cameroon examined by Waghiiwimbom *et al.* (2019a: 156) contained the following volume percentages: Lepidoptera (67.5 ± 3.3), Coleoptera (21.4 ± 2.4), Diptera (8.1 ± 1.2), Hemiptera (1.2 ± 0.5), Hymenoptera (0.8 ± 0.3), Isoptera (0.9 ± 0.8), and Trichoptera (0.1 ± 0.1). The frequency percentages for these insect orders were respectively: 91.2, 72.6, 44.4, 7.3, 10.6, 1.8, and 0.9.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 54 minutes, and the digestibility rate about 84.0 %.

PREDATORS:
Broadley (1982) [in Schätti (1984: 338)] reported the killing of a "*Pipistrellus nanus*" specimen by an opisthoglyphe treesnake (*Thelotornis capensis* A. Smith, 1849).

Nyffeler and Knörnschild (2013: 5) refer to Rosevear (1953: 267) for a dead bat being recovered by T.S. Jones from a spider's web near Kerema, Sierra Leone.

Mikula *et al.* (2016: Supplemental data) and Malan *et al.* (2022: 167) mention the Bat hawk

(*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Based on Vaughan (1976), Gual-Suárez and Medellín (2021: Suppl.) reported "*Neoromicia nanus*" as an occasional prey of *Cardioderma cor*, and accounted for 0.5 % of the prey items of *Nycteris grandis* (according to Fenton *et al.*, 1981; 1983).

Chen *et al.* (2023: 1) report on an opportunistic predation by a giant water bug (*Lethocerus cordofanus* Mayr, 1853 (Hemiptera: Belostomatidae) in Guinea-Bissau.

POPULATION:
Structure and Density
Probably not uncommon in suitable habitats (Happold, 1987).

Trend
2016: Unknown (Monadjem *et al.*, 2017bk).
2008: Unknown (Hutson *et al.*, 2008g; IUCN, 2009).

ACTIVITY AND BEHAVIOUR:
A. nanus uses territorial calls (possibly with a courtship function) consisting of a simple syllable type in series (O'Shea, 1980 in Smotherman *et al.*, 2016: 537).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

In Malawi, young were born at the beginning of the wet season, and they were lactated for about two months (Happold and Happold, 1990b: 567).

van der Merwe and Stirnemann (2007: 53) report that *A. nanus* is a seasonal monoestrous breeder. In Mpumalanga Province (South Africa), they found that spermatogensis began in late September and spermatozoa were present in the caudae epididymides from late April throughout August. Mating started in May and ovulation and fertilization occurred from the beginning of August, when the first implantations also occurred. Parturition took place between late October and the end of November. Lactating females were found until mid-January. They also indicate that reproduction timing was about one month earlier than in Malawi, where Happold and Happold (1998a: 67) found pregnant females from late August to mid-November, and births and lactating females were observed from mid-November to the end of April.

Trentin and Rovero (2011: 51) report five lactating females, captured at the end of November 2005 at Uzungwa Scarp Forest Reserve, Tanzania.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births taking place between November and early December.

Happold (2001: 397) - referring to Bernard *et al.* (1997) - indicates that sperm storage and delayed fertilisation is used to alter the interval between copulation and parturition, and as such their chronology of reproduction.

MATING:
McCracken and Wilkinson (2000: 329) indicate that *A. nanus* mating groups consist of a single male and multiple females (polygynous), but cannot be considered as harems. Males are often visited simultaneously by several females, and some males are visited more frequently by more females than others (see also Happold and Happold, 1996).

PARASITES:
PROTOZOA
Tsague *et al.* (2024: Suppl.) reported the presence of *Trypanosoma* cf. *livingstonei* in Cameroonian bats, whereas Babyesiza *et al.* (2025: 4) reported *T. dionisii* and *T. vespertilionis* from bats from the CAR.

BACTERIA
Mehl *et al.* (2021: 8) compared the intestinal microbiome of "*Neoromicia nana*" occurring around Wastewater treatment works (WWTW) and non polluted control sites in KwaZulu-Natal (RSA). In both groups, bacteria belonging to the classes Actinobacteria, Chloroplast, Bacilli, Clostridia, Planctomycetia, Alphaproteobacteria, Betaproteobacteria, Epsilonproteobactaria, Gammaproteobacteria, Spirochaetes and Mollicutes were found, although there were statistically significant differences.

ACARI
Macronyssidae
Orlova *et al.* (2020c: 951) mention *Steatonyssys afer* Radovsky and Yunker, 1963 in Angola.

Sarcoptidae
Fain (1959e: 157) described *Notoedres (Metanotoedres) miniopteri* from a "*Pipistrellus nanus*" from Bukavu, DRC.

DIPTERA
Nycteribiidae
Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108, host referred to both "*Pipistrellus nanus*" and "*Pipistrellus culex*"). *Basilia ansifera* Theodor, 1956 mainly a West

African species, reaches Lake Victoria in the east and Lake Nyasa in the south, nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110, host referred to "*P. nanus*', "*P. culex*" and "*P. stampflii*"). *Basilia robusta* Theodor, 1956 (Haeselbarth *et al.*, 1966: 111).

Dick *et al.* (2023) mentioned the nycteribiid flies *Basilia (Basilia) ansifera* Theodor, 1956, *Basilia (Basilia) robusta* Theodor, 1956 and *Nycteribia schmidlii scotti* Falcoz, 1923.

HEMIPTERA
Cicimidae
Kock *et al.* (1998b: 236, 237) reported *Cacodmus villosus* (Stål, 1855) and *Aphrania* cf. *barys* Jordan and Rothschild, 1912.

ACARINA
Dermanyssidae
Zumpt and Till (1954: 49) described *Steatonyssus eos* from "*Pïpistrellus nanus*" specimens from Kenya.

NEMATODA
Durette-Desset and Chabaud (1975: 323) described *Allintoschius dunni* from a *Myotis mystacinus* specimen from Malaysia, but also indicated that this Nematode was also found in five "*Pipistrellus nanus*" specimens from Maboké (CAR).

CESTODA
Hymenolepididae
Jenzen and Howell (1983: 135) referred to Baer (1933), who described *Vampirolepsis sandgroundi* from a bat from Zimbabwe.

VIRUSES:
Astroviridae
Neither of the two Mozambican bats tested by Hoarau *et al.* (2018: 2) was positive for this group of viruses.

Coronaviridae - Coronaviruses
SARS-CoV
During February 2008 in Ghana, Pfefferle *et al.* (2009) tested negative five fecal samples for coronavirus (CoV) RNA.

None of the 11 bats examined from the two Congos by Kumakamba *et al.* (2021: 7) tested positive for coronaviruses.

Shapiro *et al.* (2021a: 423) detected a possibly new alphacoronavirus in droppings of *A. nana* from Eswatini.

Hantaviridae (formerly included in Bunyaviridae)
Mouyassué virus - MOYV (or MOUV)
Sumibcay *et al.* (2012: 2) reported hantavirus RNA from 2 out ot 12 banana pipistrelles captured near Mouyassué village, in Côte d'Ivoire. However, Gu *et al.* (2014) were unable to find any additional bats infected with this virus. Arai *et al.* (2019b: 2) and Arai and Yanagihara (2020: 7) tentatively assigned this virus to the genus *Loanvirus*).

Paramyxoviridae
Mortlock *et al.* (2015: 1841) reported that two out of seven examined South African specimens tested positive for *Paramyxovirus* sequences.

Reoviridae
Cameron *et al.* (2023: 443) found RNA of a novel orbivirus in a bat collected in the Republic of the Congo.

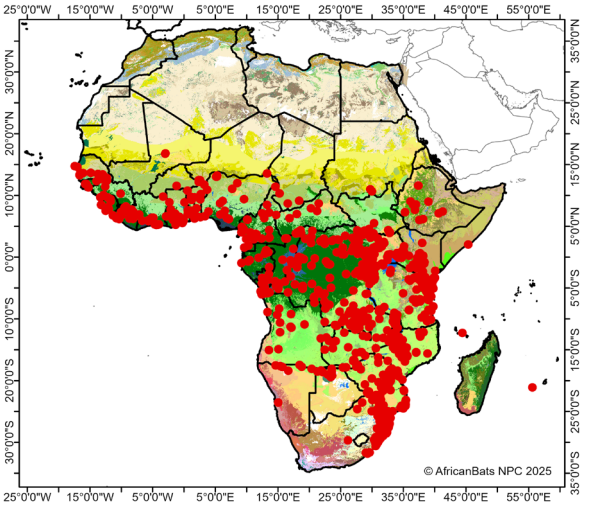

Figure 355. Distribution of *Afronycteris nanus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Comoros, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Djibouti, Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Mali, Mozambique, Namibia, Niger, Nigeria, Réunion, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Genus ***Afropipistrellus*** Thorn, Kock and Cuisin, 2007

2007. *Afropipistrellus* Thorn, Kock and Cuisin, Mammalia, 71 (1/2): 70, 75. - Etymology: From the combination of "Africa" and "Pipistrellus"; gender masculine (see Thorn *et al.*, 2007: 75).

TAXONOMY:
Based on analyses of cyt *b* sequences, Monadjem *et al.* (2020a: 1126) considered *Afropipistrellus* to be a synonym of *Nycticeinops*. However, Demos *et al.* (2025: 150) and Torrent *et al.* (2025b: 2) consider *Afropipistrellus* to be a valid taxon and raised it to genus level.

Currently recognized species in the genus *Afropipistrellus*: ***bellieri*** (De Vree, 1972), ***crassulus*** (Thomas, 1904); ***eisentrauti*** (Hill, 1968);***grandidieri*** (Dobson, 1876); ***happoldurm*** (Hutterer, Decher, Monadjem and Astrin, 2019; ***musciculus*** (Thomas, 1913).

Afropipistrellus bellieri (De Vree, 1972)

*1972. *Pipistrellus eisentrauti bellieri* De Vree, Rev. Zool. Bot. afr., 85 (3 - 4): 412. Publication date: 30 June 1972. Type locality: Côte d'Ivoire: NW of Abidjan: Adiopodoumé [05 19 N 04 08 W, 0 - 30 m]. [Goto Description]. Holotype: RMCA 35686: ad ♀, skin and skull. Collected by: Prof. Dr. Frits De Vree; collection date: 19 November 1969; original number: AX0104. Prepared and labelled in the Laboratoire d'Ecologie (L. Bellier) of the ORSTROM; see De Vree (1972). - Comments: Included in *eisentrauti* by Koopman (1993a: 221), and in *crassulus* by Simmons (2005). Considered a valid species by Fahr *et al.* (2006b: 245).
1994. *Hypsugo crassulus bellieri:* Heller, Volleth and Kock, Senckenb. biol., 74 (1/2): 1. (Name Combination).
1994. *P[ipistrellus (Pipistrellus)] e[isentrauti] bellieri:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 114.
1998. *P[ipistrellus (Hypsugo)] e[isentrauti] bellieri:* Grubb, Jones, Davies, Edberg, Starin and Hill, Mammals of Ghana, Sierra Leone and The Gambia, 84.
2003. *Nycticeinops eisentrauti:* Hoofer and Van Den Bussche, Acta Chiropt., 5 (Suppl): 38. - Comments: Although Hoofer *et al.* (2003) believed they were referring to an *eisentrauti* specimen, this was actually a *belieri* (see also the *eisentrauti bellieri* synonym by Grubb *et al.*, 1998).
2019. *Parahypsugo bellieri:* Hutterer, Decher, Monadjem and Astrin, Acta Chiropt., 21 (1): 16. Publication date: 5 October 2019. (Name Combination).
2020. *Nycticeinops bellieri:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Name Combination).
2020. *Parahypsugo cf. eisentrauti (=bellieri):* Monadjem, Richards, Decher, Hutterer, Mamba, Guyton, Naskrecki, Markotter, Wipfler, Kropff and Dalton. Publication date: 4 September 2020. (Name Combination).
2022. *Afropipistrellus bellieri:* Benda, Uvizl, Šklíba, Mazoch and Červený, Lynx, ns 53 (1): 317. (Current Combination).

TAXONOMY:
This taxon was originally described as *Pipistrellus eisentrauti bellieri*. Heller *et al.* (1994: 3) found that the holotype was more similar in size to *Hypsugo crassulus*, and transferred the taxon to that species.

Roehrs *et al.* (2011: 26, 31) mentioned that "*eisentrauti*" belongs to the genus *Nycticeinops*, but they used a specimen from Côqte d'Ivoire which should be assigned to *crassulus bellieri*. Monadjem *et al.* (2016y: 369) and Herkt *et al.* (2017: Appendix S9) report that the ecological niches for *crassulus* and *bellieri* differ and that their geographic distributions are separated by a gap, suggesting that they might represent different species.

Penis and baculum morphology as well as cranial and dental morphometrics led Hutterer *et al.* (2019: 16) to create a new genus (*Parahypsugo*), and to raise *bellieri* to full species rank.

Based on analyses of cyt *b*, Monadjem *et al.* (2020a: 1126) considered *Parahypsugo* to be a syonym of *Nycticeinops*, and transferred *bellieri* to the latter genus. However, Torrent *et al.* (2025b: 2) fransferred it subsequently to the genus Afropipistrellus.

CONSERVATION STATUS:
Global Justification
Not evaluated.

Assessment History
Global
Not evaluated.

Regional
None known.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) provide a line drawing of tragi of specimen DNSM 13222 from Mount Nimba, Liberia.

DETAILED MORPHOLOGY:
Baculum
See Hill and Harrison (1987) and Heller *et al.* (1994: 5). "*H[ypsugo] c[rassulus] bellieri*" and *P[ipistrellus] nanulus* bacula were much longer in total length than any of the *Neoromicia* species that were examined by Monadjem *et al.* (2013c). The shaft tip of "*H. c. bellieri*" was distinctly spatulate and dorsoventrally flattened baculum

shaft in both species was moderately ventrally curved, ending in a fluted base that was broader in *P. nanulus* (0.71 - 0.82 mm) than in "*H. c. bellieri*" (0.38 - 0.41 mm) (Monadjem *et al.*, 2013c: 197). Line drawing of dorsal and ventral bacula of specimen DNSM 13222 from Mount Nimba, Liberia are shown in Monadjem *et al.* (2013c: 204).

HABITAT:
Monadjem *et al.* (2016y: 369) found this species (as "*Hypsugo crassulus bellieri*") in old growth forest habitats in the Mount Nimba area.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

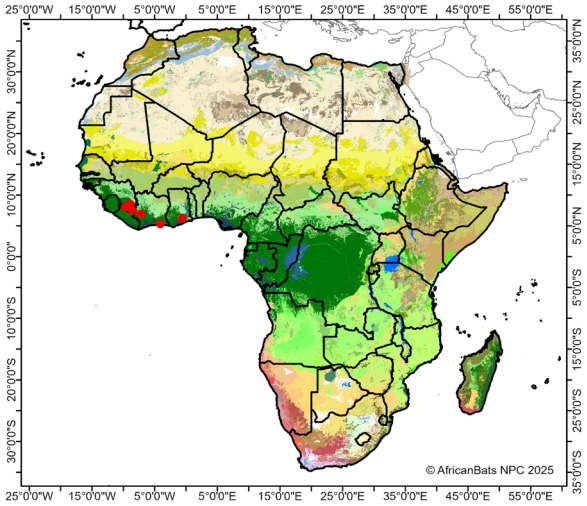

Figure 356. Distribution of *Afropipistrellus bellieri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea, Liberia.

Afropipistrellus crassulus (Thomas, 1904)

*1904. *Pipistrellus crassulus* Thomas, Ann. Mag. nat. Hist., ser 7, 13 (75): 206. Publication date: 1 March 1904. Type locality: Cameroon: Efulen [02 46 N 10 42 E]. [Goto Description]. Holotype: NHMUK 1904.2.8.1: ad ♂, skull and alcoholic. Collected by: George Latimer Bates Esq.
1966. *Pipistrellus (Pipistrellus) crassulus:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 17. (Name Combination).
1987. *[Attalepharca] crassulus:* Menu, Palaeovert., 17 (3): 126. (Name Combination).
1994. *Hypsugo crassulus:* Heller, Volleth and Kock, Senckenb. biol., 74 (1/2): 1. (Name Combination).
1994. *P[ipistrellus (Vansonia)] crassulus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 115. (Name Combination).
2019. *Hysugo eisentrauti:* Batsleer, Portelli, Borg, Kiefer, Veith and Dekeukeleire, Hystrix, It. J. Mamm., 30 (2): Suppl. (Lapsus).
2019. *Parahypsugo crassulus:* Hutterer, Decher, Monadjem and Astrin, Acta Chiropt., 21 (1): 15. Publication date: 5 October 2019. (Name Combination).
2020. *Nycticeinops cf. crassulus:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Name Combination).
2020. *Nycticeinops crassulus:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1140. Publication date: 10 September 2020. (Name Combination).
2025. *Afropipistrellus cf. crassulus:* Demos, Webala, Monadjem and Patterson, Acta Chiropt., 26 (2): 152. Publication date: 12 February 2025. (Name Combination).
2025. *Afropipistrellus crassulus:* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, Zool. J. Linn. Soc., 204 (2): 2, 12. Publication date: 13 June 2025. (Current Combination).
? *Nycticeinops cf. crassulus TD-2020*

TAXONOMY:
Mentioned in the genus *Pipistrellus* and the subgenus *Vansonia* by Koopman (1994: 116). Volleth *et al.* (2001: 27) assigned this species to the genus *Hypsugo*. Included *bellieri* but see Hutterer *et al.* (2019: 1).

Transferred to the genus *Parahypsugo* by Hutterer *et al.* (2019: 15). However, based on cyt-*b* analyses, Monadjem *et al.* (2020a: 1126) found that *Parahypsugo* should be considered a synonym of *Nycticeinops*.

Torrent *et al.* (2025b: 1) transferred *crassulus* to the genus *Afropipistrellus*.

COMMON NAMES:
Castilian (Spain): Pipistrelo. Chinese: 宽首伏翼. Czech: netopýr obtloustlý. English: Broad-headed Pipistrelle Bat, Broad-headed Pipistrelle. French: Vespère à grosse tête, Pipistrelle à grosse tête. German: Breitköpfige Zwergfledermaus, Breitköpfige Pipistrelle.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008g; IUCN, 2009; Monadjem and Fahr, 2017d).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Pipistrellus crassulus*] (Monadjem and Fahr, 2017d). 2008: LC ver 3.1 (2001) [assessed as *Pipistrellus crassulus*] (Fahr, 2008g; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as *Hypsugo crassulus*] (Fahr, 2004o; IUCN, 2004). 1996: LR/lc [assessed as *Pipistrellus crassulus*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this widespread species as a whole (Fahr, 2008g; IUCN, 2009; Monadjem and Fahr, 2017d).

CONSERVATION ACTIONS:
Fahr (2008g) [in IUCN (2009)] and Monadjem and Fahr (2017d) report that there appear to be no direct conservation measures in place, and it is not known if the species is present within any protected areas. Further studies are needed into the taxonomy, distribution and natural history of this species.

GENERAL DISTRIBUTION:
Nycticeinops crassulus has been recorded from Guinea, Liberia and Côte d'Ivoire in the west, from Cameroon, Democratic Republic of the Congo, northern Angola, southern Sudan, Uganda and western Kenya (Kakamega Forest).

Native: Angola; Cameroon; Congo (Bates *et al.*, 2013: 325 - 1st authenticated record); Congo (The Democratic Republic of the); Côte d'Ivoire; Guinea (Decher *et al.*, 2016: 266); Kenya; Liberia; Sudan; Uganda.
Presence uncertain: Nigeria.

DETAILED MORPHOLOGY:
Vomeronasal complex
In this species, the VNC is bar-shaped in cross section (Smith *et al.*, 2024: 9).

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2001) reported 2*n* = 30, FN = 56, BA = 28, a metacentric X chromosome and a metacentric Y chromosome.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

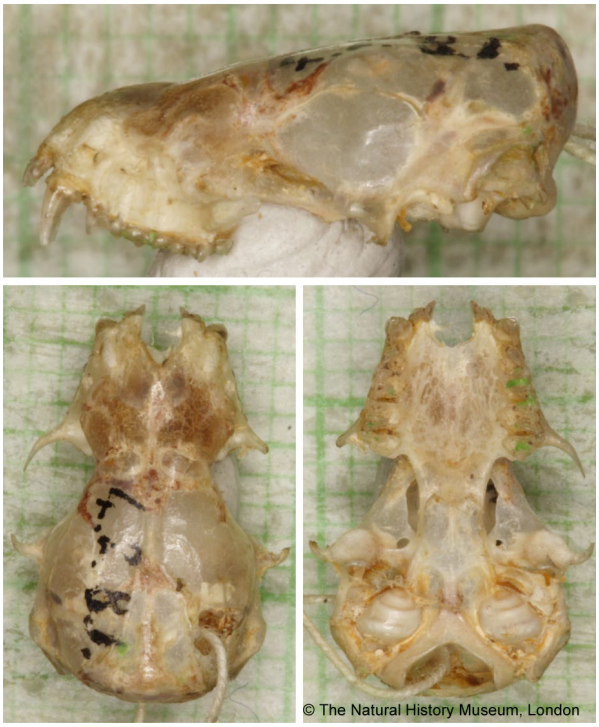

Figure 357. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1904.2.8.1, holotype of *Pipistrellus crassulus* Thomas, 1904.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 68 minutes, and the digestibility rate about 81.3 %.

POPULATION:
Structure and Density
This species has rarely been recorded (Fahr, 2008g; IUCN, 2009; Monadjem and Fahr, 2017d).

Trend
2016: Unknown (Monadjem and Fahr, 2017d).
2008: Unknown (Fahr, Fahr, 2008g; IUCN, 2009).

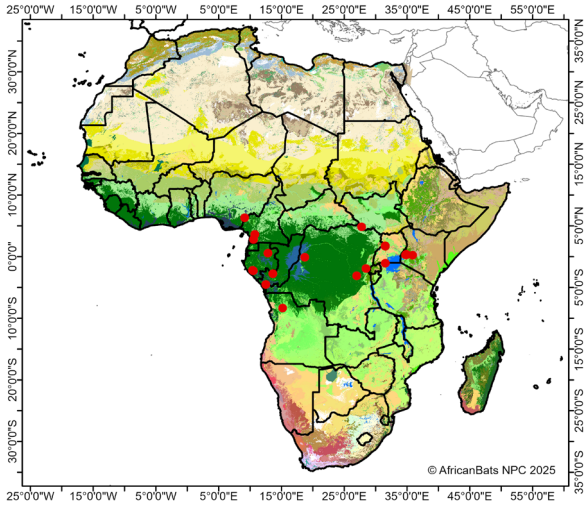

Figure 358. Distribution of *Afropipistrellus crassulus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Angola, Cameroon, Congo, Congo (Democratic Republic of the), Gabon, Kenya, Nigeria, South Sudan, Tanzania, Uganda.

Afropipistrellus eisentrauti (Hill, 1968)

*1968. *Pipistrellus eisentrauti* Hill, Bonn. zool. Beitr., 19 (1/2): 45. Publication date: 10 April 1968. Type locality: Cameroon: Western province: Rumpi Highlands, Dikume-Balue: Camp V [ca. 04 13 N 09 32 E]. [Goto Description]. Holotype: ZFMK MAM-1968.0005: ad ♂, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: 18 February 1957; original number: 498. See Hill (1968: 45), Thorn *et al.* (2007), Hutterer and Peters (2010: 12). Paratype: NHMUK 1967.2129: ad ♀, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: 30 November 1966; original number: 198. Paratype: ZFMK MAM-1968.0006: ad ♀, skin and skull. Collected by: Prof. Dr. Martin Eisentraut; collection date: 30 November 1966; original number: 198. Lager II [=Camp II], ca. 1,100 m; Mount Kupe (see Hutterer and Peters, 2010: 12). - Comments: Thorn *et al.* (2009: 53) situate Camp V at 05 00 N 09 15 E. - Etymology: In honour of Prof. Martin Eisentraut (1902 - 1994), collector of the type specimen.

1971. *Pipistrellus [(Pipistrellus)] eisentrauti:* Hayman and Hill, Mammals of Africa: Chiroptera, 39. (Name Combination).

1972. *P[ipistrellus] e[isentrauti] eisentrauti:* De Vree, Rev. Zool. Bot. afr., 85 (3 - 4): 415. (Name Combination).

1987. *Pipistrellus (Hypsugo) eisentrauti:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 274. (Name Combination).

1994. *Hypsugo eisentrauti:* Heller, Volleth and Kock, Senckenb. biol., 74 (1/2): 1. (Name Combination).

1994. *P[ipistrellus (Pipistrellus)] e[isentrauti] eisentrauti:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 114. (Name Combination).

2019. *Parahypsugo eisentrauti:* Hutterer, Decher, Monadjem and Astrin, Acta Chiropt., 21 (1): 15. Publication date: 5 October 2019. (Name Combination).

*2020. *Nycticeinops eisentrauti:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020.

2025. *Afropipistrellus eisentrauti:* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, Zool. J. Linn. Soc., 204 (2): 4. Publication date: 13 June 2025. (Current Combination).

? *Hypsugo eisentrauti bellieri:*

TAXONOMY:
Koopman (1994: 114) mentions this species as belonging to the subgenus *Pipistrellus*. Volleth *et al.* (2001: 27) assigned this species to the genus *Hypsugo*. Koopman (1993a: 221) included *bellieri*, but see Heller *et al.* (1994), Simmons (2005). Hoofer and Van Den Bussche (2003: 38) and Roehrs *et al.* (2011: 26, 31) include *eisentrauti* in *Nycticeinops*, but they used a specimen from Côte d'Ivoire, which should be assigned to *crassulus bellieri*.

Transferred to the genus *Parahypsugo* by Hutterer *et al.* (2019: 15), but Monadjem *et al.* (2020a: 1126) found that - based on cyt-*b* analyses - *Parahypsugo* should be considered a synonym of *Nycticeinops*.

Torrent *et al.* (2025b: 4) transferred *eisentrauti* to the genus *Afropipistrellus*.

COMMON NAMES:
Czech: netopýr guinejský. English: Eisentraut's Pipistrelle Bat, Eisentraut's pipistrelle. French: Pipistrelle d'Eisentraut, Vespère d'Eisentraut. German: Eisentrauts Zwergfledermaus, Eisentrauts Pipistrelle. Italian: Pipistrèllo di Eisentràut.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, status, ecological requirements and threats. This species is most probably restricted to SW Cameroon. However, there are supposedly records from four other countries. Those records may all be misidentifications. If that is the case, then it is likely that this species has a very restricted range and is probably threatened (Fahr, 2008h; IUCN, 2009; Fahr, 2019c).

Using machine learning techniques, Wieringa (2022: 535) predicted this species (as *Hypsugo eisentrauti*) to be threatened.

Assessment History
Global
2018: DD ver 3.1 (2001) assessed as "*Hypsugo eisentrauti*" (Fahr, 2019c). 2008: DD ver 3.1 (2001) assessed as "*Pipistrellus eisentrauti*" (Fahr, 2008h; IUCN, 2009). 2004: DD ver 3.1 (2001) (Fahr, 2004n; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not well known, but in Cameroon are likely to include encroachment on montane forest by subsistence agriculture (Fahr, 2008h; IUCN, 2009; Fahr, 2019c).

CONSERVATION ACTIONS:
Fahr (2008h) [in IUCN (2009)] and Fahr (2019c) reports that it is unclear if the species is present within any protected areas. Further studies are needed into the taxonomy, distribution, and threats to this species.

GENERAL DISTRIBUTION:
Nycticeinops eisentrauti was initially described from Cameroon, where it has been recorded from localities including the Rumpi Highlands, Mount Kupe and Mount Cameroon. Although there are additional records of this species from Kenya, Somalia, Uganda and from the Democratic Republic of the Congo, these are currently assigned to *Nycticeinops macrocephalus*, or need further investigation to confirm their identity.

The specimens from Kenya were identified by V. Van Cakenberghe as belonging to *eisentrauti*.

Confirmation of the possible distribution outside of Cameroon is needed.

Native: Cameroon; Nigeria (Tanshi *et al.*, 2022a: 317).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

MOLECULAR BIOLOGY:
Genetics
See Hoofer and Van Den Bussche (2003).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 68 minutes, and the digestibility rate about 81.3 %.

POPULATION:
Structure and Density
The population is little known, but it may be locally common in Cameroon (Fahr, 2008h; IUCN, 2009; Fahr, 2019c).

Trend
2018: Unknown (Fahr, 2019c). 2008: Unknown (Fahr, 2008h; IUCN, 2009).

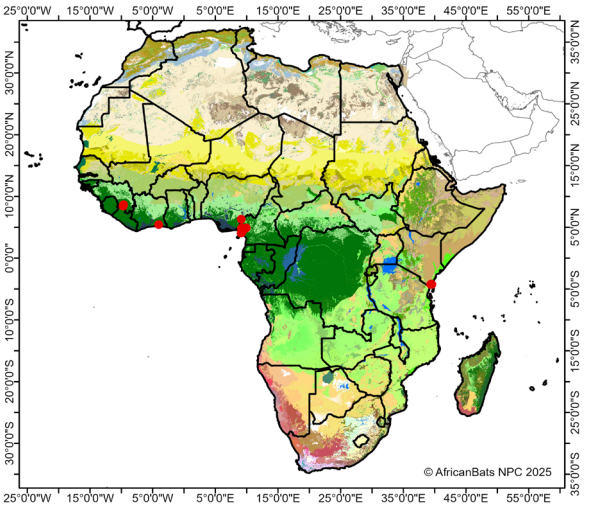

Figure 359. Distribution of *Afropipistrellus eisentrauti*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Côte d'Ivoire, Guinea, Kenya, Liberia, Nigeria.

Afropipistrellus grandidieri (Dobson, 1876)

*1876. *Vesperugo (Vesperus) grandidieri* Dobson, Ann. Mag. nat. Hist., ser 4, 18 (108): 500. Publication date: 1 December 1876. Type locality: Tanzania: Zanzibar [ca. 06 10 S 39 12 E]. [Goto Description]. Holotype:

MNHN ZM-MO-1996-2129: ad ♀, skull and alcoholic. Collected by: Alfred Grandidier; collection date: 1864. Number 215 in Rode (1941). Opened ventrally, one foetus in uterus, skull extracted in 1999.

1895. *Vesperus grandidieri:* Matschie, Säugethiere Deutsch-Ost-Afrikas, 23. (Name Combination).
1897. *Eptesicus grandidieri:* Matschie, Zur Faunistik Deutsch-Ost-Afrikas. 5. Säugethiere, 84. (Name Combination).
1900. *Vesperugo (Vesperus) flavescens* Seabra, J. Sci. mat. phys. nat., ser 2, 6: 23. Publication date: 1900. Type locality: Angola: Benguela district: East of Hanha: Galanga [12 04 S 15 09 E]. Cotype: MNHN ZM-MO-1900-536: ad? ♂, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta. Co- or topotype. Cotype: MNHN ZM-MO-1900-537: ad? ♂, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta. Co-, para- or topotype. - Etymology: From the feminine scientific Latin adjective *flavèscens*, meaning "yellowish", referring to the colour of fur and membranes (see Lanza *et al.*, 2015: 401).
1900. *Vesperugo flavescens:* Bocage, Bull. Mus. natn. Hist. nat., Paris, 6: 164. (Name Combination).
1935. *Pipistrellus flavescens:* Monard, Arq. Mus. Bocage, 6: 31. (Name Combination).
1937. *Eptesicus capensis angolensis* J.Eric Hill, Am. Mus. Novit., 916: 1, fig 1. Publication date: 17 April 1937. Type locality: Angola: Chitau [11 15 S 17 01 E, 4 900 ft]. [Goto Description]. Holotype: AMNH 85535: ad ♂, skin and skull. Collected by: Herbert Lang and The Vernay Angola Expedition; collection date: 5 August 1925; original number: 620. Co- or Topotype: AMNH 88096: ad ♀. Co- or Topotype: CM 7018b: ♀.
1939. *Eptesicus flavescens:* G.M. Allen, Bull. Mus. comp. Zool., 83: 83. (Name Combination).
1953. *Eptesicus (Eptesicus) flavescens:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).
1984. *Eptesicus (Eptesicus) capensis grandidieri:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1987. *[Attalepharca] flavescens:* Menu, Palaeovert., 17 (3): 126. (Name Combination).
1987. *Pipistrellus (Neoromicia) flavescens:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).
1993. *Eptesicus (Neoromicia) flavescens:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 201. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] grandidieri:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
2006. *Neoromicia flavescens:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 132 - 133. (Name Combination).
2007. *Pipistrellus (Afropipistrellus) grandidieri angolensis:* Thorn, Kock and Cuisin, Mammalia, 72 (1/2): 76. (Name Combination).
2007. *Pipistrellus (Afropipistrellus) grandidieri grandidieri:* Thorn, Kock and Cuisin, Mammalia, 71 (1/2): 76. (Name Combination).
2007. *Pipistrellus (Afropipistrellus) grandidieri:* Thorn, Kock and Cuisin, Mammalia, 71 (1/2): 73. (Name Combination).
2013. *Pipistrellus sp. 1:* Monadjem, Richards, Taylor and Stoffberg, Zool. J. Linn. Soc., 167 (1): 194. Publication date: 18 January 2013.
2019. *L[aephotis] flavescens:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. - Comments: Taylor (2019a 283) consider *flavescens* to be a species separate from *grandidieri*. (Name Combination).
2020. *Nycticeinops grandidieri:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Name Combination).
2022. *Afropipistrellus grandidieri:* Benda, Uvizl, Šklíba, Mazoch and Červený, Lynx, ns 43 (1): 317. (Current Combination).
? *Neoromicia grandidieri:* - Comments: . (Lapsus).
? *Pipistrellus grandidieri:* (Name Combination).

TAXONOMY:



Figure 360. *Afropipistrellus grandidieri,* Zanzibar Island.

Thorn *et al.* (2007: 73) recognize two subspecies: *P[ipistrellus] (Afropipistrellus]) g[randidieri] grandidieri* for East African specimens and *P[ipistrellus] (A[fropipistrellus]) g[randidieri] angolensis*, a slightly larger western and southern African subspecies (Angola, Malawi and Cameroon).

Monadjem *et al.* (2013c: 194) mention a specimen from Mount Nimba as "*Pipistrellus* sp. 1", which was in a later publication (Monadjem *et al.*, 2016y: 370) assigned to "*Pipistrellus* cf. *grandidieri*". The latter authors indicate that the specimen involved has very similar cranial characters as *P. grandidieri*, but that species occurs only in eastern Africa, some 2,500 km away. Pending further genetical characterisation, they tentatively named it "cf. *grandidieri*". The genetic study by Monadjem *et al.* (2020d: 550) revealed that these West-African specimens are specifically distinct from the animals from East Africa and they described these as *Pipistrellus simandouensis*.

Thorn *et al.* (2007: 70 - 71) consider "*flavescens*" to be a *nomen dubium*, since its description does

not agree with the two "syntypes" attributed to it. They indicate that one syntype (MNHN ZM-MO-1900-536) is actually a representative of *Pipistrellus* (*Afropipistrellus*) *grandidieri* Dobson, 1876.

Based on cyt *b* analyses, Monadjem *et al.* (2020a: 1126) consider *Afropipistrellus* to be a synonym of *Nycticeinops*. However, Benda *et al.* (2022: 314) indicate that as this is only based on mitochondrial DNA and the morphological traits of *Nycticeinops* are markedly distinct, they tentatively retain this species in the genus *Afropipistrellus*. Its assignment to the genus *Afropipistrellus* was confirmed by Torrent *et al.* (2025b: 5).

COMMON NAMES:
Czech: netopýr galangánský. Chinese: 黄伏翼. English: Grandidier`s Pipistrelle, Yellow Pipistrelle Bat, Yellow Serotine. French: Pipistrelle de Grandidier, Sérotine de Grandidier, Sérotine jaune, Pipistrelle jaune. German: Grandidiers Zwergfledermaus, Gelbe Zwergfledermaus, Gelbe Pipistrelle. Italian: Pipistrèllo giallàstro.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, status, ecological requirements and threats (Jacobs *et al.*, 2008s; IUCN, 2009; Jacobs *et al.*, 2017).

Assessment History
Global
2016: DD ver 3.1 (2001) [assessed as "*Pipistrellus grandidieri*"] (Jacobs *et al.*, 2017). 2008: DD ver 3.1 (2001) [assessed as "*Pipistrellus flavescens*"] (Jacobs *et al.*, 2008s; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004aa; IUCN, 2004). 1996: DD [assessed as "*Eptesicus flavescens*"] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The major threats are mining, logging and wood harvesting. It is sensitive to unintentional effects on large scale like harvesting, although the species being assessed is not the target (Jacobs *et al.*, 2017).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008s) [in IUCN (2009)] and Jacobs *et al.* (2017) report that there appear to be no conservation measures in place for this species. There is a need to clarify the taxonomic status of animals currently allocated to this species, and thereby better understand the distribution, natural history and potential threats.

GENERAL DISTRIBUTION:
Ethiopia to SE Democratic Republic of the Congo and Zambia, including Unguja [=Zanzibar]. Possibly Liberia (1st record, Monadjem and Fahr, 2007: 47; as "*Neoromicia* aff. *guineensis*"). Decher *et al.* (2016: 273) report "*N.* cf. *grandidieri*" specimens from Guinea. As "*Pipistrellus/Neoromicia flavescens*" recorded from Angola (type locality at Galanga), Burundi, Cameroon, Malawi (including the Shire Highlands (Happold and Happold, 1997b: 81), Mozambique, Uganda (Kampala); and Somalia (Shonto Forest).

Native: Angola (Crawford-Cabral, 1989; Thorn *et al.*, 2007; Monadjem *et al.*, 2010d: 571); Burundi; Cameroon; Congo (Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 571); Malawi (Happold and Happold, 1997b: 81; Thorn *et al.*, 2007; Monadjem *et al.*, 2010d: 571); Mozambique; Somalia; Tanzania; Uganda, Zambia (Benda *et al.*, 2022: 292).

DENTAL FORMULA:
Esquivel *et al.* (2021: Supp.) reported that 17 of the 32 skulls they examined had missing teeth (oligodontia).

DETAILED MORPHOLOGY:
Baculum
Thorn *et al.* (2007).

POPULATION:
Structure and Density
There are few details available on the population status of this species (Jacobs *et al.*, 2008s; IUCN, 2009; Jacobs *et al.*, 2017).

Trend
2016: Unknown (Jacobs *et al.*, 2017). 2008: Unknown (Jacobs *et al.*, 2008s; IUCN, 2009 - as "*Pipistrellus flavescens*").

PARASITES:
Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Polychromophilus* in three out of three investigated "*P.* aff. *grandidieri*" specimens from West Africa, but they indicate that the bat might represent an undescribed species. Rosskopf *et al.* (2018: Suppl.) refer to the same specimens and mention them from Guinea.

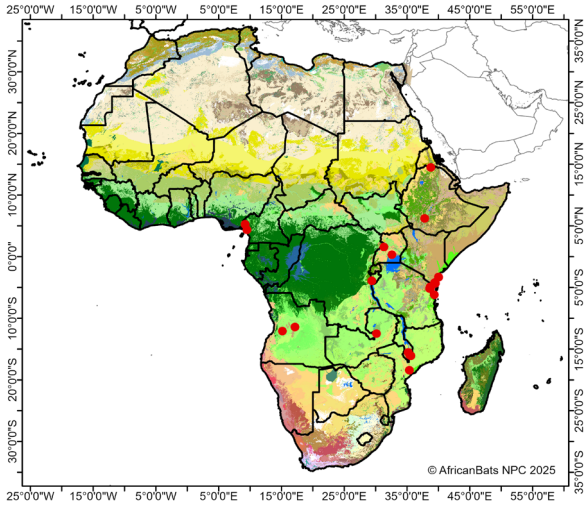

Figure 361. Distribution of *Afropipistrellus grandidieri*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Cameroon, Côte d'Ivoire, Ethiopia, Kenya, Malawi, Mozambique, Tanzania, Uganda, Zambia.

Afropipistrellus happoldorum (Hutterer, Decher, Monadjem and Astrin, 2019)

2013. *Neoromicia sp. 1:* Monadjem, Richards, Taylor and Stoffberg, Zool. J. Linn. Soc., 167 (1): 194. Publication date: 18 January 2013.

*2019. *Parahypsugo happoldorum* Hutterer, Decher, Monadjem and Astrin, Acta Chiropt., 21 (1): 9. Publication date: 5 October 2019. Type locality: Guinea: Macenta prefecture: Simandou Mountains: Western Spur Valley [08 33 26 N 08 55 17 W, 737 m]. Holotype: ZFMK MAM-2009.0029: ad ♂, skull and alcoholic. Collected by: Jan Decher, Blaise Kadjo and Juliane Schaer; collection date: 12 December 2008; original number: JD 700. Paratype: ZFMK MAM-2008.0295: ad ♀. Collection date: 8 March 2008. - Etymology: In honour of Meredith and David Happold in recognition of their studies on African bats, and particularly of their monumental work for the Mammals of Africa volume IV on hedgehogs, shrews, and bats (see Hutterer *et al.*, 2019: 10).

2020. *Nycticeinops happoldorum:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Name Combination).

2022. *Afropipistrellus happoldorum:* Benda, Uvizl, Šklíba, Mazoch and Červený, Lynx, ns 53 (1): 317. (Current Combination).

? *Neoromicia sp. 1 SaSt-2013*

TAXONOMY:
Originally described in the genus *Parahypsugo*, but based on cyt-*b* sequence analyses, Monadjem *et al.* (2020a: 1126) considered *Parahypsugo* to be a synonym of *Nycticeinops*.

Torrent *et al.* (2025b: 4) transferred *happoldorum* to the genus *Afropipistrellus*.

COMMON NAMES:
English: Happolds' Pipistrelle

CONSERVATION STATUS:
Global Justification
Not assessed.

Assessment History
Global
Not assessed.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Cameroon (1st record: Grunwald *et al.*, 2025: 281); Côte d'Ivoire; Guinea; Liberia.

However, Grunwald *et al.* (2025: 302) also indicate that the Cameroonian specimens have a different dental morphology and further analyses are needed to confirm their identity.

ECHOLOCATION:
From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 27 calls of 3 bats: F_{peak}: 46.8 ± 1.6 (43.7 - 49.4) kHz, F_{min}: 41.2 ± 1.6 (39.0 - 43.7) kHz, F_{max}: 87.4 ± 10.4 (61.5 - 100.1) kHz, duration: 2.2 ± 0.2 (2.1 - 2.6) ms.

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2023c: 42) reported 2*n*=24, FNa=44 and eight large- to medium-sized meta- to submetacentric autosomal pairs and three medium-sized subtelocentric pairs. The X chromosome is a medium-sized submetacentric and the Y chromosome a small metacentric.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ghana, Guinea, Liberia.

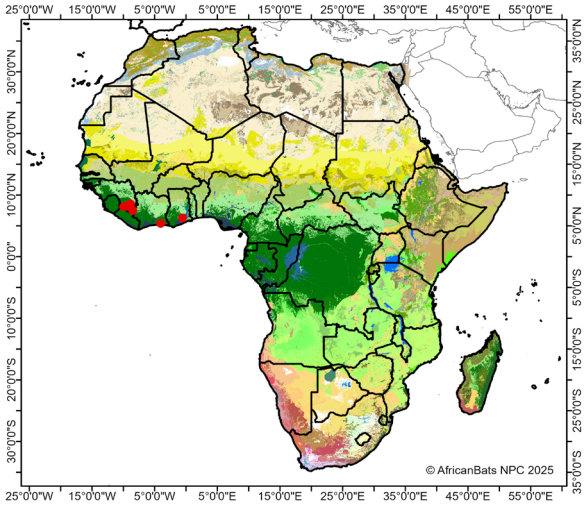

Figure 362. Distribution of *Afropipistrellus happoldorum*.

Afropipistrellus musciculus (Thomas, 1913)

*1913. *Pipistrellus musciculus* Thomas, Ann. Mag. nat. Hist., ser 8, 11 (63): 316. Publication date: 1 March 1913. Type locality: Cameroon: Ja River: Bitye [03 13 N 12 22 E, 2 000 ft]. [Goto Description]. Holotype: NHMUK 1913.2.8.1: ad ♂, skin and skull. Collected by: George Latimer Bates Esq. Collection date: 3 September 1912; original number: 622.
1966. *Pipistrellus (Pipistrellus) musciculus:* Hayman, Misonne and Verheyen, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., (8) 154: 16. (Name Combination).
1987. *Attalepharca musciculus:* Menu, Palaeovert., 17 (3): 128. - Comments: Menu used *Attalepharca* as "groupe collectif" not as genus name. (Name Combination).
1987. *Pipistrellus (Hypsugo) musciculus:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination).
2005. *Hypsugo musciculus:* Simmons, Order Chiroptera, 491. (Name Combination).
2025. *Afropipistrellus musciculus:* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards, Monadjem, Zool. J. Linn. Soc., 204 (2): 1, 13. Publication date: 13 June 2025. (Current Combination).

TAXONOMY:
Mentioned in the genus *Pipistrellus* by Hutterer *et al.* (2019: 22) and the subgenus *Pipistrellus* by Koopman (1994: 113). However, Monadjem *et al.* (2020d: 562; 2020b: 1140) confirmed that *musciculus* might not be a member of the genus *Pipistrellus*, but rather of *Hypsugo* as was suggested by Simmons (2005: 491). A recent analysis by Torrent *et al.* (2025b: 1), however, showed this species to belong to the genus Afropipistrellus.

COMMON NAMES:
Czech: netopýr mechový. English: Mouse-like Pipistrelle Bat, Least Pipistrelle Bat, Mouselike Pipistrelle, Western Africa Pipistrelle. French: Vespère murin, Pipistrelle d'Afrique occidentale, Pipistrelle murine. German: Mäuschen-Zwergfledermaus, Mäuschen-Pipistrelle, Westafrikanische Zwergfledermaus.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, status and ecological requirements (Jacobs *et al.*, 2008u; IUCN, 2009; Jacobs *et al.*, 2020b).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2020b). 2008: DD ver 3.1 (2001) [assessed as *Pipistrellus musciculus*] (Jacobs *et al.*, 2008u; IUCN, 2009). 2004: DD ver 3.1 (2001) (Jacobs *et al.*, 2004i; IUCN, 2004). 1996: LR/nt [assessed as *Pipistrellus musciculus*] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs *et al.*, 2008u; IUCN, 2009; Jacobs *et al.*, 2020b).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008u) [in IUCN (2009)] and Jacobs *et al.* (2020b) report that it is not known if the species is present within any protected area. Further studies are needed into the taxonomy,

distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:
Hypsugo musciculus has been recorded from a few localities in Ghana, Sierra Leone, southern Cameroon, Gabon, the eastern tip of Congo, and the Democratic Republic of the Congo.

Native: Cameroon; Congo (The Democratic Republic of the); Gabon; Ghana; Sierra Leone.

Bates *et al.* (2013: 339) reject the occurrence of *H. musciculus* in the Republic of Congo as Malbrant and Maclatchy (1949) only suggested it to be 'likely' occurring in that country.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 62 minutes, and the digestibility rate about 82.3 %.

POPULATION:
Structure and Density
The abundance of this species is not well known (Jacobs *et al.*, 2008u; IUCN, 2009; Jacobs *et al.*, 2020b).

Trend
2018: Unknown (Jacobs *et al.*, 2020b). 2008: Unknown (Jacobs *et al.*, 2008u; IUCN, 2009).

PARASITES:
HEMIPTERA
Cimicidae
Cacodmus villosus (Stål) recorded from the Congo (Haeselbarth *et al.*, 1966: 11; Kock *et al.*, 1998b: 236).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo (Democratic Republic of the), Gabon, Ghana, Sierra Leone.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 363. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1913.2.8.1, holotype of *Pipistrellus musciculus* Thomas, 1913.

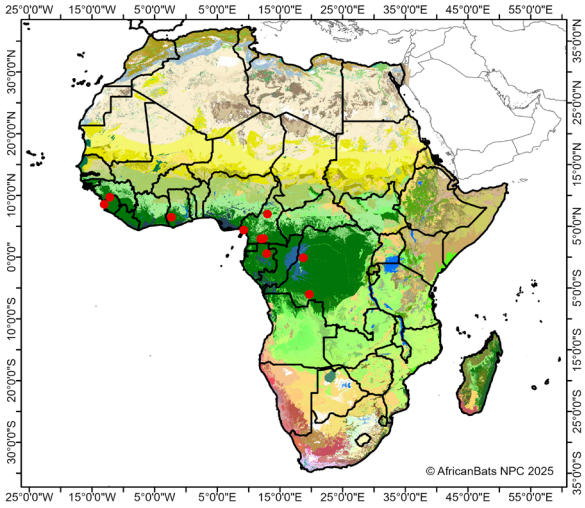

Figure 364. Distribution of *Afropipistrellus musciculus*.

Genus ***Hypsugo*** Kolenati, 1856

*1856. *Hypsugo* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (2): 131. Publication date: 1856. - Comments: Type species: *Vespertilio savii* Bonaparte, 1837. - Etymology: From the Greek "*υψι*", (hýpsi) meaning "on high" or "aloft" and the ending -"ugo" (as in *Nannugo* and *Vesperugo*) (see Palmer, 1904: 343). Lanza *et al.* (2015: 380) suggest the following "From the neuter Greek substantive "*ύψος*" (hýpsos) "height" + the suffix *-ugo* of the feminine Latin substantive *vesperùgō* 'evening star', i.e. a bright planet (as Venus), seen in the western sky after sunset, corresponding to the Latin 'stella matutina', the planet Venus, appearing first in the nocturnal sky and disappearing first from the morning one. By extension *Vesperugo* has assumed also the meaning of 'bat'; hence *Hypsugo* means 'mountain bat' as *H. maurus* Kolenati, 1856 a synonym of *savii*, was collected in the central chain of Alps". (Current Combination).
1993. *Ypsugo:* Ariagno, Le Bièvre, 13: 118. (Lapsus).

2024. *Hipsugo:* Lelli, Moreno, Canziani, Soliani, Carrera, Castelli, Faccin, Trogu, Sozzi, Cavallari, Mauri, Ferrari, Salogni, Garbarino, Chiapponi, Farioli and Lavazza, Emerg. Inf. Dis., 30 (4): 1. Publication date: April 2024. (Lapsus).

TAXONOMY:
Meester *et al.* (1986: 50) mention *Vespertilio maurus* Blasius (= *Vespertiio savii* Bonaparte) and *Vesperugo kraschenininkovii* Eversmann as type species, but this was fixed to *Vespertilio savii* Bonaparte by Wallin (1969: 329), see Corbet and Hill (1992: 133).

Helbig *et al.* (2010: 168) suggest that *Hypsugo* is actually a para- or polyphyletic group, which would become monophyletic if the African forms are transferred to the genus *Nycticeinops*.

Currently (Simmons and Cirranello, 2024a) recognized species of the genus *Hypsugo*: *affinis* (Dobson, 1871) – Cambodia, NE Burma (= Myanmar), Yunnan, SE Tibet (China), N India, Nepal, Sri Lanka; *alashanicus* Bobrinskii, 1926 – Mongolia, China, Russian Far East to Korea and Tsushima Isl (Japan) (Simmons, 2005: 489); *arabicus* (Harrison, 1979) – Oman, Iran (Simmons, 2005: 489); ***ariel*** (Thomas, 1904); *cadornae* (Thomas, 1916) – northeastern India, Burma, Thailand, Vietnam, Laos (Simmons, 2005: 490); *dolichodon* Görföl, Csorba, Eger, Son and Francis, 2014 – Lao PDR, S Vietnam, Cambodia, Myanmar; *imbricatus* (Horsfield, 1824) – Java, Kangean Isl, Bali and Lesser Suda Isls, Borneo (Simmons, 2005: 490); *kitcheneri* (Thomas, 1915) – Borneo (Simmons, 2005: 491); *lanzai* Benda, Al-Jumaily, Reiter and Nasher, 2011 – Yemen; *lophurus* (Thomas, 1915) – Burma Peninsular (Simmons, 2005: 491); *macrotis* (Temminck, 1840) – western Malaysia, Sumatra, Bali and adjacent small islands (Simmons, 2005: 491); *mordax* (Peters, 1867) – Java, Philippines; ***musciculus*** (Thomas, 1913); *petersi* (A.B. Meyer, 1899) – Borneo, Sulawesi, Buru and Ambon (Molucca Islands), Philippines (Luzon, Mindanao); *pulveratus* (Peters, 1871) – Szechwan, Yunnan, Hunan, Kiangsu, Fukien (China), Hong Kong, Thailand, Laos, Vietnam (Simmons, 2005: 491); *savii* (Bonaparte, 1837) – France, Portugal, Spain, Italy, southern Switzerland, Austria, eastern Hungary, Balkan countries, Morocco, Crimea and Caucasus, Turkey, Lebanon, Syria, Israel, Iran, Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan, Tajikistan, Afghanistan to northern India and Burma (Simmons, 2005: 491); *stubbei* (Dolch, Batsaikhan, Stubbe and Steinhauser, 2021) – Mongolia; *vordermanni* (Jentink, 1890) – Belitung Isl (Indonesia), Borneo (Sarawak, Malaysia) (Simmons, 2005: 492).

COMMON NAMES:
Czech: skalní netopýři. English: Mountain Pipistrelle Bats. French: Vespères. Italian: Ipsùghi. Ukrainian: Гіпсуг [= Hipsuh].

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Equatorial Guinea, Kenya, Madagascar.

Hypsugo ariel (Thomas, 1904)

*1904. *Pipistrellus ariel* Thomas, Ann. Mag. nat. Hist., ser 7, 14 (80): 157. Publication date: 1 August 1904. Type locality: Sudan: Kassala province: Wadi Alagi [ca. 22 N 35 E, 2 000 ft]. [Goto Description]. Holotype: NHMUK 1904.11.4.7: ad ♀, skin and skull. Collected by: Arthur M. MacKilligan; collection date: 12 August 1903; original number: 28. See Qumsiyeh (1985: 54).
1966. *Pipistrellus (Pipistrellus) ariel:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 171. (Name Combination).
1987. *Pipistrellus (Hypsugo) ariel:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination).
1991. *Pipistrellus ariel ariel:* Harrison and Bates, Mammals of Arabia, 92. (Name Combination).
2000. *Hypsugo ariel:* Horáček, Hanák and Gaisler, Bats of the Palearctic region, 126. (Current Combination).

TAXONOMY:
Mentioned in the subgenus *Pipistrellus* by Koopman (1994: 115). Harrison and Bates (1991: 93) assign the Arabian specimens to *P. a. ariel*, although they do not mention any other subspecies. Horáček *et al.* (2000: 126) mention it in the genus *Hypsugo*.

COMMON NAMES:
Arabian: Khaffash. Czech: netopýr pouštní. Dutch: Woestijndwergvleermuis. English: Pygmy Pipistrellus, Ariel Pipistrelle, Egyptian Desert Pipistrelle, Desert Pipistrelle, Fairy Pipistrelle. French: Vespère ariel, Pipistrelle ariel. German: Elfen-Zwergfledermaus, Elfen-Pipistrelle. Hebrew: Atalfon Ariel.

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of the absence of recent information on its extent of occurrence, status and ecological requirements (Benda and Aulagnier, 2008; IUCN, 2009; Benda and Aulagnier, 2020).

Assessment History
Global
2018: DD ver. 3.1 (2001) (Benda and Aulagnier, 2020). 2008: DD ver 3.1 (2001) [assessed as *Pipistrellus ariel*] (Benda and Aulagnier, 2008; IUCN, 2009). 2004: DD ver 3.1 (2001) (Benda, 2004c; IUCN, 2004). 1996: LR/nt assessed as *Pipistrellus ariel* (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
Loss of natural habitat because of agricultural intensification. The species is affected by pesticides, although this is not considered a major threat (Z. Amr *pers. comm.*, 2005 [in Benda and Aulagnier (2008) in IUCN (2009); Benda and Aulagnier, 2020)].

CONSERVATION ACTIONS:
Benda and Aulagnier (2008) [in IUCN (2009)] and Benda and Aulagnier (2020) report that no conservation actions are in place. Further research on the taxonomy, population ecology and trends is required and the extent of the range requires further clarification.

GENERAL DISTRIBUTION:
Hypsugo ariel has been recorded from Israel, Jordan and Egypt (including the Sinai) within the Mediterranean (Dietz, 2005). Outside the area the range extends to Saudi Arabia, and Yemen. In Africa it is recorded from northern Sudan (type locality, see Simmons, 2005). Approximately five localities known in northeast Africa, including Egypt and Sudan.

The specimens from Socotra (Yemen) are now considered to belong to a separate species: *Hypsugo lanzai* (see Benda *et al.*, 2011b: 37).

Native: Egypt (Sinai); Israel; Jordan; Palestinian Territory, Occupied; Saudi Arabia; Sudan; Yemen (South Yemen).

DETAILED MORPHOLOGY:
Baculum
Benda *et al.* (2011b: 38).

ECHOLOCATION:
From Jordan, Benda *et al.* (2010b: 204) reported the following parameters for 129 calls: F_{start}: 58.1 ± 4.1 (47.7 - 75.0) kHz, F_{end}: 43.0 ± 2.1 (30.0 - 47.4) kHz, F_{peak}: 46.4 ± 1.3 (43.4 - 49.0) kHz, Pulse duration: 4.1 ± 0.8 (2.4 - 7.2) ms., and Inter-pulse interval: 81.9 ± 18.9 (45.0 - 193.0) ms.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

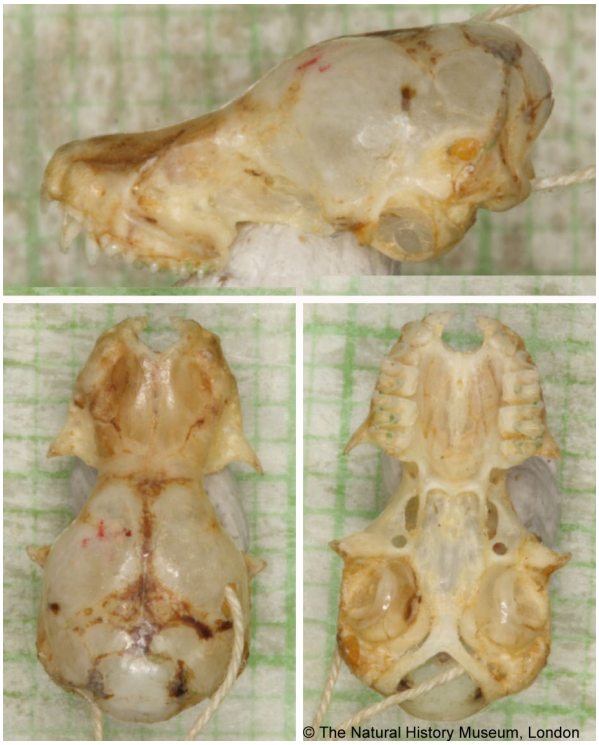

Figure 365. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1904.11.4.7, holotype of *Pipistrellus ariel* Thomas, 1904.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 62 minutes, and the digestibility rate about 82.3 %.

POPULATION:
Structure and Density
The population is apparently small but is probably stable (Z. Amr *pers. comm.*, 2005 in Benda and Aulagnier (2008) [in IUCN (2009)]; Benda and Aulagnier, 2020).

Trend
2018: Unknown (Benda and Aulagnier, 2020). 2008: Unknown (Benda and Aulagnier, 2008; IUCN, 2009). *P. ariel* populations within the Asia Minor and Levant region are unknown population trend, under predictive climate change scenarios (Bilgin *et al.*, 2012: 433).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Egypt, Kenya, Sudan.

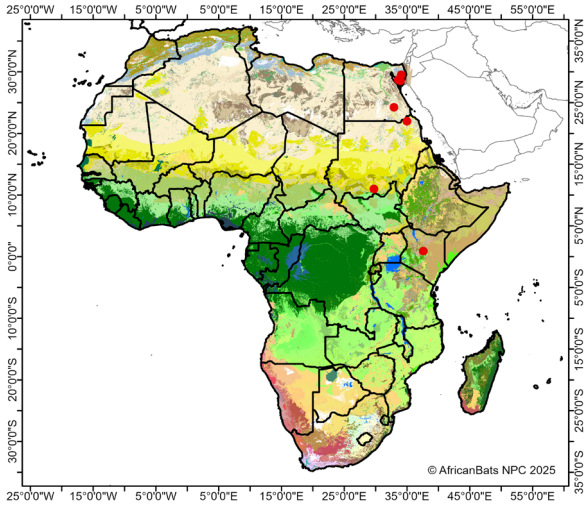

Figure 366. Distribution of *Hypsugo ariel*.

Hypsugo cf. eisentrauti Hill, 1968

*2013. *Hypsugo cf. eisentrauti:* Kerbis Peterhans, Fahr, Huhndorf, Kaleme, Plumptre, Marks and Kizungu, Bonn. Zool. Bull., 62 (2): 189. Publication date: November 2013. (Current Combination).

TAXONOMY:
As already indicated by Van Cakenberghe and Happold (2013i: 622) *eisentrauti* records from the DRC, Uganda, Kenya and Somalia do not resemble closely to the holotype and paratype of *P. eisentrauti* to be considered representatives of this species. Kerbis Peterhans *et al.* (2013: 189) therefore assigned these tentatively to *H.* cf. *eisentrauti*, indicating that they could represent a yet undescribed species. The specimens from the DRC and Rwanda have been assigned to *Parahypsugo macrocephalus* (Hutterer and Kerbis Peterhans, 2020).

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Somalia.

Hypsugo savii (Bonaparte, 1837)

*1837. *Vespertilio Savii* Bonaparte, Iconografia Fauna italiana, 1, fasc 20 and pl. Publication date: 1837. Type locality: Italy: Tuscany: Pisa [43 43 N 10 24 E]. Holotype: NHMUK 1907.1.1.732: sad, partial skeleton. Collected by: Prince Charles Lucien ("Carlo") Jules Laurent Bonaparte. - Etymology: In honour of Gaetano Savi (1769 - 1844) (see Kozhurina, 2002: 17).
1839. *V[esperugo (Vesperus)] Savii:* Keyserling and Blasius, Arch. Naturgesch. Berlin, 5 (1): 316. (Name Combination).
1853. *V[esperugo] Savii:* Blasius, Arch. Naturgesch. Berlin, 19 (1): 46. (Name Combination).
1855. *Vespertilio (Vesperugo) Savii:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 734. (Name Combination).
1856. *Vesperus (Meteorus) Savii:* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (5): 166. (Name Combination).
1856. *Vesperus Savii:* Kolenati, Allg. deutsche naturh. Zeitung, NF, 2 (4): 132. (Name Combination).
1859. *Scotophilus darwini* Tomes, Proc. zool. Soc. Lond., 1859, I (OS 27): 70. Publication date: February - June 1859. Type locality: Canary Islands (Spain): La Palma [28 40 N 17 50 W]. [Goto Description]. Holotype: NHMUK 1907.1.1.423: ad ♀, skull and alcoholic. Presented/Donated by: Charles Robert Darwin. Although Dobson (1878: 219) mentioned it was presented by Rev. R.T. Lowe. Formerly in Tomes collection.
1862. *Vespertilio (Meteorus) Savii:* Koch, Das Wesentliche der Chiroptern, 393. (Name Combination).
1871. *Vesperugo Savi:* Doderlein, Alcune generalita Intorno la Fauna Sicula de Vertebrati, ???. (Name Combination, Lapsus).
1885. *Vesperugo Savii:* Lataste, Act. Soc. Linn. Bordeaux, 39: 190?. (Name Combination).

1887. *Scotophilus darwinii:* Doria, Ann. Mus. civ. Stor. nat. Genova, 4 (2): 71. (Lapsus).
1904. *Vespertilio ochromixtus* Cabrera, Mem. Soc. espan. Hist. nat., 2 (5): 267, pl 3, fig 1 and 4. Type locality: Spain: Balearic Islands, Menorca Island. [Goto Description]. Holotype: MNCN 1.094: ♂. However, Ibáñez and Fernández (1989: 41) referred to this specimen as the holotype. However, Jelle Zijlstra (pers. comm., 26/02/2023) indicated that this specimen is a syntype as Cabrera mentioned two specimens and no lectotype has been designated since. Cabrera Latorre (1904: 268) explicitly mentions one male specimen and also refers to a second specimen, but concludes on this specimen as: "There are, however, between Mr. de Seabra's description and my *V. ochromixtus* some differences which make it impossible to decide the question without prior comparison of the specimens" Therefore, we agree with Ibáñez and Fernández (1989) and consider this specimen as a holotype. - Comments: Some authors, e.g. Ellerman and Morrison-Scott (1951: 170), Gharaibeh (1997: 95) mention "Sierra de Guadarrama, Madrid, Spain" as type locality, but Ibáñez and Fernández (1989: 41) - explicitly referring to the type specimen - mention Menorca as type locality.
1912. *Pipistrellus savii:* Miller, Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British Museum, 219. (Name Combination).
1956. *Pipistrellus savii savii:* Kahmann and Goerner, Mammalia, 20: 358. (Name Combination).
1964. *Pipistrellus savii sevii:* Hanák, Acta Soc. Zool. Bohem., 28 (1): 83. (Lapsus).
1966. *Pipistrellus (Pipistrellus) savii darwini:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 170. (Name Combination).
1966. *Pipistrellus (Pipistrellus) savii savii:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 169. (Name Combination).
1966. *Pipistrellus (Pipistrellus) savii:* Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals 1758 to 1946. (Second Edition), 169. (Name Combination).
1971. *Pipistrellus (Hypsugo) savii savii:* Lanza and Azzaroli, Lav. Soc. ital. Biogeog., nov ser 1: 698 (for 1970). (Name Combination).
1986. *[Hypsugo] savii:* Horáček and Hanák, Myotis, 23-24: 9. (Current Combination).
1987. *Hypsugo savii:* Menu, Palaeovert., 17 (3): 127. (Name Combination).
1987. *Pipistrellus (Hypsugo) savii:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 281. (Name Combination).
1997. *Pipistrellus savii ochromixus:* Gharaibeh, Systematics, distribution, and zoogeography of mammals of Tunisia, 95. Publication date: December 1997. (Lapsus).
2000. *Hypsugo savii savii:* Horáček, Hanák and Gaisler, Bats of the Palearctic region, 125. (Name Combination).
2002. *H[ypsugo] s[avii] darwini:* Trujillo, Ibáñez and Juste, Rev. suisse Zool., 109 (3): 549. (Name Combination).
2003. *H[ypsugo] savii darwinii:* Pestano, Brown, Suárez and Fajardo, Mol. Phylogenet. Evol., 26 (1): 57. (Lapsus).
2007. *Hypsugo cf. darwinii:* Mayer, Dietz and Kiefer, Front. Zool., 4: 4. (Name Combination).
? *Pipistrellus savi:* (Name Combination, Lapsus).

Taxonomy:

Koopman (1994: 114) considers this species to belong to the (sub)genus *Pipistrellus (Pipistrellus)*. Horáček *et al.* (2000: 125) and Volleth *et al.* (2001: 27) assigned this species to the genus *Hypsugo*.

Based on mitochondrial DNA, Veith *et al.* (2011: 95, 98) report the presence of "*H.* cf. *darwinii*" on Sardinia, Turkey, the Canary Islands, Morocco, and Sicily), but they also indicate that "taxonomic conclusions, which are solely based on mitochondrial genes, may be misleading due to effects such as incomplete lineage sort ing, introgression, and selection on mitochondrial loci". However, as indicated by Puechmaille *et al.* (2012: 226), the mitochondrial data suggest the presence of cryptic species within "*H. savii*", which led these authors to use "*H.* cf. *savii*" for the North African populations. However, Mayer *et al.* (2007: Suppl.) and Borloti *et al.* (2020: 2) use "*H.* cf. *darwinii*" for the bats from North African and the Canarian Islands. Gojznikar and Mayer (2024: 7) found that the mitochondrial DNA of specimens from Cape Verde, the Canary Islands and northern Africa belongs to the same lineage as that of the Italian specimens, and therefore "*H.* cf. *darwinii*" should be considered a synonym of "*H. savii savii*". However, they also indicate (p. 10) that analyses of nuclear DNA is necessary to confirm any subspecific division.

Common Names:

Albanian: Pipistrel i Savi-it. Arabian: Khaffash. Armenian: Մաշեղանման փոքրաչղջիկ. Azerbaijani: Savi şəbpərəsi. Basque: Savi saguzar, Savi saguzarra. Belarusian: Нетапыр Саві. Bengali: Savir Chamchika. Bosnian: Savijev šišmiš. Breton: Gousper Savi. Bulgarian: Савиево прилепче. Castilian (Spain): Murciélago montañero, Murciélago de montaña. Catalan (Spain): Ratpenat muntanyenc, Rat penat muntanyero, Ratapinyada muntayenca. Croatian: Primorski šišmiš. Czech: Netopýr Saviův, Netopýr alpský. Danish: Savis flagermus. Dutch: Alpendwergvleermuis, Alpenvleermuis, Savi's dwergvleermuis. English: Savi's Pipistrelle, Savi's Pipistrelle Bat. Estonian: Alpi nahkhiir. Finnish: Vuoristopiippa. French: Vespère de Savi, Pipistrelle de Savi. Frisian: Lytse Alpenflearmûs. Galician (Spain): Morcego montañeiro, Morcego do monte. Georgian: სავის ღამორი. German: Alpenzwergfledermaus, Alpenfledermaus, Alpen-Pipistrelle, herzohrige Abendfledermaus. Greek: Βουνονυχτερίδα. Hebrew: עטלפון סאבי, atalefon savi, Atalfon Savi. Hungarian: Alpesi denevér, Nycteris i alpios. Irish Gaelic: Ialtóg Savi. Italian: Pipistrello di Savi. Latvian: Sāvi sikspārnis. Lithuanian: Savio

šikšniukas. Luxembourgish: Alpen-Fliedermaus. Macedonian: Савиев лилјак [= Saviev Liljak]. Maltese: Pipistrell ta' Savi. Montenegrin: Savijev slijepi mišić. Norwegian: Klippeflaggermus. Polish: Pzymroczek Saviego. Portuguese: Morcego de Savii. Rhaeto-Romance: Pipistrel da Savi, Pipistrel da las alps. Romanian: Liliacul lui Savi. Russian: Нетопырь кожановидный, Кожановидный нетопырь [= Kozhanovidny netopyr]. Serbian: Дугодлаки сл[ij]епи мишић [= Dugodlaki sl[ij]epi mišić]. Scottish Gaelic: Ialtag Savi. Slovak: Večernica Saviho. Slovenian: Savijev netopir. Swedish: Alpfladdermus. Turkish: Savi'nin Cüce Yarasası. Ukrainian: Нетопир скельний (Саві), Гіпсуг гірський [= Hipsuh hirs'kyy]. Welsh: Ystlum lleiaf Savi.

CONSERVATION STATUS:
Global Justification
The species is widespread and abundant and there is no evidence of population decline. Consequently, it is assessed as Least Concern (LC ver 3.1 (2001)) (Hutson *et al.*, 2008p; IUCN, 2009; Juste and Paunović, 2016b).

Assessment History
Global
2016: LC ver 3.1 (2001) (Juste and Paunović, 2016b). 2008: LC ver 3.1 (2001) [assessed as *Pipistrellus savii*] (Hutson *et al.*, 2008p; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
No major threats are known (Hutson *et al.*, 2008p; IUCN, 2009; Juste and Paunović, 2016b). Water stress and the aerial hawking feeding style are, however, identified as being major risk factors linked with climatic change (Sherwin *et al.*, 2012: 174). Bilgin *et al.* (2012: 434) predict that the range retraction for *H. savii* as a result of climatic change may pose severe threats to its survival as this species has the bulk of its range in the Mediterranean region.

CONSERVATION ACTIONS:
Hutson *et al.* (2008p) [in IUCN (2009)] report that it is protected by national legislation in some range states. There are also international legal obligations for its protection through the Bonn Convention (Eurobats) and Bern Convention in parts of its range where these apply. It is included in Annex IV of EU Habitats and Species Directive. It occurs in protected areas.

GENERAL DISTRIBUTION:
Hypsugo savii has a wide range in the Palaearctic (and marginally in Indomalaya), extending from southern Europe and north Africa (Morocco, Algeria, Tunisia, the Canary Islands of La Palma, Tenerife, La Gomera, Gran Canaria, and El Hierro, and the Cape Verde Islands of Santiago and San Vicente) through the Middle East and the Caucasus to Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan, Tajikistan, Afghanistan and northern India (Horáček and Benda, 2004; Simmons, 2005). It occurs from sea level to 3,000 m.

Bilgin *et al.* (2012) examining climate change scenarios within the Asia Minor and Levant region, predict *H. savii* to have a range contraction, which may pose severe threats to the survival of this species.

Native: Afghanistan; Albania; Algeria; Andorra; Austria; Azerbaijan; Bangladesh; Bosnia and Herzegovina; Bulgaria; Cape Verde Islands (Azzaroli Puccetti and Zava, 1988; Borloti *et al.*, 2020: 2); China; Croatia; Cyprus; Czech Republic; France [Corse]; Georgia; Gibraltar; Greece [East Aegean Is., Kriti]; Holy See [Vatican City State]; Hungary; India; Iran, Islamic Republic of; Iraq; Israel; Italy [Sardinia, Sicily]; Japan; Kazakhstan; Korea, Democratic People's Republic of; Korea, Republic of; Lebanon; Monaco; Mongolia; Montenegro; Morocco (Benda *et al.*, 2010a: 157; El Ibrahimi and Rguibi Idrissi, 2015: 362; Dbiba *et al.*, 2025: 8); Palestinian Territory, Occupied; Portugal; Russian Federation; San Marino; Serbia; Slovakia; Slovenia; Spain [Baleares, Canary Is.]; Switzerland; Syrian Arab Republic; Tunisia (Dalhoumi *et al.*, 2014: 53); Turkey; Turkmenistan; Ukraine.

Regionally extinct: Germany.

Vagrant: United Kingdom (Great Britain).

Presence uncertain: Armenia; Bhutan; Macedonia, the former Yugoslav Republic of.

DENTAL FORMULA:
Esquivel *et al.* (2021: Suppl.) reported that 3 out of 24 examined museum skulls showed oligodontia (missing teeth).

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Benda *et al.* (2011b: 38).

Tongue
Park and Lee (2009: 267) found three types of lingual papillae in Korean specimens: filiform, fungiform, and circumvallate.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) mention a wing loading value of 8.0 Pa, aspect ratio 5.8 for a wingspan of 22 cm and a wing area of 86 cm^2 and a body mass of 7 g.

SEXUAL DIMORPHISM:
In Italian *H. savii* specimens, Rughetti and Toffoli (2014: 149) found a seasonal variability in body conditions, which was sex dependent. In late spring equal sized (Fa) females were heavier than males, although these differences were small in late summer. Additionally, the female's body mass decreased during late spring and summer most probably as the result of higher energy requirements for lactation. The male's mass did not change during this period.

ECHOLOCATION:
Papadatou *et al.* (2008b: 133) report the following data for 53 Greek specimens: F_{start}: 55.5 ± 10.64 kHz, F_{end}: 33.7 ± 1.43 kHz, F_{peak}: 36.7 ± 1.23 kHz, bandwidth: 8.7 ± 2.18 kHz, duration 6.8 ± 1.57 ms and interpulse interval: 148.5 ± 59.63 ms.

For 32 calls from animals from France, Greece and Switzerland, Walters *et al.* (2012: suppl.) present the following numbers: duration: 8.23 ± 3.19 ms, F_{max}: 46.59 ± 12.95 kHz, F_{min}: 32.64 ± 2.26 kHz, bandwidth: 13.95 ± 11.88 kHz, F_{peak}: 34.87 ± 3.15 kHz.

Five calls of animals from Iran had the following values reported by Benda *et al.* (2012a: 182): F_{start}: 42.5 ± 2.1 (40.9 - 45.9) kHz, F_{end}: 36.1 ± 0.3 (35.7 - 36.3) kHz, F_{peak}: 37.4 ± 0.7 (36.7 - 38.4) kHz, duration: 9.4 ± 0.4 (8.8 - 9.7) ms, and interpulse interval: 185.6 ± 4.0 (182.1 - 191.3) ms.

In Morocco, Disca *et al.* (2014: 226) report the type of call for "*Hypsugo* cf. *savii*" as FM-QFC, with the following parameters: F_{start}: 52.7 ± 7.2 kHz, F_{end}: 32.3 ± 0.7 kHz, F_{peak}: 34.0 ± 1.0 kHz, bandwidth: 20.3 ± 6.8 kHz, duration: 6.8 ± 0.7 ms.

Ait-Abdesselam *et al.* (2025: 40) mentioned an F_{max} value of 32.40 ± 1.71 kHz for Algerian bats.

Luo *et al.* (2019a: Supp.) reported the following data (from two calls): F_{peak}: 36.7, 34.6 kHz, F_{start}: 55.5, 47.3 kHz, F_{end}: 33.7, 32.8 kHz, Band width: 21.8, 14.5 kHz, and duration: 6.8, 8.1 ms.

MOLECULAR BIOLOGY:
Karyotype
Capanna (1968), Zima (1982) and Volleth *et al.* (2001) reported 2*n* = 44, Fna = 50, BA = 8, a metacentric X and a submetacentric Y chromosome. Rushton (1970: 465) reported 2*n* = 44, FN = 50, X = metacentric, and Y = acrocentric. Arslan and Zima (2014: 13) added that the autosomal complement consists of three large and one small metacentrics, 15 acrocentrics and two dot-like pairs. Capanna and Manfredi Romanini (1971: 474) described the autosomal chromosomes as 3 pairs of metacentric, 1 submetacentric and 17 acrocentrics.

Genetics
See Hoofer and Van Den Bussche (2003), Mayer *et al.* (2007), and García-Mudarra *et al.* (2009).

Pestano *et al.* (2003b: 59) found a 6.3 to 7.2 % difference in (uncorrected) cyt b and 3.8 to 4.4 % difference in 16S rRNA between bats from Spain and the Canary Islands.

Mayer *et al.* (2007: Suppl. 5) reported that European and Moroccon bats differed by 9.6 % in their mtDNA (nd1) and 16S rRNA (see also Kipson *et al.*, 2023: 102).

16S rRNA from Maltese specimens examined by Batsleer *et al.* (2019: 172) indicated that these bats belonged to a mainly north African lineage.

Gojznikar and Mayer (2024:) reviewed published data for four mitochondrial genes (ND1, CytB, COI and 16 S) and assigned records from the Cape Verdian Islands through the Canary Islands and northern Africa, and the Apennine Peninsula to the Alps to Lineage B (previously referred to as *Hypsugo* cf. *darwinii*).

HABITAT:
In northern Algeria, Ait-Abdesselam *et al.* (2025: 45) reported this species to be primarily active in rural sites, especially at water bodies.

DIET:
Benda *et al.* (2012a: 402 - 403) report the following major food groups for different areas, indicating that this species is an opportunistic feeder: *Lepidoptera, Diptera, Hymenoptera and Neuroptera (Switzerland); * Homoptera, Heteroptera and smaller representatives of Lepidoptera (Balkans and West Turkestan); * Formicoidea, Heteroptera, Coleoptera and Lepidoptera (Syria); *Coleoptera and Formicoidea (Turkey); *Auchenorrhyncha, small Lepidoptera, Coleoptera (mainly Staphilinidae), nematoceran Diptera (Chironomidae, Culicidae), Sternorrhyncha (Aphididae), Neuroptera

(Chrysopidae, Hemerobiidae), Heteroptera, Hymenoptera (small Apocrita), and Trichoptera (Iran: Fars); *Small Lepidoptera, Neuroptera (Chrysopidae), Sternorrhyncha (Aphididae), Heteroptera, Coleoptera,and nematoceran Diptera (Culicidae) (Iran: Khorasan).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 69 minutes, and the digestibility rate about 81.1 %.

POPULATION:
Structure and Density
In the western part of its range it generally occurs at low densities and is restricted by its habitat requirements, but it is abundant in some European areas bordering the Mediterranean. Summer maternity colonies usually number 20 - 70 females. In the Canary Islands it is the commonest bat species. In the eastern part of its range population size and trends are not known (Molur *et al.*, 2002).

Trend
2016: Stable (Juste and Paunović, 2016b). 2008: Stable (Hutson *et al.*, 2008p; IUCN, 2009). *H. savii* populations within the Asia Minor and Levant region are predicted to have a stable population trend, under climate change scenarios (Bilgin *et al.*, 2012: 433).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

PARASITES:
In Italy, Voyron *et al.* (2011: 193) reported *Aspergillus sydowii* and *Cladosporium cladosporioides* (Fungi) from live *H. savii* specimens.

In Algeria, Bendjeddou *et al.* (2013: 325) found *Rhipicephalus sanguineus* (Latreille, 1806) (Arachnidae: Ixodida: Ixodidae). The following ectoparasites were reported by Bendjeddou *et al.* (2017: 15): Siphonaptera: *Ischnopsyllus octactenus* (Kolenati, 1856); Heteroptera: *Cimex pipistrelli* Jenyns, 1839; Arachnida: *Argas transgariepinus* White, 1846. Mechouk *et al.* (2022: 8) mentioned the ixodid mite *Rhipicephalus sanguineus* (Latreille, 1806).

In their checklist of arthropod parasites of North African bats, Bendjeddou *et al.* (2023: 4 - 7) mention the following species: Argasidae: *Secretargas transgariepinus* (White, 1846); Cimicidae: *Cimex pipistrelli* Jenyns, 1839; Ischnopsyllidae: *Ischnopsyllus octactenus* (Kolenati, 1856); and Macronyssidae: *Rhipicephalus sanguineus* s.l.

VIRUSES:
Adenoviridae
Mastadenovirus
Bat mastadenovirus wa reported by Nieto-Rabiela *et al.* (2019: Suppl.).

Coronaviridae
Alphacoronavirus
This virus was reported by Kohl and Kurth (2014: 3112) from Italy.

Betacoronavirus
Kohl and Kurth (2014: 3112) reported this virus from Spain and Italy.

Herpesviridae
Cytomegalovirus
Nieto-Rabiela *et al.* (2019: Supp;) reported this virus.

Orthomyxoviridae
Despite sampling and testing of 2 individuals of this species, no evidence of influenza A-like viruses (*Orthomyxoviridae*) were obtained (Fereidouni *et al.*, 2015).

Poxviridae
Lelli *et al.* (2019) described a new pox virus (Hypsugopoxvirus - HYPV) from (*Hypsugo savii* from Northern Italy.

Rhabdoviridae
"Various European bat lyssaviruses" were reported by Kohl and Kurth (2014: 3114) from various European countries.

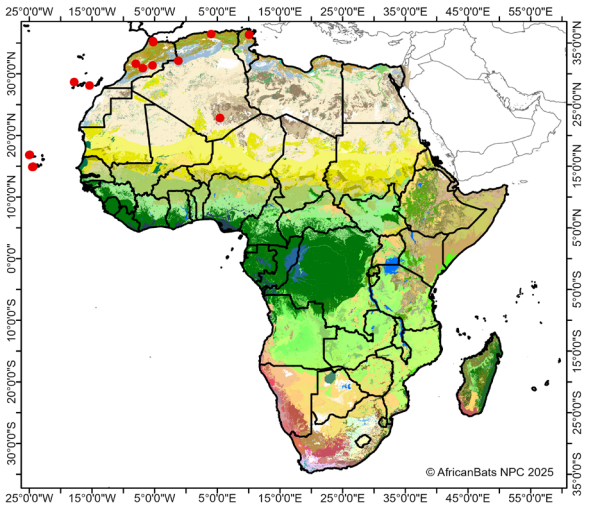

Figure 367. Distribution of *Hypsugo savii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Algeria, Canary Islands (Spain), Cape Verde, Italy, Morocco, Spain, Tunisia.

Genus ***Laephotis*** Thomas, 1901

1829. *Vespertilio:* A. Smith, Zool. Journ., 4 (16): 435. Publication date: May 1829. - Comments: In part. Not of Linnaeus, 1758 (see Monadjem *et al.*, 2020a: 1127).
1860. *Hypsugo:* Kolenati, Monographie der Europäischen Chiroptern, 20. - Comments: In part. Not of Kolenati, 1856 (see Monadjem *et al.*, 2020a: 1127, 1138).
1861. *Scotophilus:* Tomes, Proc. zool. Soc. Lond., 1861, I (old XXIX): 31. Publication date: May 1861. - Comments: In part. Not of Leach, 1821 (see Monadjem *et al.*, 2020a: 1127, who erroneously attributed the name to Thomas, 1861).
1878. *Vesperugo:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 183. Publication date: 15 June 1878. - Comments: In part. Not of Keyserling and Blasius, 1839 (see Monadjem *et al.*, 2020a: 1127, 1138).
1887. *Vesperus:* Jentink, Notes Leyden Mus., 9 (2): 275. Publication date: April 1887. - Comments: In part. Not of Keyserling and Blasius, 1839 (see Monadjem *et al.*, 2020a: 1127).
1897. *Eptesicus:* Matschie, Arch. Naturg., 63 (1): 84. Publication date: October 1897. - Comments: In part. Not of Rafinesque, 1820 (see Monadjem *et al.*, 2020a: 1127).
*1901. *Læphotis* Thomas, Ann. Mag. nat. Hist., ser 7, 7 (41): 460. Publication date: 1 May 1901 [Goto Description]. - Comments: Type species: *Læphotis Wintoni* Thomas, 1901. - Etymology: From the Greek "*laephotis*" meaning cloaked, veiled. Although, a note in the description of the genus suggested the name meant "sail" in Greek (Thomas, 1901d: 460). Palmer (1904: 359) mentions it as from the Greek "*λαίφος*", meaning sail and "*oύς*" or "*ώτός*", meaning ear, referring to the large ears. Gardner (2005: 184) considers this name to be masculine (*Leaph* = sail + *ot* = ear(ed) + is (Latin third declension ending).
1908. *Scabrifer* G.M. Allen, Bull. Mus. comp. Zool., 52 (3): 46. Publication date: July 1908. - Comments: Type species: *Scabrifer notius* G.M. Allen, 1908. Originally described as substitute for *Rhinopterus* Miller, preoccupied by *Rhinoptera* Kuhl, 1841 (see Allen, 1908: 46; 1939a: 97).
1939. *Rhinopterus:* G. M. Allen, Bull. Mus. comp. Zool., 83: 97. Publication date: February 1939. - Comments: In part. Not of Miller, 1906 (see Monadjem *et al.*, 2020a: 1127).
1984. *Pipistrellus:* Heller and Volleth, Z. zool. Syst. Evolut.-forsch., 22:. - Comments: In part. Not of Kaup, 1829 (see Monadjem *et al.*, 2020a: 1127). However, the only name currently assigned to *Laephotis* by Heller and Volleth (1984) is *capensis*, of which they state: "*"Eptesicus" capensis* has to be placed here [in *Pipistrellus*] as well", but they never explicitly do so. The first explicit use of *Pipistrellus* in combination with names currently assigned to *Laephotis* seems to be Hill and Harrison (1987: 274).
1987. *Nycterikaupius* Menu, Palaeovert., 17 (3): 108, pl 4, fig 1. Publication date: 15 November 1987 [Goto Description]. - Comments: In part. The species assigned to this genus by Menu (1987: 109) are currently (sensu Monadjem *et al.*, 2020a: 1140) included in the genera *Laephotis, Neoromicia, Pipistrellus* and *Pseudoromicia*.
2001. *Neoromicia:* Volleth, Bronner, Göpfert, Heller, von Helversen and Yong, Chromosome Res., 9 (1): 26.
? *Laephotis:* (Current Spelling).
? *Neoromicia sp. DMR-2017*

TAXONOMY:
The genus *Laephotis* was considered monotypic with two subspecies (Hayman and Hill, 1971). But Peterson (1971b) introduced *wintoni* and *angolensis* as distinct species, while Setzer (1971) described two further species, *namibensis* and *botswanae*. However, inter-specific relations remain unresolved largely because specimens are few and in scattered collections (Kock and Howell, 1988, Stanley and Kock, 2004). Several specimens from South Africa were assigned to *L. wintoni* and *L.* cf. *wintoni* on the basis of multivariate analyses (Rautenbach and Nel, 1978b, Watson, 1990a, Kearney and Taylor, 1997). Given the distance of South African localities from other populations of *L. wintoni* in Kenya and Ethiopia, this identification was considered with some scepticism and not followed by Honacki *et al.* (1982) or Andrianaivoarivelo *et al.* (2007). Specimens described by Rautenbach and Nel (1978b) were subsequently provisionally placed with *L. namibensis* (Skinner and Smithers, 1990: 105). Kock and Howell (1988) and Stanley and Kock (2004) identified several cases where specimens identified as *L. angolensis* have been re-identified as *L. botswanae* or *L.* cf. *angolensis*. Morphometric analyses that included palatal and post-palatal measurements (Kearney and Seamark, 2005) allowed the distinction of *L. botswanae* and *L.* cf. *angolensis* from other species of *Laephotis*, and suggested the assignment of specimens from KwaZulu Natal previously identified as *L.* cf. *wintoni* to *L. botswanae*. However, the distinction between *L. wintoni* and *L. namibensis* was not confirmed and still remains to be clarified (Kearney and Seamark, 2005).

In his initial description of the genus *Laephotis*, Thomas (1901d) suggested the genus was most closely allied to *Vespertilio*. Tate (1942) considered *Laephotis* the closest relative of the Neotropical big-eared genus, *Histiotus*, which in turn was considered an offshoot of *Eptesicus*. However, the ears in *Laephotis* are not as greatly enlarged as in *Histiotus*, nor are they connected across the forehead (Hayman and Hill, 1971). On geographic grounds, Williams and Mares (1978) doubted the association with *Histiotus*. Hill (1974a) considered *Laephotis* an independent offshoot of *Eptesicus*.

Placed in tribe Vespertilionini by Hill and Harrison (1987) on basis of baculum morphology and retained in that tribe by Simmons (2005).

In a cladistic analysis of bacular morphology *Laephotis* nested within *Neoromicia* (Kearney *et al.*, 2002). The molecular results of Stadelmann *et al.* (2004b) support this, and those of Hoofer and Van Den Bussche (2003) would be similar, if the suggestion that *nanus* is moved to the genus *Neoromicia*, as indicated by chromosomal analysis and bacular morphology (Kearney *et al.*, 2002), had been followed.

Although considered monotypic by Hayman and Hill (1971), four species are currently recognised (Simmons, 2005); *L. angolensis* Monard, 1935, *L. botswanae* Setzer, 1971, *L. namibensis* Setzer, 1971, and *L. wintoni* Thomas, 1901, see review by Jobling (1939). Specimens of this rarely caught bat, from the Western Cape Province in South Africa, were initially identified as *Laephotis wintoni* (Rautenbach and Nel, 1978b), and then later as *Laephotis namibensis* (Skinner and Smithers, 1990). This change in species identification has led to considerable confusion in the literature (Honacki *et al.*, 1982; Corbet and Hill, 1991; Koopman, 1994; Bronner *et al.*, 2003; Jacobs *et al.*, 2005; Simmons, 2005). Separation of *L. namibensis* and *L. wintoni* using morphometric analyses of cranial and dental characters, which include Hill (1974a)'s palatal and post-palatal measurements, that Stanley and Kock (2004) found useful in the separation of *L. botswanae* and *L. wintoni*, remains problematic (Kearney and Seamark, 2005).

Bacular studies have also failed to show differences between some species of *Laephotis* (Kearney *et al.*, 2002). Monadjem *et al.* (2010d: 430) suggests that molecular studies may be necessary to sort out the current confusion over species limits within this genus.

Without mentioning a reason, Taylor (2019a: 282, 283) - followed by Simmons and Cirranello (2020) - transferred all of the *Neoromicia* species (as well as *Hypsugo anchietae*) to the genus *Laephotis*. This was undone by Monadjem *et al.* (2020a: 1114, 1140).

Taylor *et al.* (2024: 7) mention the crown age for this genus as 3.46 (0.6 - 11.9) Mya, and 1.46 (0.19 - 4.43) Mya for the long-eared clade.

Traditionally recognized species of the genus *Laephotis*: ***angolensis*** Monard, 1935; ***botswanae*** Setzer, 1971; ***namibensis*** Setzer, 1971; ***wintoni*** Thomas, 1901.

Currently (Simmons and Cirranello, 2024a) recognized species within this genus: ***angolensis*** Monard, 1935; ***capensis*** (A. Smith, 1829); ***kirinyaga*** Monadjem, Patterson, Webala and Demos, 2020; ***malagasyensis*** (Peterson, Eger and Mitchell, 1995); ***matroka*** (Thomas and Schwann, 1905); ***namibensis*** Setzer, 1971; ***robertsi*** (Goodman, Taylor, Ratrimomanarivo and Hoofer, 2021); ***stanleyi*** (Goodman, Kearney, Ratsimbazafy and Hassanin, 2017); ***wintoni*** Thomas, 1901.

COMMON NAMES:
Czech: de Wintonovi netopýři. English: Long-eared Bats, African Long-eared Bats, Tropical Long-eared Bats. French: Oreillards d'Afrique, Noctophiles, Chauves-souris à longues oreilles. German: Afrikanische Langohrfledermäuse. Italian: Lefòti.

GENERAL DISTRIBUTION:
A small genus with four species, endemic to Africa south of the Sahara (Kearney, 2013a: 578).

BIOGEOGRAPHY:
A fairly wide range of biotic zones and habitats are exploited by this genus: the Somalia Masai Bushland, Zambezian Woodland, the Southern Rainforest—Savanna Mosaic (marginally), Afromontane Afroalpine, Highveld, South West Arid and South West Cape BZs (Kearney, 2013a: 579).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
The genus *Laephotis* is distinguished from all other African vespertilionid in part by the relatively long ears (> 16.5 mm, almost half the length of the FA) and large triangular tragus (Monadjem *et al.*, 2010d: 430). Distinguishing the four species of *Laephotis* from each other is not currently possible on external features (Monadjem *et al.*, 2010d: 430). There is a slight difference in mean size between *L. botswanae* and *L. angolensis*, with the former being larger, but this difference may be due to the very small sample size of measured *L. angolensis* (Monadjem *et al.*, 2010d: 430).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32 (like *Otonycteris* but as in *Glauconycteris*, *Eptesicus*, some *Pipistrellus* and *Mimitellus*) (Kearney, 2013a: 578).

The upper and lower premolars are tall teeth, almost the same height as the canines, and this, together with toothwear on the canines, might account for the suggestion that the canines are

extremely reduced (Hayman and Hill, 1971, Kingdon, 1974).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
Kearney and Seamark (2005) identified four cranial measurements based on a multivariate morphometric analysis to separate *L. botswanae* from the other three congeners. The post-palatal measurement of the distance from a line across the rear margins of the third upper molar to the anterior edge of the mesopterygoid fossa is shorter than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars in the *L. botswanae*/*L. angolensis* group, but longer in the *L. namibensis*/*L. wintoni* group (Hill, 1974a,Stanley and Kock, 2004, Kearney and Seamark, 2005).

DETAILED MORPHOLOGY:
Baculum
Bacular studies have also failed to show differences between some species of *Laephotis* (Kearney *et al.*, 2002). Monadjem *et al.* (2010d: 430) suggests that molecular studies may be necessary to sort out the current confusion over species limits within this genus.

ECHOLOCATION:
In Benin, the call of a non-specified *Laephotis* was categorized as a FMd (Frequency modulation downward) sonotype by Roemer *et al.* (2021: Suppl.).

HABITAT:
Marsden *et al.* (2023: 7) indicate that bats of the genus *Laephotis* are generally urban avoiders. This can probably be attributed to their roost specificity and the rarity of these species.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Gabon, Ghana, Kenya, Liberia, Mozambique, Rwanda, Somalia, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Laephotis 'incertae-sedis'

1857. *Vespertilio pusillus* Leconte, Proc. Acad. nat. Sci. Philad., 10. Publication date: 25 February 1857. Type locality: "Africa": "Western Africa". - Comments: Kock (1969a: 228) indicates that this paper was published in 1858.
1897. *Vesperugo (Vesperus) pusillus:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 110. (Name Combination).
1929. *Eptesicus pusillus:* Thomas, Proc. zool. Soc. Lond., 101. - Comments: Thomas (1929: 101) assigned this name to Noack. (Name Combination).
1953. *Eptesicus (Eptesicus) pusillus:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 76. (Name Combination).
2013. *Neoromicia cf. nana:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. (Name Combination).
2013. *Neoromicia cf. somalica:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. (Name Combination).
? *Neoromicia "incertae-sedis"*
? *Neoromicia capensis B:*

TAXONOMY:
Allen (1939a: 86) indicates that *Vespertilo pusillus* might possibly be the same form as *Vesperugo pusillus* Noack, 1887, but that the description is insufficient to identify the species. Ansell (1978: 25) - referring to Rosevear (1962) and Hayman and Hill (1971) - indicates that the status of *pusillus* Leconte is uncertain in relation to *Eptesicus minuta* Temminck, *"Eptesicus" somalicus* and *"Eptesicus" capensis*. Crawford-Cabral (1989) also points out that in southern Africa, *"Eptesicus" zuluensis* might be involved too.

Koopman (1965) and Kock (1969a: 138) consider this name to be indeterminable, and they suggest placing the small northern African *Eptesicus* specimens in the species *guineensis* Bocage, 1889.

According to Kock it is even uncertain that *pusillus* Leconte represents *Eptesicus* [= *Neoromicia/Laephotis* in the current context].

Kock (1969a: 159) also pointed out that the skull of the type of *Vesperugo pusillus* Noack, 1887 actually represents a non-adult "*Pipistrellus nanus*".

The fact that *pusillus* Leconte and *pusillus* Noack have been considered synonyms throughout the literature, also render much of the literature data indeterminable, unless these are supported by voucher specimens.

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

PARASITES:
In their description of the Nematode parasite *Molinostrongylus richardae*, Durette-Desset and Chabaud (1975: 312) also mention an "*Eptesicus pusillus* from Tananarive, Madagascar as an additional host. From the same host (species) and locality, Richard (1966: 413, 419) reported the Trematode *Plagiorchis (Plagiochis) vespertilionis* (Müller, 1784) Braun, 1900 and described another one: *Papillatrium (Papillatrium) inversum*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Burkina Faso.

Laephotis angolensis Monard, 1935

*1935. *Laephotis angolensis* Monard, Arq. Mus. Bocage, 6: 45. Type locality: Angola: 15 km W Dala: Tyihumbwe [=Tschiumbe / Tyiumbwe / Tyhumbwe / Chiu [11 02 S 20 04 E]. [Goto Description]. Holotype: MHNC 32-4-816: ♀. Collection date: September 1932. - Etymology: Referring to the country where the type specimen was collected. (Current Combination).
1953. *Laephotis wintoni angolensis:* Ellerman, Morrison-Scott and Hayman, Southern African Mammals 1758 to 1951: a reclassification, 78. Publication date: 23 December 1953. (Name Combination).
1971. *Laephotis botswanae* Setzer, Proc. Biol. Soc. Wash., 84 (32): 260, fig 1b, 1d. Publication date: 4 November 1971. Type locality: Botswana: 50 mi (80 km) W and 12 mi (19 km) S Shakawe [18 21 S 21 52 E]. [Goto Description]. Holotype: USNM 425349: ad ♀, skin and skull. Collected by: S.W. Goussard; collection date: 24 May 1967; original number: 691. - Comments: Although Schmidt *et al.* (2008: 35) mention the coordinates of the type locality as 18 32 S 21 05 E. - Etymology: The specimen from which the species was described originated near Shakawe in north-western Botswana (Taylor, 2005).
1974. *Laephotis wintoni:* Hill, Bull. Br. Mus. (nat. Hist.) Zool., 27 (2): 75. Publication date: 18 July 1974. - Comments: Not of Thomas, 1901. (Name Combination).
1999. *Laephotis cf. wintoni:* Taylor, S. Afr. J. Zool., 34 (1): 22. (Name Combination).
2005. *Laephotis cf. angolensis:* Kearney and Seamark, Ann. Transv. Mus., 42: 71. (Name Combination).
2024. *Laephotis cf. botswanae:* Taylor, Kearney, Clark, Howard, Mdluli, Markotter, Geldenhuys, Richards, Rakotoarivelo, Watson, Balona, and Monadjem, Glob. Ch. Biol., 30 (6):4. Publication date: 5 June 2024. (Name Combination).
? *Laephotis cf. botswanae:* (Name Combination).

TAXONOMY:
Described, as a distinct species, from a single specimen, ♀ with damaged skull, but subsequently considered a subspecies of *L. wintoni* (Ellerman *et al.*, 1953, Hayman and Hill, 1971). Although currently treated as a distinct species, the relationship between *L. angolensis* and *L. botswanae* is obscure, partly because specimens of *L. angolensis* are so scarce that variation within this form cannot be assessed (Kearney, 2013b: 580). Peterson (1973) suggests that *L. botswanae* may prove to be a larger, southern race of *L. angolensis*. However, both species occur together in S DR Congo (Setzer, 1971). Several specimens originally considered to represent *L. w. angolensis* were later reassigned to *L. botswanae* (Smithers, 1971, Hill, 1974a).

Laephotis botswanae and *L. angolensis* are currently considered to be conspecific, which makes the former a larger race of the latter (Peterson, 1971b, Kearney and Seamark, 2005). This is reflected in records of both taxa from southeastern Katanga, DRC (Monadjem *et al.*, 2010d: 430).

Stanley and Kock (2004), being concerned about the correct assignment of the species that is known from very few specimens, referred to specimens in the Natural History Museum, London collection, as cf. *angolensis*. In a morphometric analysis with specimens of the other *Laephotis* taxa, these specimens were distinct from *L. botswanae*, and *L. wintoni* / *L. namibensis*, however, it was suggested this small difference, based on two specimens of *angolensis*, may disappear with the addition of more specimens of both *angolensis* and *botswanae* (Kearney and Seamark, 2005: 85). Peterson (1973: 602) had suggested that "*L. bostwanae* may prove to be a larger, southern race of *L. angolensis*".

No subspecies currently recognized.

COMMON NAMES:
Czech: netopýr angolský. English: Angolan Long-eared Bat. French: Oreillard d'Angola, Chauve-souris à longues oreilles d'Angola, Noctophile d'Angola. German: Angola-Langohrfledermaus.

SIMILAR SPECIES:
Not easily distinguished from other *Laephotis* (Monadjem *et al.*, 2010d: 430, Kearney, 2013b: 580).

L. wintoni - Forearm longer (37 - 41 mm). Ears longer (21 - 24 mm) and broader. Skull longer and broader (GLS: 15.6 - 16.3 mm, GWS: 8.8 - 9.5 mm, C-M3: 5.1 - 5.3 mm).
L. namibensis - Forearm usually longer 37.8 (36 - 40 mm). Ears longer (22 - 25 mm). Skull larger (GLS: 16.1 - 17.0 mm, GWS: 8.4 - 9.2 mm, C-M3: 4.8 - 5.4 mm).

CONSERVATION STATUS:
Global Justification
Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing doubts as to its taxonomic validity as well as absence of recent information on its extent of occurrence, status, ecological requirements and threats (Jacobs *et al.*, 2008m; IUCN, 2009; Jacobs *et al.*, 2019e).

Assessment History
Global
2018: DD ver 3.1 (2001) (Jacobs *et al.*, 2019e). 2008: DD ver 3.1 (2001) (Jacobs *et al.*, 2008m; IUCN, 2009). 2004: NT ver 3.1 (2001) (Jacobs *et al.*, 2004c; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known (Jacobs *et al.*, 2008m; IUCN, 2009; Jacobs *et al.*, 2019e).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008m) [in IUCN (2009)] and Jacobs *et al.* (2019e) report that there appear to be no direct conservation measures in place, and it is not known if the species is present within any protected areas. Further studies are needed into the taxonomy, distribution, natural history and potential threats to this poorly known species.

GENERAL DISTRIBUTION:
Laephotis angolensis is known from two localities in Angola (including the type locality of Tyihumbwe [Chiumbe], 15 km west of Dala) and a single locality in the Democratic Republic of the Congo (Mumeme, East of Likasi, Shaba Province). Hill and Carter (1941) suggest that the species may occur throughout eastern Angola, but more sampling is needed here.

Laephotis angolensis is endemic to southern Africa (Kearney and Seamark, 2005). Apparently restricted to the Zambezian Woodland BZ and the southern fringe of the Southern Rainforest Savanna Mosaic (Kearney, 2013b: 580). *Laephotis angolensis* is known from just four specimens collected at three localities (Kearney and Seamark, 2005) in Angola and SE DR Congo (Peterson, 1973, Setzer, 1971, Hill, 1974a).

Native: Angola (Monard, 1935; Hill and Carter, 1941; Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 563; Taylor *et al.*, 2018b: 60); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Stanley and Kock, 2004; Kearney and Seamark, 2005: 87 as *L.* cf. *angolensis*); Kearney and Seamark, 2005: 85; Simmons, 2005; Monadjem *et al.*, 2010d: 563).
As *Laephotis botswanae*, it was reported from: Angola (Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 563); Botswana (Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 563); Congo (The Democratic Republic of the) (Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 564); Malawi (Ansell and Dowsett, 1988; Happold and Happold, 1997a; Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 564); Mozambique (Monadjem *et al.*, 2010c: 383); Namibia (Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 564); South Africa (Kearney and Seamark, 2005: 87; Simmons, 2005; Monadjem *et al.*, 2010d: 564); Tanzania (Kock and Howell, 1988; Bauer, 1992; Stanley and Kock, 2004: 176; Kearney and Seamark, 2005: 87); Zambia (Ansell, 1960a, Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 564); Zimbabwe (Cotterill, 1996a; Kearney and Seamark, 2005: 87; Monadjem *et al.*, 2010d: 564).

GEOGRAPHIC VARIATION:
None (Kearney, 2013b: 580).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Laephotis angolensis is a small bat with an estimated mass of around 5 - 6 g (Monadjem *et al.*, 2010d: 430), it is very similar in size and appearance to the slightly larger *L. botswanae*, from which it cannot be reliably separated on external characters (Kearney and Seamark, 2005, Monadjem *et al.*, 2010d: 430).

The face is plain, without noseleaf and with tail more or less fully enclosed in interfemoral membrane.

Dorsal pelage yellowish-brown to reddish-brown; hairs distinctly bicoloured (Monadjem *et al.*, 2010d: 430), mid-dorsal hairs ca. 7 mm: basal 5 mm blackish-brown, terminal 2 mm yellowish-brown or reddish-brown (Kearney, 2013b: 580). Ventral pelage pale grey on chin, paler on throat, becoming cream or white in pelvic region; hairs (except pelvic region) blackish-brown with pale grey, cream or white tip. Ventral hairs in pelvic region pure white (Kearney, 2013b: 580).

The naked skin on muzzle and around eyes is dark brown.

The long ears are dark brown, roughly triangular but very elongated; tip rounded; inner margins almost meeting on forehead but not joined at base. Ears may he held erect above head or (when resting) held sideways at right angles to head (Kearney, 2013b: 580). Ears separated, of medium length for a vespertilionid (15 – 18 mm) and of medium relative length (45 - 46 % of FA, n = 2) (Kearney, 2013b: 580).

Tragus with notch at base of posterior margin as in *L. botswanae*, but diagnostic differences between the tragi of these species, if present, are not known (Kearney, 2013b: 580).

Wings dark brown (Monard, 1935); arm-wing with whitish hind border. Interfemoral membrane medium-brown, more translucent.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32.

Four upper and five lower cheekteeth and two upper incisors on each side.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
In lateral profile the braincase is slightly flattened, but raises slightly above the rostrum (Monadjem *et al.*, 2010d: 430); rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull apparently shorter and usually narrower than in other *Laephotis* but data very limited (GLS: 13.7 13.8 mm; GWS: 6.7, 8.1 mm, n 2). Palatal length 6.1, 6.2 mm (n 2) (cf. > 6.4 mm in *L. botswanae* and *L. wintoni*) (Hill 1974a).

The upper premolar is sharply pointed and rises above the molars (Monadjem *et al.*, 2010d: 430).

DETAILED MORPHOLOGY:
Karyotype
Not recorded (Monadjem *et al.*, 2010d: 430, Kearney, 2013b). Monadjem *et al.* (2010d: 430) suggests the diploid number is likely to be 2n = 34 as in other species of *Laephotis*.

FUNCTIONAL MORPHOLOGY:
For *Laephotis botswanae*: Aspect ratio low; wing-loading very low (Malawi; M. Happold *pers. comm.* in Kearney (2013c: 582)). Flight highly manoeuvrable; turns by banking (minimum radius < 25 cm) and by stalling-and-twisting; individuals were able to sustain flight in a 1 x 1 x 1 m enclosure for up to three circuits/flight (6 bats, 10 flights each; M. Happold *pers. comm.* in Kearney (2013c: 582)). Can take off from ground. Not easily able to climb or scuttle.

SEXUAL DIMORPHISM:
No information (Kearney, 2013b: 580).

ECHOLOCATION:
Weier *et al.* (2020: Suppl.) reported on nine calls from the Okavango River Basin with the following characteristics: F_{max}: 74.79 ± 11.44 kHz, F_{min}: 42.51 ± 1.93 kHz, F_{knee}: 47.75 ± 4.49 kHz, F_{char}: 43.72 ± 3.23 kHz, slope: 165.40 ± 83.15 OPS, duration: 2.77 ± 0.57 ms.

For "*L. botswanae*", Pierce *et al.* (2012: 41) reported a mean peak frequency of 37.13 ± 2.37 kHz, and a mean bandwidth of 26.43 ± 11.49 kHz, with a duration of 2.68 ± 1.09 ms. Hand-released specimens from Malawi produced slightly longer FM-QCF (quasi-constant frequency) calls that had similar frequency parameters: duration: 4.73 ± 1.10 ms, mean peak frequency: 32.34 ± 1.42 kHz, and mean bandwidth of 29.72 ± 9.62 kHz. The maximum frequency in cluttered space was found to be 48.94 ± 4.6 kHz, as compared with 60.78 ± 9.33 kHz in open space. "*Laephotis botswanae*" produces LD-FM echolocation calls with an intermediate peak frequency (33 kHz), broad bandwidth (22 kHz), and intermediate duration (5 ms). Besides the fundamental, the second and third harmonics are often present on the spectrogram (Fenton and Bell, 1981; also see Fenton and Thomas (1980).

Search-phase call-shape (Malawi) (a) steep FM/ QCF and (b) smooth steep/shallow FM (six bats recorded as released, one tethered; M. Happold *pers. comm.* in Kearney (2013c: 582). Start-frequency 60 - 72 kHz; end-frequency 29 - 33 kHz; peak- frequency 29 - 33 kHz; call-duration ca. 3 - 5 ms (155 calls). (b) Start- frequency 47 - 49 kHz; end-frequency 32 - 33 kHz; call-duration 15 ms (12 calls). Fenton and Bell (1981) reported

calls from *Laephotis* of uncertain identity from Zimbabwe (see above) for which call-shape (based on one illustrated call) was angular steep/shallow FM; start- frequency 55 kHz; end-frequency 32 kHz; peak-frequency 33 kHz; maximum call-duration 5 ms. Although call shapes differed, the peak-frequency was the same in calls from Malawi and Zimbabwe, suggesting that the bats in both localities represent "*L. botswanae*" (Kearney, 2013c: 582).

Taylor *et al.* (2013b: 17) recorded two "*L. botswanae*" calls in Waterberg, South Africa, with the following parameters: F_{max}: 51.6 (50.3 - 53.0) kHz, F_{min}: 32.0 (31.8 - 32.2) kHz, F_{knee}: 35.6 (35.3 - 35.8) kHz, F_{char}: 33.0 (32.8 - 33.3) kHz, duration: 3.0 (2.9 - 3.1) ms. In the Mapungubwe National Park (RSA), Parker and Bernard (2018: 57) recorded 20 calls with F_{char}: 31.46 ± 1.47 kHz, F_{max}: 53.20 ± 7.20 kHz, F_{min}: 30.75 ± 1.28 kHz, F_{knee}: 37.38 ± 1.77 kHz, duration: 6.49 ± 2.68 ms and 6.79 ± 2.71 calls/sec.

3 "*L. botswanae*" calls recorded by Adams and Kwiecinski (2018: 4) had the following characteristics: F_{char}: 38.8 ± 0.7 kHz, F_{max}: 68.5 ± 0.5 kHz, F_{min}: 37.9 ± 0.9 kHz, duration: 2.2 ± 0.3 ms.

Moir (2020: 30) and Moir *et al.* (2021a: 371) reported 269 calls of 10 "*L. botswanae*" bats from southern KwaZulu-Natal and Eastern Cape (RSA): F_{max}: 59.63 ± 3.62 (53.43 - 62.9) kHz, F_{min}: 33.25 ± 0.66 (32.02 - 34.00) kHz, F_{char}: 33.73 ± 0.75 (32.88 - 35.38) kHz, F_{knee}: 38.85 ± 2.43 (35.54 - 44.38) kHz, and duration: 1.54 ± 0.21 (1.07 - 1.72) ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 6 *L. botswanae*" bats: F_{max}: 45.58 ± 10.03 kHz, F_{min}: 30.24 ± 1.16 kHz, F_{knee}: 33.66 ± 1.14 kHz, F_{char}: 30.73 ± 1.21 kHz, slope: 309.65 ± 145.86 OPS, duration: 4.92 ± 1.98 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 4 "*Laephotis botswanae*" calls from the Kruger Park (RSA): F_{min}: 32.9 ± 1.1 (31.7 - 34.2) kHz, Duration: 2.1 ± 0.1 (2.0 - 2.2) ms, F_{max}: 66.3 ± 1.6 (64.5 - 68.4) kHz, F_{knee}: 35.7 ± 1.1 (34.5 - 37.2) kHz, F_{char}: 33.3 ± 0.7 (32.5 - 34.2) kHz,

2 pulses of "*L. botswanae*" recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 31 - 32 kHz, F_{max}: 50 - 53 kHz, F_{char}: 32 - 33 kHz, F_{knee}: 35 kHz and duration 2 - 34 ms.

Taylor-Boyd *et al.* (2025: 116) report the following values for 11 calls from Zambia: Interpulse interval: (70.8 ± 16.7 (44.3 - 94.9) ms; F_{max}: 40.8 ± 3.4 (36.9 - 46.4) kHz; Start slope: -16.0 ± 3.3 (-11.0 - -21.6) kHz/ms; End slope: -7.9 ± 2.6 (-11.0 - -9.3) kHz/ms; Ledge duration: 0.4 ± 0.1 (0.3 - 0.6) ms.

Molecular Biology:

Karyotype

Rautenbach *et al.* (1993) reported 2*n* = 34, FN = 50, BA = 18, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa (as *Laephotis botswanae*).

Habitat:

Nothing is currently known on the habitat of *L. angolensis* (Monadjem *et al.*, 2010d: 430, Kearney, 2013b: 580). All records have come from the savanna biome (Kearney and Seamark, 2005: 85).

Most specimens of "*Laephotis botswanae*" have been caught in mist-nets, usually over or close to water, in riverine woodland or woodland savanna (Monadjem *et al.*, 2010d: 435, Kearney, 2013c: 582). Their association with rocky outcrops has been noted in some localities (Herholdt, 1989, Cotterill, 1996a). In Malawi, recorded near streams, and lakes in montane and sub montane evergreen forest at 1520 - 1700 m, from miombo woodland near sub-montane rainforest at 1350 - 1500 m, from mosaic of miombo woodland, farmland and riverine woodland near rocky hills, dams, streams and marshes at 1000 m, and in ornamental gardens in the town of Zomba (800 900 m), with rocky hills nearby (Happold and Happold, 1997b).

Furthermore, "*L. botswanae*" was reported occurring in both savanna (75 % of specimen records) and grassland biomes (25 % of specimen records) (Kearney and Seamark, 2005: 85). However, since all the grassland biome records are from high altitude localities in Malawi (Happold and Happold, 1997b), it was suggested the identification of the specimens from Malawi should be confirmed using palatal and post-palatal measurements (Kearney and Seamark, 2005: 85). Cooper-Bohannon *et al.* (2016: Table S2) mention its habitat preferences as Savanna (83 %) and Afromontane (16 %).

Habits:

For "*Laephotis botswanae*" the following was reported: Becomes torpid during day at ambient temperatures 21 - 24 °C. Predicted mean maximum urine concentration is medium (3745 mOsmol/kg); captive bats drank regularly every night (Kearney, 2013c: 582).

Forages by slow hawking. A light-tagged individual, released in an area with marshland, a large dam, some woodland and farmland, observed for 53 min, foraged mainly between 1 - 3 m over the marsh, making straight level traverses to and fro with some jerky zig-zagging and some wide circling, but no diving or swooping upwards or any other acrobatic manoeuvres; also foraged over tall grass in spaces between trees, and flew over a banana plantation; did not fly above other trees and did not forage over the open water (M. Happold *pers. comm.* in Kearney (2013c: 582)).

Of 20 individuals sampled in Malawi, one post-lactating ♀ and one sub adult ♂ were mist netted together; one reproductively inactive ♀, one lactating ♀ and one ♂ with abdominal testes were caught in one mist-net at intervals of 15 mm and 5 mm respectively; and all others were caught singly on different dates and at different localities (M. Happold *pers. comm.* in Kearney (2013c: 582). All of four individuals mist-netted by Herholdt (1989) in the Waterberg area in the Limpopo Province of South Africa were caught singly.

ROOST:
A pair of "*Laephotis botswanae*" was found roosting under the bark of a broken limb of a tree (HZM specimen label written by W F. H. Ansell); no other roosts known (Kearney, 2013c: 582).

DIET:
There is no information on the diet of this species (Monadjem *et al.*, 2010d: 430), but in Zimbabwe, "*Laephotis botswanae*" has been recorded feeding on Coleoptera, Lepidoptera and Trichoptera (Fenton *et al.*, 1977a, Fenton and Thomas, 1980). Fenton (1985) reported Coleoptera, Lepidoptera and Trichoptera in cool season diet of *Laephotis* in Zimbabwe, and Lepidoptera only in wet season; however, he was not sure if the bats represented *L. botswanae* or *L. angolensis* and this is still unresolved.

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 76 minutes, and the digestibility rate about 80.1 %. For "*L. botswanae*, the reported numbers were slightly different: 74 minutes and about 80.4 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
The populations abundance is not well known, however, 25 specimens were collected at one locality (Jacobs *et al.*, 2008m; IUCN, 2009; Jacobs *et al.*, 2019e). Rare (Kearney, 2013b: 580).

As *Laephotis botswanae* it seems to be rarely collected, and may be naturally rare (Schlitter, 2008e; IUCN, 2009; Monadjem and Schlitter, 2017a). Rare in some parts of their distribution, although Herholdt (1989) and Happold and Happold (1997b) have suggested it is not uncommon, but seldom caught at other localities (Kearney, 2013c: 582). There was a marked change in numbers recorded in Malawi between a survey in 1984 - 85 with three specimens (Happold *et al.*, 1988), and 1993 - 94 with 17 specimens (Happold and Happold, 1997b). Herholdt (1989) suggested that their being caught singly might indicate they are not easily captured in mist-nets.

Numbers in museum collections are growing (Kearney, 2013c:582).

Trend
2018: Unknown (Jacobs *et al.*, 2019e). 2008: Unknown (Jacobs *et al.*, 2008m; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Data for *Laephotis botswanae* indicate that the litter-size not known (Kearney, 2013c: 582), nor is the reproductive chronology (data inconclusive) (Monadjem *et al.*, 2010d: 435, Kearney, 2013c: 582). At 15° 31' 5 (near Namadzi, Malawi), 2 of 3 adult ♀♀ were lactating and one was reproductively inactive in Dec; 2 of 2 were reproductively inactive in Jan; 2 of 2 were post-lactating in Feb; no data for other months (M. Happold *pers. comm.* in Kearney (2013c: 582)). Two subadults were captured in Jan and Feb. These data suggest that ♀♀ might not reach sexual maturity until second year.

PARASITES:
ACARI
Ixodidae
Rhipicephalus simus, (Anciaux de Faveaux, 1984), although the information is uncertain because the identity of the host still needs to be confirmed (Kearney, 2013b: 580).

Spinturnicidae
Spinturnix walkei, (Anciaux de Faveaux, 1984), although the information is uncertain because the identity of the host still needs to be confirmed (Kearney, 2013b: 580).

Macronyssidae
Steatonyssus sp., (Anciaux de Faveaux, 1984), although the information is uncertain because the identity of the host still needs to be confirmed (Kearney, 2013b: 580).

HEMIPTERA
Cimicidae
Cacodmus villosus (Stâl, 1855) (Kock and Aellen, 1987: 876; Kock *et al.*, 1998b: 236; Kearney, 2013b: 580).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Congo (Democratic Republic of the), Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe.

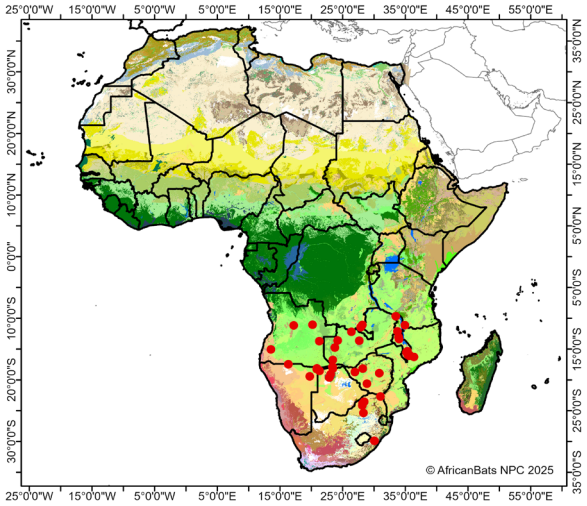

Figure 368. Distribution of *Laephotis angolensis*.

Laephotis capensis (A. Smith, 1829)

*1829. *Vespertilio Capensis* A. Smith, Zool. Journ., 4 (16): 435. Publication date: May 1829. Type locality: South Africa: Cape province: Grahamstown [33 18 S 26 32 E]. [Goto Description]. Lectotype: NHMUK 1848.6.12.18: ad, skin only. Collected by: Dr. J.A. Smith. This skin should match skull NHMUK 1848.6.12.21. Lectotype: NHMUK 1849.8.16.21: ad, skull only. Collected by: Dr. J.A. Smith. This skull should match skin NHMUK 1849.8.16.18. - Comments: Thorn *et al.* (2009: 56) mention that the "Lectotype (Thomas 1926) probably does not match the Grahamstown type-locality selected by Roberts (1951), see Thorn (1988a).". - Etymology: The name *capensis* refers to the Cape, where the type specimen was collected.
1840. *Vespertilio minuta* Temminck, Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome Seconde, 2 (13): 209. Publication date: 1840. Type locality: South Africa: Cape of Good Hope [ca. 33 56 S 18 28 E]. [Goto Description]. - Comments: Preoccupied by *Vespertilio minutus* Montagu, 1808.
1855. *Vespertilio (Vesperus) minutus:* Wagner, in: Schreber, Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, Suppl 5: 747.
1860. *Hypsugo minutus:* Kolenati, Monographie der Europäischen Chiroptern, 20.
1861. *Scotophilus capensis:* Tomes, Proc. zool. Soc. Lond., 1861, I: 36. (Name Combination).
1861. *Scotophilus minutus:* Tomes, Proc. zool. Soc. Lond., 1861, I: 32.
1878. *Vesperugo (Vesperus) capensis:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 198. Publication date: 15 June 1878. (Name Combination).
1878. *Vesperugo (Vesperus) minutus:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 197. Publication date: 15 June 1878.
1886. *Vesperugo capensis?:* Nehring, Katalog der Säugethiere, 5. (Name Combination).
1887. *Vesperus minutus:* Jentink, Mus. Hist. nat. Pays-Bas, Leyden, 275.
1889. *Vesperus damarensis* Noack, Zool. Jb. Syst., 4: 213, pl 5, fig 59. Publication date: 28 February 1889. Type locality: Namibia: Damaraland: Omburu and Golabie. [Goto Description]. Syntype: ZMB 86231: ad ♀, skin and skull. Collected by: Heinrich Rudolph Schinz; collection date: August 1886. Formerly A4902; see Turni and Kock (2008: 65). Syntype: ZMB A.4903: ad ♀, alcoholic (skull missing). Collected by: Heinrich Rudolph Schinz; collection date: August 1886. From Omburo; see Turni and Kock (2008: 65) [missing]. Syntype: ZMZ |TS389|: ad ♀, skin and skull. Collected by: Heinrich Rudolph Schinz. Locality Golabie, see Turni and Kock (2008: 65).
1897. *Eptesicus minutus:* Matschie, Arch. Naturgesch. Berlin, 63 (1): 84.
1897. *Vesperugo (Vesperus) damarensis:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 110.
1901. *Vespertilio (Eptesicus) capensis:* Sclater, Mammals of South Africa, 123, 125. (Name Combination).
1901. *Vespertilio (Eptesicus) damarensis:* Sclater, Mammals of South Africa, 123, 128.
1901. *Vespertilio (Eptesicus) minutus:* Sclater, Mammals of South Africa, 123, 124.
1905. *Vespertilio capensis gracilior* Thomas and Schwann, Proc. zool. Soc. Lond., 1905, I, II: 257. Publication date: 10 August 1905. Type locality: South Africa: KwaZulu-Natal: Eshowe [28 54 S 31 28 E]. Holotype: NHMUK 1904.8.31.3: ad? ♂, skin and skull. Collected by: Captain Claude Henry Baxter Grant and C.D. Rudd; collection date: 15 February 1904; original number: 678.
1907. *Vespertilio (Vespertilio) minutus:* Elliot, Field Columbian Mus., Zool. Ser., 115 (8): 512.
1908. *Scabrifer notius* G.M. Allen, Bull. Mus. comp. Zool., 52 (3): 46. Publication date: July 1908. Type locality: South Africa: SW Cape province: [=Western Cape]: Cape Town [33 56 S 18 28 E]. [Goto Description]. Holotype: MCZ 4555: ad ♂, skull and alcoholic. Collected by: Edgar Leopold Layard; collection date: August 1864. Presented/Donated by: Edgar Leopold Layard. See Allen (1908: 46); Helgen and McFadden (2001: 147).
1917. *Eptesicus garambæ* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 445. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Garamba [04 11 N 30 00 E]. [Goto Description]. Holotype: AMNH 49340: ad ♂, skull and alcoholic. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 14 March 1912; original number: 1888.

1917. *Eptesicus minutus minutus:* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 410, 445.
1919. *Eptesicus melckorum* Roberts, Ann. Transv. Mus., 6(3): 113. Type locality: South Africa: SW Cape province: Berg River: Kersfontein [32 51 S 18 42 E]. [Goto Description]. Holotype: TM 2283: ad ♀, skin and skull. Collected by: Austin Roberts and Adendorff; collection date: 21 November 1917; original number: 533. Note: In loft, under eaves of house. - Etymology: In honour of R. Melck of Kersfontein, Berg River, Cape Province, on whose property the original specimen was taken (Smithers, 1983: 102).
1923. *Eptesicus capensis:* Kershaw, Rev. Zool. afr., 11 (4): 358. (Name Combination).
1924. *Eptesicus capensis gracilior:* Roberts, Ann. Transv. Mus., 10: 60. (Name Combination).
1926. *Eptesicus damarensis:* Thomas, Proc. zool. Soc. Lond., 1926, I: 286.
1932. *Eptesicus capensis nkatiensis* Roberts, Ann. Transv. Mus., 15 (1): 16. Publication date: 1 October 1932. Type locality: Botswana: N Bechuanaland: Nkate [20 00 S 26 10 E]. [Goto Description]. Holotype: TM 6549: ad ♀, skin and skull. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 18 August 1930; original number: 999.
1934. *Eptesicus capensis capensis:* Shortridge, Mammals of South West Africa, 61. (Name Combination).
1939. *Rhinopterus notius:* G.M. Allen, Bull. Mus. comp. Zool., 83: 97.
1953. *Eptesicus (Eptesicus) capensis capensis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 75. (Name Combination).
1953. *Eptesicus (Eptesicus) capensis damarensis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 75. (Name Combination).
1953. *Eptesicus (Eptesicus) capensis gracilior:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 75. (Name Combination).
1953. *Eptesicus (Eptesicus) capensis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 75. (Name Combination).
1953. *Eptesicus (Rhinopterus) notius:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination).
1961. *Eptesicus notius:* Bateman, Koedoe, 4: 82. (Name Combination).
1965. *Eptesicus capensis garambae:* Koopman, Am. Mus. Novit., 2219: 15. (Name Combination).
1975. *Eptiscus capensis:* Dean, Zool. Afr., 10: 218. (Lapsus).
1984. *[Pipistrellus] capensis:* Heller and Volleth, Z. zool. Syst. Evolut.-forsch., 22: 72. (Name Combination).
1984. *Eptesicus (Eptesicus) capensis garambae:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1984. *Eptesicus (Eptesicus) capensis grandidieri:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1987. *Nycterikaupius capensis:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination).
1987. *Pipistrellus (Neoromicia) capensis:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).
1988. *P[ipistrellu]s c[apensis] notius:* Thorn, Mammalia, 52 (2): 202. (Name Combination).
1988. *Pipistrellus (Neoromicia) capensis capensis:* Ansell and Dowsett, Mammals of Malawi, 41. (Name Combination).
1988. *Pipistrellus (Neoromicia) capensis gracilior:* Ansell and Dowsett, Mammals of Malawi, 41. (Name Combination).
1988. *Pipistrellus capensis capensis:* Thorn, Mammalia, 52 (2): 199. (Name Combination).
1988. *Pipistrellus capensis gracilior:* Thorn, Mammalia, 52 (2): 204. (Name Combination).
1988. *Pipistrellus capensis:* Thorn, Mammalia, 52 (2): 199. (Name Combination).
1993. *Eptesicus (Neoromicia) capensis:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 201. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] damarensis:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] garambae:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] grandidieri:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] matroka:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
1994. *P[ipistrellus (Neoromicia)] c[apensis] notius:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 55. (Name Combination).
2001. *Hypsugo capensis:* Volleth, Bronner, Göpfert, Heller, von Helversen and Yong, Chromosome Res., 9 (1): 25. - Comments: Possibly a lapsus since this combination is only mentioned once in the abstract, as is *Pipistrellus (Neoromicia) capensis*. All other references to this taxon refer to it as *Neoromicia capensis*. (Name Combination, Lapsus).
2001. *Neoromicia capensis:* Volleth, Bronner, Göpfert, Heller, von Helversen and Yong, Chromosome Res., 9 (1): 26. (Name Combination).
2006. *Neuromicia capensis:* Watson, Koedoe, 49 (1): 114. Publication date: 18 December 2006. (Lapsus).
2010. *Neromicia capensis:* Traylor-Holzer, Tawes, Bayless, Valenta, Rayman and Songsasen, N., Insectivorous Bat Captive Population Feasibility Workshop Report, 49. (Lapsus).
2019. *L[aephotis] capensis:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2019. *Laephotis capensis:* M. Taylor, Bats: An illustrated guide to all species, 285. Publication date: 11 April 2019. (Current Combination).
? *Eptesicus capensis damarensis:* (Name Combination).
? *Eptesicus capensis notius:* (Name Combination).
? *Eptesicus capensis subsp.:*
? *Neoromicia capensis A2:*
? *Neoromicia capensis capensis:* (Name Combination).
? *Neoromicia capensis damarensis:* (Name Combination).

? *Neoromicia capensis garambae:* (Name Combination).
? *Neoromicia capensis gracilior:* (Name Combination).
? *Neoromicia capensis nkatiensis:* (Name Combination).
? *Neoromicia cf. capensis*

TAXONOMY:



Figure 369. *Laephotis capensis* (SMG-15768) caught at Marloth Park, Mpumalanga, South Africa.

Includes *notius*; see Koopman (1975: 405). Mentioned in the genus *Pipistrellus* by Koopman (1994: 117). Most of the West African populations have not been allocated to subspecies. Volleth *et al.* (2001: 27) assigned this species to the genus *Neoromicia*. Koopman (1993a: 201) included *matroka*, but see Peterson *et al.* (1995: 104).

Thorn *et al.* (2007: 70) removed *grandidieri* Dobson, 1876.

Helbig *et al.* (2010: 168) suggest transferring *capensis* to the genus *Laephotis*.

COMMON NAMES:

Afrikaans: Kaapse dakvlermuis. Chinese: 南非伏翼. Czech: netopýr kapský, netopýr hnědý, netopýr damarský. English: Cape bat, Cape Serotine, Cape Pipistrelle Bat, Cape Serotine Bat, Cape House Bat. French: Sérotine du Cap. German: Kap-Zwergfledermaus, Kap-Pipistrelle, Capische Abendfledermaus. Italian: Pipistrèllo capènse. Kiluba (DRC): Kasusu. Portuguese: Morcego caseiro do cabo.

ETYMOLOGY OF COMMON NAME:

The colloquial name serotine is derived from the Latin *serotinus*, late in the evening (*serus*) (Taylor, 2005). The name serotine is referring to *Eptesicus serotinus* and was in general use when the current species was still considered to belong to that genus.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

This species has been recovered from the upper Pleistocene at Border Cave (Avery, 1991: 6) and Wonderwerk (Avery and Avery, 2011: 19), South Africa, as well as from Holocene deposits at Blinkklipkop, Limerock, Wonderwerk (Avery and Avery, 2011: 19).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008r; IUCN, IUCN, 2009; Monadjem *et al.*, 2017cs).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Neoromicia capensis*] (Monadjem *et al.*, 2017cs). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus capensis*"] (Jacobs *et al.*, 2008r; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004t; IUCN, 2004). 1996: LR/lc [assessed as "*Eptesicus capensis*"] (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016w). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

There appear to be no major threats to this species as a whole (Jacobs *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017cs), although Doty and Martin (2012: 75) report on fatalities due to wind turbines in the Eastern Cape, South Africa. Aronson (2022: 225) indicated that this species accounted for 18.9 % of the carcasses he found during his study on the impact of wind energy facilities in the RSA.

CONSERVATION ACTIONS:

Jacobs *et al.* (2008r) [in IUCN (2009)] and Monadjem *et al.* (2017cs) report that in view of the species wide range and adaptability it is expected to occur in many protected areas (such as the Udzungwa Mountains National Park (Stanley *et al.*, 2005b)). There are no direct conservation measures currently needed for this species as a whole.

GENERAL DISTRIBUTION:

Laephotis capensis is widespread over much of sub-Saharan Africa. It has been recorded from Guinea Bissau in the west, to Somalia, southern Sudan and Eritrea in the east, ranging south to

most of South Africa. In South Africa, the species' distribution is linked with land use/land cover (Babiker Salata, 2012: 50).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,719,255 km^2.

Benda *et al.* (2025: 98) [referring to Monadjem *et al.* (2024)] indicate that the distribution of Laephotis capensis is restricted to the southern half of the continent, from central DRC, Burundi, central Tanzania to the Cape. West African records represent *Laephotis* cf. *capensis*. The records from Kenya should be referred to referred to *Laephotis kirinyaga*. However, they do report a new *capensis* specimen from Hells Gate National Park, which confirms the occurrence of the species in Kenya. They also suggest that some of the records currently assigned to *kirinyaga* might actually represent *capensis*.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 565; Taylor *et al.*, 2018b: 60); Botswana (Archer, 1975; Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 565); Burundi; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 565); Eswatini (Monadjem *et al.*, 2010d: 567, Monadjem *et al.*, 2021: 5); Kenya (Benda *et al.*, 2025: 31, 98); Lesotho (Lynch, 1994: 195; Monadjem *et al.*, 2010d: 565); Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 565); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 565; Monadjem *et al.*, 2010c: 384); Namibia (Monadjem *et al.*, 2010d: 565); South Africa (Seamark and Kearney, 2007; Monadjem *et al.*, 2010d: 566); Tanzania; Zambia (Ansell, 1967; Ansell, 1969; Ansell, 1973; Monadjem *et al.*, 2010d: 567); Zimbabwe (Monadjem *et al.*, 2010d: 567).

Presence uncertain (might tentavively need to be assigned to *Laephotis* cf. *capensis* or another form): Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 619); Cameroon; Central African Republic; Côte d'Ivoire; Djibouti; Equatorial Guinea; Eritrea; Ethiopia (Largen *et al.*, 1974; Yalden *et al.*, 1996; Lavrenchenko *et al.*, 2004b: 142); Gabon; Ghana (Decher and Fahr, 2007: 16 as "*N.* cf. *capensis*"); Guinea (Ziegler *et al.*, 2002: 78); Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Rainho and Ranco, 2001: 63); Liberia (Fahr, 2007a: 104); Nigeria; Sierra Leone; Somalia; Sudan; Togo; Uganda (Kityo and Kerbis, 1996: 62);

Bates *et al.* (2013: 339) reject the presence of *L. capensis* in the Republic of Congo as the data presented by Lavrenchenko *et al.* (2004b: 142) are actually from the DRC.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Fisk (1890: 97) reported on an albino specimen shot at Broadlands farm (Somerset West, South Africa), see also Allen (1939b), Lucati and López-Baucells (2016: Suppl.) and Zortéa and Silva (2017: 80).

Schoeman and Jacobs (2002: 157) mention the following parameters for 10 specimens from the Algeria Forestry Station (RSA): Fa: 35.9 ± 1.2 mm, Wing area: 87.6 ± 7.4 cm^2, Wing span: 24.0 ± 0.8 cm, Wing loading: 7.3 ± 1.0 N/m^2, and aspect ratio: 6.6 ± 0.4.

DETAILED MORPHOLOGY:
Penis
Fasel *et al.* (2020: 1394) described the penis as having a medial ridge widening toward its distal extremity, which separates it from the five other pipistrelloid species they examined. The hairs on the prepuce are shorter than in the other species.

Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

Other
van der Weyden *et al.* (2024: 2) reported the first case of a tumor (plasmacytoma) on the skin over the left lateral chest area in a Cape serotine bat.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 7.1 Pa, aspect ratio 6.4 for a wingspan of 25 cm and a wing area of 97 cm^2 and a body mass of 7 g.

ECHOLOCATION:
See Jacobs (1996), Taylor (1999b) and Taylor *et al.* (2005).

For the Algeria Forest Station (RSA), Schoeman and Jacobs (2002: 157) reported the call type to be a low duty echolocation dominated by frequency modulated calls, with a F_{peak}: 41.9 ± 1.4 kHz.

Schoeman and Waddington (2011: 291) and Luo *et al.* (2019a: Supp.) mention a peak frequency of 39.4 ± 1.1 kHz and duration of 5.1 ± 1.2 ms for specimens from Durban, South Africa.

Taylor *et al.* (2013b: 17) recorded the following parameters for 7 calls from Soutpansberg, South Africa: F_{max}: 48.9 ± 6.15 (41.4 - 61.4) kHz, F_{min}: 37.6 ± 1.86 (34.7 - 40.9) kHz, F_{knee}: 40.0 ± 1.92

(37.0 - 42.4) kHz, F_{char}: 38.2 ± 1.68 (35.8 - 41.2) kHz, duration: 3.6 ± 1.05 (2.1 - 5.0) ms.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg (RSA): F_{min}: 34 - 39 kHz, F_{char}: 36 - 41 kHz, F_{knee}: 37 - 42 kHz, slope: 254 - 509 OPS, duration: 2 - 5 ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 40 (37 - 42) kHz. 10 calls from the Kalahari Desert, recorded by Adams and Kwiecinski (2018: 4), had the following values: F_{char}: 36.9 ± 0.6 kHz, F_{max}: 39.6 ± 4.3 kHz, F_{min}: 36.7 ± 0.6 kHz, duration: 3.5 ± 0.5 ms. 20 calls from the Mapungubwe National Park (RSA) recorded by Parker and Bernard (2018: 57) had the following features: F_{char}: 39.54 ± 1.17 kHz, F_{max}: 63.06 ± 5.75, F_{min}: 38.59 ± 1.21 kHz, F_{knee}: 46.16 ± 3.94 kHz, duration: 5.18 ± 1.45 ms and 7.36 ± 2.31 calls/sec.

In the Telperion Nature Reserve (RSA), Kearney *et al.* (2019: 37) recorded the release calls of 37 bats (559 pulses) with the following characteristics: F_{char}: 37.10 ± 1.42 (32.65 - 42.11) kHz, slope at start of call: 53.67 ± 42.21 (-42.66 - 261.53), time from start of call to F_{char}: 4.25 ± 1.14 (1.66 - 7.64) ms and duration: 4.61 ± 1.12 (3.01 - 8.19). Subdivided according to sex, these data were respectively: ♂♂:37.26 ± 1.46 (32.65 - 42.11) kHz, 58.29 ± 46.30 (-18.07 - 261.53), 4.24 ± 1.09 (1.66–6.99) ms, 4.63 ± 1.07 (3.01 - 7.74) ms;♀♀: 36.93 ± 1.36 (33.20 - 40.20) kHz, 48.68 ± 36.75 (-42.66 - 205.01), 4.26 ± 1.19 (1.76–7.64) ms, 4.59 ± 1.18 (3.02 -8.19) ms. As February is probably in the mating season of *N. capensis*, this dimorphism in calls might be playing a social role within the reproductive context (Kearney *et al.* (2019: 41). This dimorphism was also reported by De Jong *et al.* (2025: 322) for 135 calls from 27 females: F_{char}: 37.93 ± 1.32 kHz, F_{knee}: 40.47 ± 2.05 kHz, F_{min}: 37.61 ± 1.32 kHz, F_{max}: 73.11 ± 9.73 kHz, Bandwidth: 35.50 ± 9.97 kHz, Duration: 3.94 ± 1.08 ms; and 125 calls from 25 males: F_{char}: 38.45 ± 1.34 kHz, F_{knee}: 42.57 ± 2.10 kHz, F_{min}: 38.06 ± 1.29 kHz, F_{max}: 74.80 ± 11.47 kHz, Bandwidth: 36.74 ± 11.51 kHz, Duration: 3.64 ± 1.08 ms. De Jong *et al.* (2025: 324) therefore state that the sexe of the bat needs to be taken into account when identifying bats based on their echolocation calls.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 39.54 ± 1.17 kHz, F_{max}: 63.06 ± 5.75 kHz, F_{min}: 38.59 ± 1.21 kHz.

Weier *et al.* (2020: Suppl.) reported on 12 calls from the Okavango River Basin with the following characteristics: F_{max}: 48.36 ± 7.29 kHz, F_{min}: 37.18 ± 1.79 kHz, F_{knee}: 40.26 ± 2.23 kHz, F_{char}: 37.55 ± 1.93 kHz, slope: 41.91 ± 24.41 OPS, duration: 5.15 ± 2.13 ms.

2384 calls of 78 bats recorded by Moir (2020: 30) and Moir *et al.* (2021a: 371) from southern KwaZulu-Natal and Eastern Cape (RSA) had the following parameters: F_{max}: 68.15 ± 9.29 (46.23 - 82.68) kHz, F_{min}: 39.2 ± 1.36 (35.64 - 42.26) kHz, F_{char}: 39.63 ± 1.35 (35.85 - 43.09) kHz, F_{knee}: 42.5 ± 2.20 (36.79 - 48.17) kHz, and duration: 3.09 ± 0.65 (1.93 - 4.87) ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 9 bats: F_{max}: 50.69 ± 4.25 kHz, F_{min}: 33.67 ± 6.67 kHz, F_{knee}: 39.85 ± 1.03 kHz, F_{char}: 35.9 ± 1.34 kHz, slope: -864.75 ± 7241.84 OPS, duration: 2.47 ± 0.56 ms.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 12 "*Neoromicia capensis*" calls from the Kruger Park (RSA): F_{min}: 39.4 ± 4.9 (36.2 54.2) kHz, Duration: 4.1 ± 1.1 (2.3 5.7) ms, F_{max}: 53.1 ± 8.0 (40.1 65.1) kHz, F_{knee}: 40.2 ± 2.0 (36.7 43.5) kHz, F_{char}: 38.7 ± 1.5 (36.2 41.2) kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype [as "*Neoromicia capensis*"].

112 pulses from "*Neoromicia capensis*" recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 35 - 41 kHz, F_{max}: 41 - 61 kHz, F_{char}: 35 - 41 kHz, F_{knee}: 37 - 42 kHz and duration 5 - 5 ms.

In the Mountain Zebra National Park, RSA, Parker (2022: 20) recorded 41 passes with: F_{min}: 36.25 ± 4.80 kHz, F_{char}: 39.25 ± 3.51 kHz and F_{max}: 45.09 ± 10.21 kHz.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 54) reported F_{char}: 39.54 ± 1.17 kHz, F_{max}: 63.06 ± 5.75 kHz and F_{min}: 38.59 ± 1.21 kHz.

Taylor-Boyd *et al.* (2025: 116) report the following values for 46 calls from Zambian bats: Interpulse interval: 71.3 ± 17.6 (29.4 - 132.0) ms; F_{max}: 46.0 ± 4.3 (41.1 - 58.7) kHz; Start slope: -23.0 ± 3.9 (-15.4 - -31.5) kHz/ms; End slope: -8.2 ± 3.3 (-1.4 - -9.9) kHz/ms; Ledge duration: 0.4 ± 0.1 (0.3 - 0.6) ms.

MOLECULAR BIOLOGY:
Karyotype
Peterson and Nagorsen (1975), Rautenbach *et al.* (1993), Volleth *et al.* (2001), and Kearney *et al.* (2002) all reported 2*n* = 32, FN = 50, BA = 20. While Rautenbach *et al.*, 1993) and Kearney *et al.* (2002) reported a metacentric X chromosome, Peterson and Nagorsen (1975) reported a submetacentric X chromosome. Peterson and Nagorsen (1975) and Rautenbach *et al.* (1993) both reported an acrocentric Y chromosome. GTG-bands identified three Robertsonian fusion chromosomes (7/11, 8/9, 10,12), considered as distinguishing characters for the genus *Neoromicia* Kearney *et al.* (2002).

Protein / allozyme
See Morales *et al.* (1991) for results from seven specimens from South Africa.

HABITAT:
Sirami *et al.* (2013: 34) recorded in the Western Cape Province, South Africa that *N. capensis* activity was significantly and positively influenced by size of wetland, while habitats 100 m surrounding wetlands were also significantly and positively influenced by the water body. *L. capensis* favoured open habitats surrounding wetlands (Sirami *et al.*, 2013: 35).

Minnaar *et al.* (2014a: 522) found that moth consumption by *L. capensis* was low under unlit conditions (mean percentage volume ± SD: 5.91 ± 6.25 %), while moth consumption increased six fold (35.42 ± 17.90 %) under artificially lit conditions despite a decrease in relative moth abundance. They conclude (p. 529) that the "introduction of artificial lights into previously unlit environments may allow syntonic bats [such as *N. capensis*, which are audible to eared moths] access to an historically unavailable resource in eared moths".

ROOST:
Taylor *et al.* (1999: 69) reported on a single roost found in the Durban area, which was located in the roof and spaces between wooden shutters and the outer wall of a school building in the Kloof suburb.

Kearney *et al.* (2019: 30) indicate that there seems to be a shift in roosting sites from natural crevice and vegetation types to man-made structures, which seems to be accompanied by a change in roosting group size. Vegetation roosts were usually inhabited by two or three individuals, whereas buildings can house groups of over 50 animals.

Czenze *et al.* (2021: 3) classified these bats as hot-roosting species as they preferred to roost at sites where the temperature approached the bat's normothermic body temperature.

DIET:
From the Algeria Forestry Station (RSA), Schoeman and Jacobs (2002: 157) reported the following prey groups based on 89 faecal pellets from 10 bats (in volume percent): Hemiptera (46.6 ± 33.7), Diptera (37.6 ± 28.4), Coleoptera (12.5 ± 21.5), Ephemeroptera (2.3 ± 5.5), and unknown (1 ± 3.2).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 67 minutes, and the digestibility rate about 81.4 %.

PREDATORS:
Thomas and Jacobs (2013: 127) [referring to Avery *et al.* (2005)] indicate that *L. capensis* is more often taken by owls due to its clutter-edge foraging style, which combines slow flight with foraging at the edge of the vegetation.

Dean (1975: 218) reports on one specimen being found in a barn owl (*Tyto alba* (Scopoli, 1769) pellet in South Africa (see also Avery *et al.*, 2005: 1054). Avery *et al.* (2003: 7) found *L. capensis* to be the best represented prey in barn owl pellets collected in the Free State during the summer.

Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850), the Pied crow (*Corvus albus* Statius Muller, 1776) and the Southern fiscal (*Lanius collaris* Linnaeus, 1766) as diurnal avian predators of "*Eptesicus capensis*".

Based on Fenton *et al.* (1983), Gual-Suárez and Medellín (2021: Suppl.) reported that this species was part of the food items taken by *Nycteris grandis*.

POPULATION:
Structure and Density
In general, this is a locally common species (Jacobs *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017cs).

Trend
2016: Stable (Monadjem *et al.*, 2017cs). 2008: Stable (Jacobs *et al.*, 2008r; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
van der Merwe and Rautenbach (1990: 540) reported that "*Eptesicus capensis*" commonly gives birth to twins and occasionally even triplets (= polytocy, see Garbino *et al.*, 2021: Suppl.). van der Merwe (1990: 202) examined five

pregnant females and found three of them having two foetuses (one in each uterine horn), one had three foetuses (two in the right and one in the left uterine horn) and one even four foetuses.

Happold and Happold (1990b: 567) reported births early in the wet season in Malawi.

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births from late October to November.

PARASITES:
Genov *et al.* (1992) reported the Nematode *Molinostrongylus omatus* (Mönnig, 1927) from an "*Eptesicus capensis*" specimen from South Africa.

Schaer *et al.* (2013a: 17416) report the presence of hemosporidian parasites of the genus *Polychromophilus* in one out of three investigated bats.

Clément *et al.* (2019a: 5) refer to four southern African bats, of which two were infected by *Trypanosoma dionisii*_AF5 and *Trypanosoma vespertilionis*_AF2.

BACTERIA
Dietrich *et al.* (2016a: 4) found *Rickettsia* in the faeces of bats from South Africa. Federici *et al.* (2022: 5) [referring to Dietrich *et al.* (2016a)] mentions Proteobacteria *Burkholderia, Helicobacter* and *Bartonella*.

ACARI
Myobiidae
Bochkov and Fain (2003: 12) reported three female and one tritonymph of *Acanthophthirius capensis* (de Meillon and Lavoipierre, 1944) from Tanzanian bats.

HEMIPTERA
Cimicidae
Kock *et al.* (1998b: 236, 137) reported the presence of *Cacodmus sparsilis* Rothschild, 1914 and *Cacodmus villosus* (Stål, 1855) on bats from South Africa and Malawi; and Haeselbarth *et al.* (1966: 11) reported *Cacodmus villosus* (Stål, 1855) in the Transvaal, South Africa. Haeselbarth *et al.* (1966: 11) suggests that Bedford (1932)'s record of *Cimex pipistrelli* Jenyns from Cape Town most probably refers to *Cacodmus villosus* (Stål, 1855) (see also Reinhardt and Jacobs, 2006).
Szentiványi *et al.* (2022: 12) reported *Aphrania barys* Ferris and Usinger, 1957 from Namibia and South Africa, and *Cacodmus villosus* (Stål, 1855) from Namibia.

DIPTERA
Nycteribiidae
Nycteribia schmidlii Schiner, 1853 (Haeselbarth *et al.*, 1966: 108). Dick *et al.* (2023) mentioned that the nycteribiid flies *Basilia (Basilia) robusta* Theodor, 1956, *Nycteribia latitergum* Theodor, 1957 and *Nycteribia schmidlii scotti* Falcoz, 1923 have been found on this bat species.

SIPHONAPTERA
Ischnopsyllidae
Ischopsyllus emminus Jordan and Rothschild, 1921 only known from the type series collected at Greenwood Park, Natal, South Africa (Haeselbarth *et al.*, 1966: 187). *Dampfia grahami* (Waterston, 1915) from Malawi (Beaucournu and Kock, 1996); *Araeopsylla scitula* (Rothschild, 1909) a single record from Kanye, Botswana (Haeselbarth *et al.*, 1966: 189).

Brennan *et al.* (2015: 145) found no antibodies against *Pseudogymnoascus destructans* (White-nose syndrome) in blood samples from bats from Botswana.

VIRUSES:
Bunyaviridae
Hantavirus
Těšíková *et al.* (2017: 279) found Hantavirus RNA in dried blood samples of *L. capensis* from the Dhati Walel National Park in Ethiopia. Arai and Yanagihara (2020: 7) assigned this virus to the genus *Loanvirus* (Mouyassué virus).

Coronaviridae - Coronaviruses
Geldenhuys *et al.* (2013: 516) found one *L. capensis* specimen (out of 10) testing positive for CoV RNA in Taung, RSA. Ithete *et al.* (2013: 1697) reported on a new virus from a *L.* cf. *capensis* (incorrectly identified as *L.* cf. *zuluensis*) from South Africa, which is related to Middle East respiratory syndrome (MERS)-CoV. Corman *et al.* (2014) determined the full genome sequence of the MERS-related CoV identified in Ithete *et al.* (2013: 1697) and found that 85 % of its genome was identical to Middle East respiratory syndrome (MERS)-CoV (subgenus *Merbecovirus*; see Markotter *et al.*, 2020: 5).

In South Africa, Cronjé *et al.* (2019: 2) found that female *N. capensis* [and bats trapped at low altitude sites with low body condition scores] were most likely to be infected with coronaviruses.
Joffrin *et al.* (2020: 6) reported Beta-C coronaviruses from RSA bats.

Phenuiviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)

Oelofsen and Van der Ryst (1999) tested 28 individuals from four localities in the Free State Province, South Africa for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies
Oelofsen and Smith (1993) tested 101 individuals from 5 localities using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) tested 145 individual brains, from 12 localities by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Botswana, Burundi, Cameroon, Congo (Democratic Republic of the), Eritrea, Eswatini, Ethiopia, Ghana, Guinea, Kenya, Lesotho, Liberia, Malawi, Mozambique, Namibia, Nigeria, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

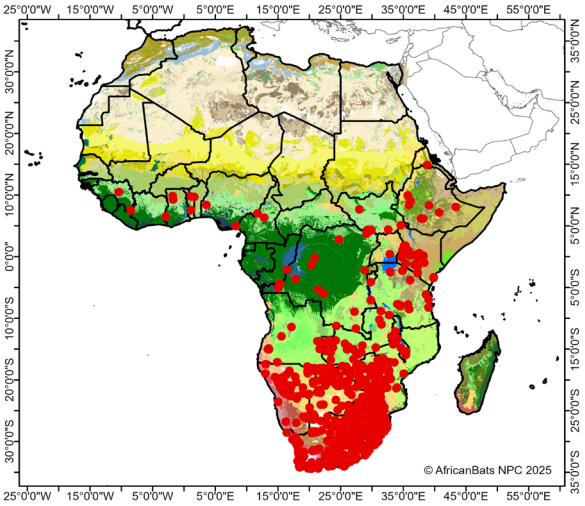

Figure 370. Distribution of *Laephotis capensis*.

Laephotis kirinyaga Monadjem, Patterson, Webala and Demos, 2020

1974. *Eptesicus capensis:* Kingdon, East African Mammals. - Comments: Not of A. Smith, 1829 (see Monadjem *et al.*, 2020a: 1128).
2008. *Pipistrellus capensis garambae:* Thorn and Kerbis Peterhans, Small mammals of Uganda, 56. - Comments: In part (see Monadjem *et al.*, 2020a: 1128).. (Name Combination).
2012. *Neoromicia capensis:* Patterson and Webala, Field. Life Earth Sc., 6: 42. Publication date: 29 November 2012. - Comments: Not of A. Smith, 1829 (see Monadjem *et al.*, 2020a: 1128).
2016. *Neoromicia somalica:* Benda, Reiter, Uhrin and Varadínová, Acta Chiropt., 18 (2): 323. Publication date: October 2016. - Comments: In part (see Monadjem *et al.*, 2020a: 1128, 1132).
2020. *Laephotis cf. kirinyaga:* Monadjem, Patterson, Webala and Demos, Zool. J. Linn. Soc., 191 (4):1120. Publication date: 10 September 2020. (Name Combination).
*2020. *Laephotis kirinyaga* Monadjem, Patterson, Webala and Demos, in: Monadjem et al., Zool. J. Linn. Soc., 191 (4): 1120, 1128, figs 5A, 7, 8. Publication date: 10 September 2020. Type locality: Kenya: Marsabit county: Marsabit Nat. Park, 1.3 km SE campsite, near HQ [02 18 32 N 38 00 00 E, 1250 m]. Holotype: FMNH 234558: ad ♂, skull and alcoholic and tissue. Collected by: Bruce D. Patterson, Paul W. Webala, Carl W. Dick and Beryl Makori; collection date: 27 July 2015; original number: BDP-7516. Paratype: FMNH 234546: ♂. Collected by: Bruce D. Patterson; collection date: 16 July 2015; original number: BDP-7291. Paratype: FMNH 234549: ♀. Collected by: Bruce D. Patterson; collection date: 22 July 2015; original number: BDP-7382. Paratype: FMNH 234550: ♂. Collected by: Bruce D. Patterson; collection date: 22 July 2015; original number: BDP-7388. Paratype: FMNH 234551: ♂. Collected by: Bruce D. Patterson; collection date: 22 July 2015; original number: BDP-7391. Paratype: FMNH 234552: ♀. Collected by: Bruce D. Patterson; collection date: 22 July 2015; original number: BDP-7393. Paratype: FMNH 234553: ♂. Collected by: Bruce D. Patterson; collection date: 22 July 2015; original number: BDP-7395. Paratype: FMNH 234556: ♂. Collected by: Bruce D. Patterson; collection date: 25 July 2015; original number: BDP-7441. Paratype: FMNH 234557: ♂. Collected by: Bruce D. Patterson; collection date: 26 July 2015; original number: BDP-7454. Paratype: FMNH 234559: ad ♂. Collected by: Bruce D. Patterson; collection date: 27 July 2015; original number: BDP-7517. - Etymology: *kirinyaga* is a Kikuyu word for Mount Kenya and refers to the distribution of this species (Monadjem *et al.*, 2020a 1129). (Current Combination).
2022. *Neoromicia kirinyaga:* Benda, Uvizl, Šklíba, Mazoch and Červený, Lynx, ns 53 (1): 317. (Name Combination).
? *Laephotis cf. kirinyaga TD-2020*
? *Pipistrellus capensis garambe:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1128. (Lapsus).

COMMON NAMES:
English: East African Serotine

CONSERVATION STATUS:
Monadjem *et al.* (2020a: 1132) suggest that this species should be listed as "Least Concern".

GENERAL DISTRIBUTION:
This species occurs infrequently across the highlands of Kenya on both sides of the Rift Valley, as well as in Murchison Falls National Park (Uganda), Ethiopia, and Senegal (Monadjem *et al.*, 2020a: 1131).

The single record on the border of Senegal and Guinea (IVB S1787) seems aberrant, but that specimen is explicitly mentioned by Monadjem *et al.* (2020a) so it is assumed to be correct (or possibly might represent an undescribed species).

Native: Ethiopia, Kenya, Senegal, Uganda.

ECHOLOCATION:
Monadjem *et al.* (2020a: 1132) reported the following echolocation parameters for the type specimen: F_{peak}: 44.9 kHz, F_{start}: 74.3 kHz, F_{end}: 41.6 kHz. The peak frequency for 14 additional specimens was 43.9 ± 0.91 kHz (73.9 ± 9.43 to 41.8 ± 1.64 kHz).

MOLECULAR BIOLOGY:
Karyotype:
Volleth *et al.* (2023c: 39) reported 2*n*=32, Fna=50 and nine large-to-medium-sized meta- to submetacentric, one small metacentric and five small acrocentric autosomal chromosome pairs. The X chromosome is a medium-sized metacentric chromosome and the Y chromosome is about of the same size as chromosome 23.

HABITAT:
Monadjem *et al.* (2020a: 1131) indicate that this species occurs in in wet tropical forest (e.g., Kakamega forest, with ~1900 mm of rainfall per annum), less mesic montane forest (Marsabit National Park) and relatively dry savanna woodlands (e.g., Lolldaiga Hills conservancy ~600 mm).

PARASITES:
Babyesiza *et al.* (2025: 4) found *Trypanosoma dionisii* and *T. vespertilionis* in *Laephotis kirinyaga* specimens from the CAR.

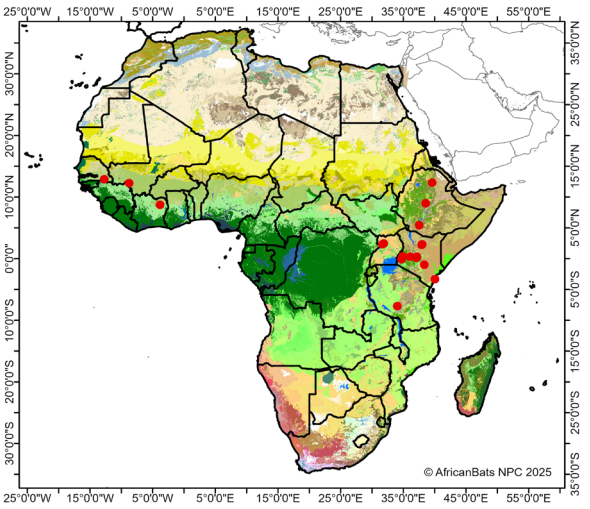

Figure 371. Distribution of *Laephotis kirinyaga*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Côte d'Ivoire, Ethiopia, Kenya, Mali, Senegal, Tanzania, Uganda.

Laephotis malagasyensis (Peterson, Eger and Mitchell, 1995)

*1995. *Eptesicus somalicus malagasyensis* Peterson, Eger and Mitchell, Faune de Madagascar, Chiroptères, 84: 100, fig 49. Type locality: Madagascar: Sakaraha sous-prefecture: 220 km NE Tuléar [=Toleara]: Ilakaka, East of [22 41 S 45 13 E]. [Goto Description]. Holotype: ROM 42713: ad ♀, skin and skull. Collected by: Randolph Lee Peterson, John George Williams and Robert M. Glen; collection date: 13 May 1967. See Peterson *et al.* (1995: 100), Goodman and Ranivo (2004: 434). - Comments: Bates *et al.* (2006: 313) situated the type locality at Maninday [22 47 S 44 48 E].
2004. *N[eoromicia] malagasyensis:* Goodman and Ranivo, Mamm. biol., 69 (6): 436. (Name Combination).
2004. *Neoromicia somalicus malagasyensis:* Goodman and Ranivo, Mamm. biol., 69 (6): 434. (Name Combination).
2012. *Neoromicia cf. malagasyensis:* Goodman, Taylor, Ratrimomanarivo and Hoofer, Zootaxa, 25: 25. (Name Combination).
2019. *L[aephotis] malagasyensis:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2019. *Laephotis malagasyensis:* M. Taylor, Bats: An illustrated guide to all species, 391. (Name Combination).
2020. *Laephotis malagasyiensis:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (1): 1140. Publication date: 10 September 2020. (Lapsus).
2020. *Neoromicia somalicus malagasyiensis:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (1): 1140. Publication date: 10 September 2020. (Lapsus).
? *Eptesicus malagasyensis:* (Name Combination).
? *Neoromicia malagasyensis:* (Name Combination).

TAXONOMY:
Only known from a very limited number of specimens. Originally considered a subspecies of *somalicus* Thomas, 1901 by Peterson *et al.* (1995), but see Goodman and Ranivo (2004: 438), who elevate it to species rank, which is supported by Bates *et al.* (2006). However, they did not discuss the relation of this form with *humbloti* A. Milne-Edwards, 1881.

COMMON NAMES:
English: Isalo Serotine. French: Sérotine de Sakahara, Sérotine de l'Isalo. German: Madagaskar-Zwergfledermaus, Madagaskar Pipistrelle.

CONSERVATION STATUS:
Global Justification
This species is listed as Vulnerable (VU B1ab(iii)+2ab(iii) ver 3.1 (2001)) because it has an extent of occurrence (EOO) of only 7,301 km², and is currently known only from the area around the Isalo Massif (likely having a maximum area of occupancy (AOO) of <2,000 km²), where it is presumed to be at risk of habitat loss (Monadjem *et al.*, 2019b).

Assessment History
Global
2016: VU B1ab(iii)+2ab(iii) ver 3.1 (2001) assessed as *Neoromicia malagasyensis* (Monadjem *et al.*, 2019b). 2008: EN B1ab(iii) ver 3.1 (2001) [as "*Eptesicus malagasyensis*"] (Andriafidison *et al.*, 2008c; IUCN, 2009).

Regional
None known.

MAJOR THREATS:
The threats to this species are not known, but its habitat is presumably undergoing some decline. It has yet to be recorded from synanthropic settings and probably relies on natural roost sites in trees and other vegetation (Andriafidison *et al.*, 2008c; IUCN, 2009; Monadjem *et al.*, 2019b).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008c) [in IUCN (2009)] and Monadjem *et al.* (2019b) report that this species is present in Parc National d'Isalo. Future conservation measures should focus on roosting sites, but further research is needed to investigate the roosting and foraging habitats of this species.

GENERAL DISTRIBUTION:
Laephotis malagasyensis is endemic to Madagascar, where it is restricted to an area of 1,905 km² around the Isalo Massif (Bates *et al.*, 2006). It has been recorded between 450 and 700 m above sea level (Goodman and Ranivo, 2004) and is currently known from four localities in the centre-south (Bates *et al.*, 2006; Garbutt, 2022: 100).

Native: Madagascar (Peterson *et al.*, 1995; Goodman and Ranivo, 2004: 438; Bates *et al.*, 2006).

ECHOLOCATION:
Kofoky *et al.* (2009: 382) reported the calls of six individuals which consisted of FM/QCF components produced at low duty cycle, with maximum energy in the fundamental at about 45.8 kHz.

POPULATION:
Structure and Density
There is no information on the population status of this species (Monadjem *et al.*, 2019b).

Trend
2016: Unknown (Monadjem *et al.*, 2019b).

PARASITES:
Ramasindrazana *et al.* (2016: 7) report the presence of an unnamed filarial Nematode.

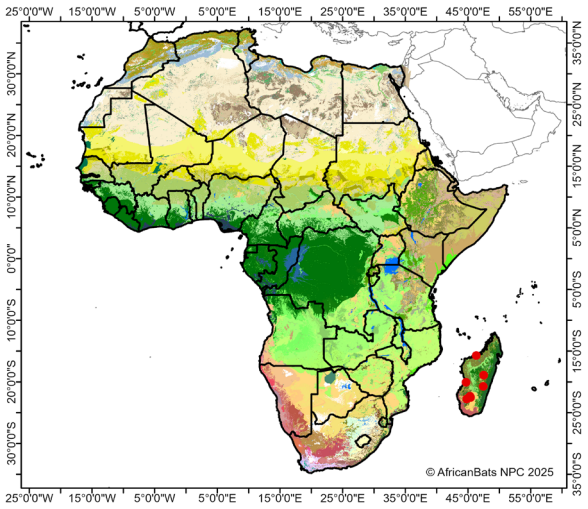

Figure 372. Distribution of *Laephotis malagasyensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Laephotis matroka (Thomas and Schwann, 1905)

*1905. *Vespertilio matroka* Thomas and Schwann, Proc. zool. Soc. Lond., 1905, I, II: 258. Publication date: 10 August 1905. Type locality: Madagascar: Betsileo: Ambositra [20 31 S 47 15 E, 1 100 m]. Holotype: NHMUK 1897.9.1.32: ad ♂, skull and alcoholic. Collected by: Dr. Charles Immanuel Forsyth-Major; collection date: 2 February 1875; original number: 177. See Peterson *et al.* (1995: 104).
1939. *Eptesicus matroka:* G.M. Allen, Bull. Mus. comp. Zool., 83: 86. (Name Combination).
1987. *Nycterikaupius matroka:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination, Lapsus).
2006. *Neoromicia matroka:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 136. (Name Combination).
2019. *L[aephotis] matroka:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2019. *Laephotis matroka:* M. Taylor, Bats: An illustrated guide to all species, 391. (Name Combination).

TAXONOMY:
Considered a synonym of *capensis* by Hayman and Hill (1971) and Koopman (1993a: 201), but see Peterson *et al.* (1995: 104), Russ *et al.* (2001), Simmons (2005: 456) who consider it a valid species.

Simmons (2005: 456) placed *matroka* within the genus and subgenus *Eptesicus*.

COMMON NAMES:
Czech: netopýr malgašský. English: Madagascar serotine, Matroka Bat, Malagasy Serotine. French: Sérotine de Madagascar. German: Matroka-Zwergfledermaus, Matroka-Pipistrelle.

CONSERVATION STATUS:
Global Justification
This species is listed as Least Concern (LC ver 3.1 (2001)) because there is no evidence of a severe decline in habitat or population size and it occurs across a wide range of habitats which includes built-up areas (Andriafidison *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017bt).

Assessment History
Global
2016: LC ver 3.1 (2001) [as *Neoromicia matroka*] (Monadjem *et al.*, 2017bt). 2008: LC ver 3.1 (2001) [as "*Eptesicus matroka*"] (Andriafidison *et al.*, 2008r; IUCN, 2009). 2000: Data Deficient.

Regional
None known.

MAJOR THREATS:
There are no known major threats to this species (Andriafidison *et al.*, 2008r; IUCN, 2009; Monadjem *et al.*, 2017bt).

CONSERVATION ACTIONS:
Andriafidison *et al.* (2008r) [in IUCN (2009)] and Monadjem *et al.* (2017bt) report that this species has yet to be recorded from inside protected areas, but is known to use agricultural land adjacent to Parc National de Mantadia (Randrianandriananina *et al.*, 2006).

GENERAL DISTRIBUTION:
Laephotis matroka is endemic to Madagascar and appears to be largely restricted to an area in the eastern highlands (approximately Ambohitantely / Zahamena in the north, to Andringitra / Zazafotsy in the south) between 970 and 1,300 m above sea level, where it occurs in humid montane forest, degraded forest and anthropogenic grassland areas (Bates *et al.*, 2006; Garbutt, 2022: 101).

Native: Madagascar (Peterson *et al.*, 1995: 105; Bates *et al.*, 2006; Randrianandriananina *et al.*, 2006).

GEOGRAPHIC VARIATION:
Goodman *et al.* (2012b: 3) found geographical variation in the cranio-dental measurements, which lead them to divide this species into geographical units or Operational Taxonomic Units (OTUs): OTU 1 - the Central Highlands above 1,000 m, which includes the type locality near Ambositra (Thomas and Schwann, 1905b: 258); OTU 2 - areas in central western Madagascar less than 900 m; OTU 3 - eastern lowlands from sea-level to 200 m; and OTU 4 - eastern lowlands from 201 - 900 m.

DETAILED MORPHOLOGY:
Baculum
See Bates *et al.* (2006).

HABITAT:
It is found alongside humid forests and has also been recorded from open anthropogenic agricultural and grassland areas (Bates *et al.*, 2006; Randrianandriananina *et al.*, 2006).

ROOST:
It has been netted emerging from buildings (Bates *et al.*, 2006).

DIET:
On Madagascar, Rakotondramanana *et al.* (2015: 74) report the following volume percentages for: Coleoptera: 49.7 ± 22.44; Hymenoptera: 18.7 ± 17.57; Lepidoptera: 16.3 ± 16.34; Trichoptera: 9.2 ± 8.74; Homoptera: 5.5 ± 6.93; Arachnida: 0,2 ± 0,80. The frequencies for these groups were: Coleoptera: 97.6 ± 6.63; Hymenoptera: 64.0 ± 37.86; Lepidoptera: 55.2 ± 42.54, Trichoptera: 48.0 ± 40.82; Homoptera: 25.6 ± 28.0, and Arachnida: 0.8 ± 4.00. Rasoanoro *et al.* (2015: 64) mention the following volume percentages: Coleoptera: 53.4, Diptera: 11.0, Hemiptera: 17.6, and Hymenoptera: 18.0.

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 71 minutes, and a digestibility rate of about 81 %.

POPULATION:
Structure and Density
The population and local abundance of this species are not known, but it is thought to be locally common (Bates *et al.*, 2006).

Trend
2016: Unknown (Monadjem *et al.*, 2017bt). 2008: Unknown (Andriafidison *et al.*, 2008r; IUCN, 2009).

PARASITES:
Zhu *et al.* (2014: 2160) report the presence of the flea *Dampfia grahami grahami* (Waterston, 1915) (Ischnopsyllidae), which is a carrier of *Bartonella* bacteria. This flea was also reported by Hastriter (2016: 16) and Duchemin *et al.* (2022: 1076)..

Ramasindrazana *et al.* (2016: 6) report the presence of an unnamed filariod in this bat species.

Richard (1966: 413) reported the Trematode *Plagiorchis (Plagiochis) vespertilionis* (Müller, 1784) Braun, 1900.

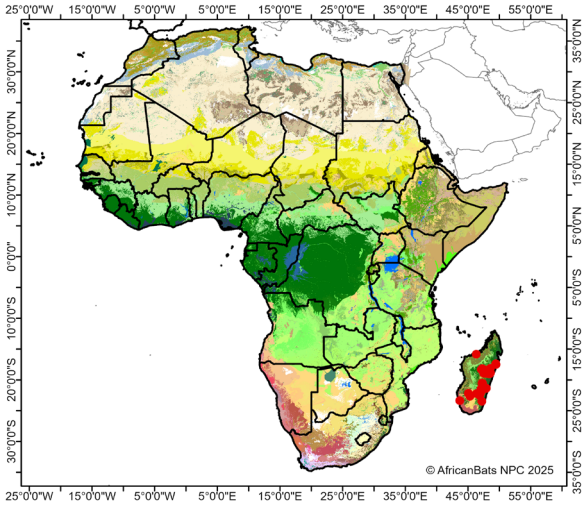

Figure 373. Distribution of *Laephotis matroka*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Laephotis namibensis Setzer, 1971

*1971. *Laephotis namibensis* Setzer, Proc. Biol. Soc. Wash., 84 (32): 259, fig 1a, 1c. Publication date: 4 November 1971. Type locality: Namibia: Namib Desert, Kuiseb River: Gobabeb (Namib Desert Research Station) [23 30 S 15 03 E, 407 m]. [Goto Description]. Holotype: USNM 342152: ad ♀, skin and skull. Collected by: Ronald E. Cole; collection date: 22 November 1963; original number: 270. Paratype: USNM 342153: ♀. See Setzer (1971: 259). - Etymology: Referring to the country where the type specimen was collected. (Current Combination).
2024. *Laephotis cf. namibensis:* Taylor, Kearney, Clark, Howard, Mdluli, Markotter, Geldenhuys, Richards, Rakotoarivelo, Watson, Balona and Monadjem, Glob. Ch. Biol., 30 (6): 4. Publication date: 5 June 2024. (Name Combination).
? *Laephotis cf. wintoni:*

TAXONOMY:
In a morphometric analysis with specimens of the other *Laephotis* taxa, specimens of *L. wintoni* and *L. namibensis* were not clearly separated (Kearney and Seamark, 2005: 85). Additional characters, or other systematic techniques will be required to clarify the species distinction. Unfortunately, specimens from the Western Cape province in South Africa have been identified as both *L. wintoni* (Rautenbach and Nel, 1978b) and *L. namibensis* (Skinner and Smithers, 1990). Hence, see also the account for *L. wintoni* for the results of a study based in the Western Cape province of South Africa that identified the specimens as *L. wintoni* (Jacobs *et al.*, 2005).

Laephotis namibensis and *L. wintoni* may be conspecific, which would make the former a paler, western race of *L. wintoni* (Kearney and Seamark, 2005).

Bacular studies have also failed to show differences between selected species of *Laephotis* (Kearney *et al.*, 2002). Kearney and Seamark (2005) could not find a clear distinction between *L. namibensis* and *L. wintoni* and echoed the suggestion that they might be geographic races of the same species (Peterson, 1973). These results endorse the use of molecular studies to clarify the current confusion over species limits within this genus (Monadjem *et al.*, 2010d).

No subspecies are currently recognized.

COMMON NAMES:
Afrikaans: Namib-langoorvlermuis. Czech: netopýr namibský. English: Namibian Long-eared Bat, Namib Long-eared Bat. French: Oreillard de Namibie, Oreillard du Namib, Chauve-souris à longues oreilles de Namibie, Noctophile du Namib. German: Namibia-Langohrfledermaus.

SIMILAR SPECIES:
Not easily distinguished from other *Laephotis*:
Laephotis angolensis - FA shorter (34.3 (32 - 36) mm). Ears shorter, 15 -18 mm and narrower. Skull smaller, GLS: 13.7 - 13.8 mm; GWS: 6.7 - 8.1 mm; C-M^3: 4.3 mm.

L. botswanae - Skull shorter, GLS: 14.1 - 15.5 mm.

L. wintoni - Skull usually shorter, GLS: 15.6 - 16.3 mm. Dorsal pelage and wings apparently never creamy-brown (as far as is known).

CONSERVATION STATUS:
Global Justification
Although this species is known mainly from isolated records from a relatively large area, it is listed as Least Concern (LC ver 3.1 (2001)), as most of the range is within well protected areas, where there are no significant threats, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Schlitter, 2008f; IUCN, 2009; Monadjem and Schlitter, 2017b). Type locality (Gobabeb) is close to Namib Naukluft Park, which includes some of the Naukluftberge where this species probably roosts (Kearney, 2013d: 583).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Schlitter, 2017b). 2008: LC ver 3.1 (2001) (Schlitter, 2008f; IUCN, 2009). 2004: LC ver 3.1 (2001) (Schlitter, 2004b; IUCN, 2004). 1996: EN (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: VU D2 ver 3.1 (2001) (Jacobs *et al.*, 2016a). 2004: considered a vagrant not assessed, not recorded in SA, Cederberg specimens considered to be *L. wintoni* (Friedmann and Daly, 2004). 1986: Indeterminate, assessed as *L. wintoni* (Smithers, 1986).

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Schlitter, 2008f; IUCN, 2009; Monadjem and Schlitter, 2017b).

CONSERVATION ACTIONS:
Schlitter (2008f) [in IUCN (2009)] and Monadjem and Schlitter (2017b) reports that much of the range of this species is protected within the Namib-Naukluft National Park, Namibia. Further studies are needed into the distribution and general natural history of this species.

GENERAL DISTRIBUTION:
Laephotis namibensis has been recorded from a few localities in Namibia (Kuiseb River, Gobabeb, Zwartmodder, Klein Aus and Helmeringshausen), and a single area in South Africa (Algeria in the Cedarberg Mountains of the Western Cape) (Skinner and Chimimba, 2005).

Found in the South West Arid BZ (Namib Desert) and in the South West Cape BZ. Recorded from Namibia (Gobabeb, Zwartmodder, Klein Aus, Helmeringshausen) and South Africa (Algeria Forest) (Setzer, 1971, Kearney, 2013d: 583).

Although, specimens from South Africa have also been identified as *L. wintoni*, see the discussion in the generic account.

Native: Namibia (Setzer, 1971; Kearney and Seamark, 2005: 87; Simmons, 2005; Monadjem *et al.*, 2010d: 564); South Africa (Kearney and Seamark, 2005: 87; Simmons, 2005; Monadjem *et al.*, 2010d: 564).

GEOGRAPHIC VARIATION:
Specimens from Namibia have much paler pelage and flight-membranes than those from South Africa (Kearney, 2013d: 583).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Laephotis namibensis is a small bat with a mass of around 10 g, without noseleaf and with tail more or less fully enclosed in interfemoral membrane; ears separated, of medium length for a vespertilionid (22 - 25 mm) and of medium relative length (54 - 65 % of FA, n= 11).

Pelage soft, slightly shaggy on rump; mid-dorsal hairs ca. 7 mm. Dorsal pelage creamy-brown or yellowish-brown, varies geographically: the upper parts are pale brown in the Namib, but buffy-brown in the Western Cape; hairs distinctly bicoloured, basal 4 mm dark brown, terminal 3 mm creamy-brown or yellowish-brown. Ventral pelage (except in pelvic region) pale cream to whitish; hairs with basal 4 mm blackish-brown, terminal 3 mm pale cream or white (Kearney, 2013d: 583). Hairs in pelvic region pure white. The naked skin on muzzle and around eyes is pale brown. Ears pale to medium-brown, roughly triangular but elongated; tip rounded; inner margins almost meeting on forehead but not joined. Ears may be held erect above the head or (when resting) held horizontally at right-angles to head. Tragus shape much like that of *L. botswanae* except that in *L. namibensis* the bulge above the basal, posterior notch extends further out, making the tragus much wider at that point (Kearney, 2013d: 583). Wings pale creamy-brown (when dorsal pelage is pale) or dark brown (when dorsal pelage is yellowish- brown); arm-wing usually with whitish hind-border. Interfemoral membrane paler and more translucent (Kearney, 2013d: 583).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32.

Four upper and five lower cheekteeth and two upper incisors on each side. The upper premolar is sharply pointed and rises above the molars.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:
As in all *Laephotis* spp. with braincase slightly flattened (rises slightly above the rostrum); rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull on average long and wide for the genus (GLS: 16.1 - 17.0 mm; GWS: 8.4 - 9.2 mm). Palatal length: 8.0 (7.6 - 8.7) mm, n = 10 (Kearney and Seamark, 2005).

DETAILED MORPHOLOGY:
Baculum
See Kearney *et al.* (2002), which showed no difference to *L. botswanae*.

FUNCTIONAL MORPHOLOGY:
Laephotis namibensis has relatively broad wings with intermediate wing loading (7.0 N/m^2) and low aspect ratio (5.7) (Jacobs *et al.*, 2005; Monadjem *et al.*, 2010d; Amador *et al.*, 2019;also see Schoeman and Jacobs (2008). It is a clutter-edge forager.

SEXUAL DIMORPHISM:
Sexes similar (Monadjem *et al.*, 2010d, Kearney, 2013d: 583).

ECHOLOCATION:
Laephotis namibensis produces low- intensity LD-FM echolocation calls with a low peak frequency (22 ± 0.6 kHz, n = 5), narrow bandwidth (13.5 ± 2.9 kHz, n = 5), and short duration (2.6 ± 0.8 ms, n = 5) (Jacobs *et al.*, 2005; also see Schoeman and Jacobs (2008). Besides the fundamental, the second harmonic is often present on the spectrogram (Monadjem *et al.*, 2010d).

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 34, FN = 50, BA = 18, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from Namibia. Rautenbach *et al.* (1993) also obtained the same results for specimens from the Western Cape, which were identified as *L. wintoni*, but reassigned to *L. namibensis* (Skinner and Smithers, 1990).

Genetics
See Hoofer and Van Den Bussche (2001) for the results of a specimen from Namibia. See Stadelmann *et al.* (2004b) for the results of a specimen from the Western Cape in South Africa identified as *L. wintoni*, but from a locality where the species identification has also been assigned to *L. namibensis* (Skinner and Smithers, 1990).

HABITAT:
Found in desert (60 % of specimen records), fynbos (20 % of specimen records), and savanna (20 % of specimen records) biomes (Kearney and Seamark, 2005: 85). Arid, mountainous habitat, in close proximity to open water (Kearney, 2013d: 583). Sirami *et al.* (2013: 35) recorded in the Western Cape Province, South Africa that *L. namibensis* activity was not significantly, nor positively influenced by size of wetland or habitats located 100 m from surrounding these wetlands. *L. namibensis* preferentially near trees, orchards surrounding wetlands and over these wetlands (Sirami *et al.*, 2013: 35).

HABITS:
The holotype and paratype were mist-netted over a waterhole in the bed of the Kuiseb R. near Namib Desert Research Station (Setzer, 1971). Individuals from Algeria Forest were mist netted as they flew along a water course, close to the water surface, between 20:30 and 21:00h.

ROOST:
Roosts not known, but the association of this bat with cliffs (in South Africa) indicates that it might roost in cracks and crevices of cliff faces (Jacobs *et al.*, 2005, Kearney, 2013e: 585). Specimens have been caught while foraging for insects from early to mid-evening (18h30 - 21h40).

Three radio tagged females in the Western Cape province of South Africa roosted in different crevices or narrow fissures in a cliff face above the valley where they foraged (Jacobs *et al.*, 2005). They also moved roost from one day to the next (Jacobs *et al.*, 2005).

DIET:
In the Cedarberg, Western Cape, its diet comprised mainly Lepidoptera and Coleoptera (Jacobs *et al.*, 2005, Schoeman 2006).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 76 minutes, and the digestibility rate about 80.1 %.

POPULATION:
Structure and Density
Although the species appears to be naturally rare in the Namib desert, it is rather commonly captured in mist-nets set around water tanks outside of the Namib (Schlitter, 2008f; IUCN, 2009; Monadjem and Schlitter, 2017b). Rare (Kearney, 2013d: 583).

Trend
2016: Stable (Monadjem and Schlitter, 2017b).
2008: Stable (Schlitter, 2008f; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In the Cedarberg, Western Cape, a pregnant ♀ was caught in November (Jacobs *et al.*, 2005) and a post-lactating ♀ was collected in late January (Seamark and Brand, 2005).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Namibia, South Africa.

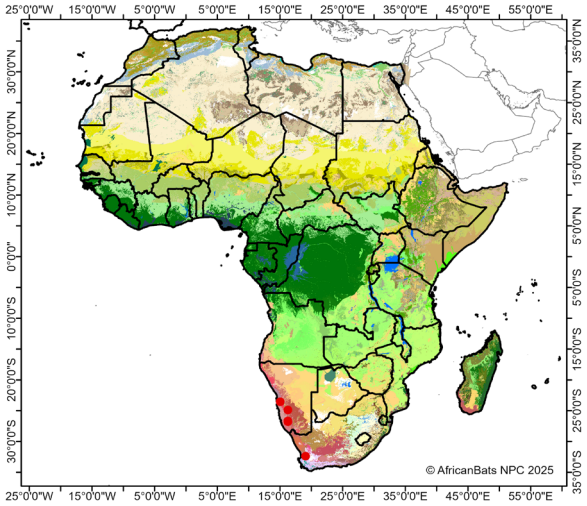

Figure 374. Distribution of *Laephotis namibensis*.

Laephotis robertsi (Goodman, Taylor, Ratrimomanarivo and Hoofer, 2012)

*2012. *Neoromicia robertsi* Goodman, Taylor, Ratrimomanarivo and Hoofer, Zootaxa, 3250: 1, 11, figs 3A, 4, 5A, 6A. Publication date: 29 March 2012. Type locality: Madagascar: Province d'Antananarivo, Anjozorobe, Amboasary [18 24.295 S 47 56.699 E]. Holotype: UADBA 43677: ad ♂, skull and alcoholic. Collected by: Richard K.B. Jenkins; collection date: 25 September 2002; original number: RBJ 105. Paratype: FMNH 213931: ad ♂, skull and alcoholic. Collected by: Richard K.B. Jenkins; original number: RBJ 119. Formerly UADBA 43679. Madagascar: Province de Toamasina, Parc National de Mantadia, between PK 9 and PK 10, 18 48.941 S, 48 25.633 E (see Goodman *et al.*, 2012b: 11). Paratype: UADBA 43678: ad ♀, skull and alcoholic. Collected by: Richard K.B. Jenkins; original number: RBJ 118. Madagascar: Province de Toamasina, Parc National de Mantadia, between PK 9 and PK 10, 18 48.941 S, 48 25.633 E (see Goodman *et al.*, 2012b: 11). - Etymology: In honour of Austin Roberts, who conducted systematic research on African mammals at the Transvaal Museum in Pretoria, and studied southern Africa bats, including small vespertilionids, during which he provided important insights into sorting out their generic affiliations (see Goodman *et al.*, 2012b: 11).
2017. *N[eoromicia] roberti:* Goodman, Kearney, Ratsimbazafy and Hassanin, Zootaxa, 4236 (2): 358. Publication date: 23 February 2017. (Lapsus).
2019. *L[aephotis] robertsi:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2019. *Laephotis robertsi:* M. Taylor, Bats: An illustrated guide to all species, 391. (Name Combination).

TAXONOMY:
Bates *et al.* (2006: 303) previously assigned these Madagascan specimens to *Laephotis melckorum*, but see Goodman *et al.* (2012b: 2).

Goodman *et al.* (2012b: 7) indicate that *L. robertsi* forms a sister-species pair with *L. malagasyensis*.

COMMON NAMES:
English: Robert's serotine. French: Sérotine de Robert. German: Roberts Zwergfledermaus.

CONSERVATION STATUS:
Global
Goodman (2017d) report that this species is known from two regions of the eastern portion of Madagascar, both within or at the edge of existing protected areas. As it is apparently not forest-dependent, few bat surveys have been conducted in the general region it is known to occur, and it is not uncommon where it has been captured, we await further field data to properly assess this taxon.

Assessment History
Global
2016: DD ver. 3.1 (2001) [assessed as *Neoromicia robertsi*] (Goodman, 2017d).

Regional
None known.

MAJOR THREATS:
Current threats to this species are not known (Goodman, 2017d).

CONSERVATION ACTIONS:
Goodman (2017d) report this species is known to occur in the Anjozorobe-Angavo and Mantadia-Analamazaotra protected areas.

GENERAL DISTRIBUTION:
Eastern Madagascar, where it is known from two localities (Anjozorobe-Angavo and Andasibe-Mantadia National Park). It occurs between 900

and 1,300 m in forests and partially degraded habitats (Garbutt, 2022: 101).

BIOGEOGRAPHY:
Only known from two localities in eastern Madagascar, at altitudes between 900 and 1,300 m (see Goodman *et al.*, 2012b: 20).

MOLECULAR BIOLOGY:
Genetics
L. robertsi is separated from its sister-species (*L. malagasyensis*) by a 1.8 % (12S rRNA) and 2.3 % (16S rRNA) sequence divergence. It is separated by a 3.3 % (12S rRNA) and 5.1 % (16S rRNA) sequence divergence from the other sister-species pair: *L. matroka* and *L. capensis*. The divergence between *L. robertsi* and other related taxa is greater than 6.0 % (12S rRNA) and 8.0 % (16S rRNA) (see Goodman *et al.* (2012b: 7).

DIET:
Rakotondramanana *et al.* (2015: 74) report the following prey volume percentages: Coleoptera: 55.0 ± 9.01; Hymenoptera: 25.3 ± 15.73; Lepidoptera: 7.5 ± 7.87; Trichoptera: 2.5 ± 2.95, and Homoptera: 9.7 ± 14.00. The frequency by which these occur are: Coleoptera: 96.7 ± 8.16; Hymenoptera: 80.0 ± 25.30; Lepidoptera: 50.0 ± 45.16; Trichoptera: 26.7 ± 30.11, and Homoptera: 40.0 ± 33.47.

POPULATION:
Structure and Density
Population size is not known for this species, but presumably it is substantial as it is found in degraded habitats that have been modified by human actions (Goodman, 2017d).

Trend
2016: Stable (Goodman, 2017d).

PARASITES:
BACTERIA
Gomard *et al.* (2016: 5) found the single specimen they tested to be positive for *Leptospira*.

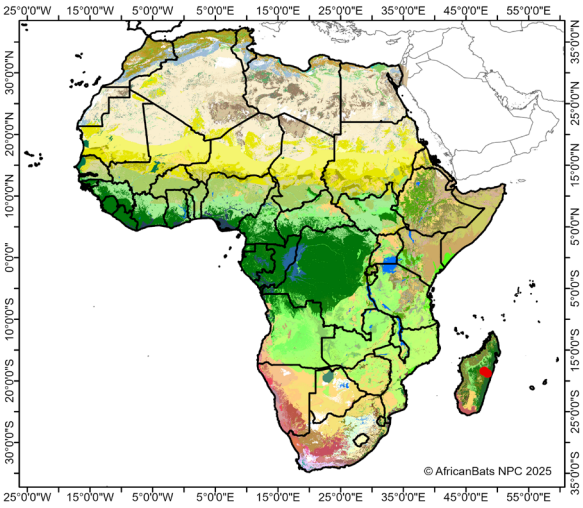

Figure 375. Distribution of *Laephotis robertsi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Madagascar.

Laephotis stanleyi (Goodman, Kearney, Ratsimbazafy and Hassanin, 2017)

1971. *Eptesicus melckorum:* Hayman and Hill, in: Meester and Setzer, Order Chiroptera, 44. - Comments: in part. (Name Combination).
1987. *Pipistrellus (Neoromicia) melckorum:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52: 249, 274. - Comments: in part. (Name Combination).
1993. *Eptesicus (Neoromicia) melckorum:* Koopman, in: Wilson and Reeder, Order Chiroptera, 202. - Comments: in part. (Name Combination).
1993. *Pipistrellus cf. melckorum:* Rautenbach, Bronner and Schlitter, Koedoe, 36 (2): 93. (Name Combination).
1995. *Eptesicus cf. melckorum:* Rautenbach, Fenton and Braack, Koedoe, 28: ???. (Name Combination).
2002. *Neoromicia cf. melckorum:* Kearney, Volleth, Contrafatto and Taylor, Acta Chiropt., 4 (1): 58. (Name Combination).
2005. *Neoromica melckorum:* Simmons, in: Wilson and Reeder, Order Chiroptera, 494. - Comments: in part. (Name Combination).
2011. *Neoromicia sp. aff. melckorum:* ACR, African Chiroptera Report 2011. (Name Combination).
*2017. *Neoromicia stanleyi* Goodman, Kearney, Ratsimbazafy and Hassanin, Zootaxa, 4236 (2): 351, 361, figs 2A, 4, 5, 6A, 7,. Type locality: Botswana: Okavango Delta, Chitabe, Gomoti River, Highbanks [19.41979 S 23.40413 E, 950m]. Holotype: TM 48487: ad ♂, skull and alcoholic. Collected by: Dr. Teresa Catherine Kearney and Ernest Charles James Seamark; collection date: 11 April 2009; original number: ECJS 48/2009. - Etymology: Named in honour of the William ("Bill") T. Stanley (1957 - 2015), who conducted active field and systematic research on African small mammals, particularly in east Africa, until his sudden death.
2017. *Pipistrellus krugeri* Herkt, Skidmore and Fahr, Global Ecol. Biog., 26 (8): Appendix S9. Publication date: 16 June 2017. - Comments: Herkt *et al.* (2017: Appendix S9) refer to the IUCN (2013) attribute table for the shapefile for "*Pipistrellus melckorum*", which notes "that these records must be referred to *Pipistrellus* sp., which will probably become *Pipistrellus krugeri*". As such, the name has no taxonomic value whatsoever.
2019. *L[aephotis] stanleyi:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2019. *Laephotis stanleyi:* M. Taylor, Bats: An illustrated guide to all species, 391. (Name Combination).
? *Eptesicus melckorum subsp.:*
? *Neoromicia cf. melckorum KMN-2014*

? *Pipistrellus melckorum:*

TAXONOMY:



Figure 376. *Laephotis stanleyi* (TM 48487) holotype caught at Chitabe, Okavango, Botswana.

Bronner *et al.* (2003) state that most previous authors recognised "*Eptesicus* (= *Neoromicia*) *melckorum*" as distinct from *Laephotis capensis* (Roberts, 1951); Ellerman *et al.*, 1953; Hayman and Hill, 1971; Corbet and Hill, 1980; Meester *et al.*, 1986). Koopman (1982), however, questioned the status of *L. melckorum*, since it cannot be clearly distinguished from *L. capensis*. Specimens from the type locality (Kersefontein Farm in the Western Cape Province) are morphologically and karyotypically indistinguishable from *L. capensis*, but specimens from the Kruger National Park with a unique karyotype (2*n* = 40, aFN = 50) agree with the original description of *melckorum* (Rautenbach *et al.*, 1993; Kearney *et al.*, 2002 for Kersefontein chromosomal data). The Kruger National Park specimens are also well differentiated from *L. capensis* by allozymes (Morales *et al.*, 1991). *Laephotis melckorum* should thus be synonymised under *L. capensis*, whereas specimens from the Kruger National Park probably represent a distinct species that remained unnamed (Koopman, 1994), and which were referred to as *Laephotis* cf. *melckorum*. It seems likely that the Zimbabwe specimens reported by Cotterill (1996a) represent this latter species. Goodman *et al.* (2017a) studied these (and other southern African) specimens and provided a name and description for this taxon: "*Neoromicia stanleyi*".

COMMON NAMES:

English: Kruger serotine bat (Taylor, 2005: 305 - first use). French: Pipistrelle des Melcks. German: Stanleys Serotine bat.

CONSERVATION STATUS:

Global Justification

Listed as Data Deficient (DD ver 3.1 (2001)) in view of continuing problems with its taxonomy as well as absence of recent information on its extent of occurrence, status and ecological requirements (Jacobs, 2019a).

Assessment History

Global

2018: DD ver 3.1 (2001) assessed as "*Neoromicia melckorum*" (Jacobs, 2019a). 2008: DD ver 3.1 (2001) assessed as "*Pipistrellus melckorum*" (IUCN, 2009).

Regional

South Africa: 2016: LC ver 3.1 (2001) [assessed as "*Neoromicia* cf. *melckorum*"] (Taylor *et al.*, 2016c). 2004: considered a vagrant ("*Pipistrellus spp*" - Kruger Serotine bat) not assessed, single locality (Friedmann and Daly, 2004).

MAJOR THREATS:

The threats to this species are not known. In Madagascar it has been recorded from degraded or modified habitats (Jacobs, 2019a).

CONSERVATION ACTIONS:

Jacobs (2019a) states that this species was not known from any protected areas in southern Africa, but these is incorrect as has been recorded from a number of protected areas (e.g., Kruger National Park). Further studies to better determine the species distribution, habitat requirements and any potential threats.

GENERAL DISTRIBUTION:

Kenya to Zambia and N South Africa (Simmons, 2005). For South Africa, Babiker Salata (2012: 49) found that "*Neoromicia melckorum*" has a distribution which is strongly associated with the amount of precipitation in the coldest quarter of the year.

Native: Botswana (Monadjem *et al.*, 2010d: 568); Malawi (Happold *et al.*, 1988: 568); South Africa (Monadjem *et al.*, 2010d: 568); Zambia (Ansell, 1967; Monadjem *et al.*, 2010d: 568); Zimbabwe (Monadjem *et al.*, 2010d: 568).

DETAILED MORPHOLOGY:

Baculum

In general appearance, this is very similar to the bacula of the closely related *L. capensis, L. matroka, L. robertsi* and *L. malagasyensis*. They all have a ventrally deflected tip, with a small dorsally projecting heel. Compared with the one of *capensis*, its longer and has a broader, shorter tip. The lateral tip flanges in *L. stanleyi* are only curved or notched on the distal edge, whereas there are distally and proximally curved edges on the tip flanges of *L. capensis*. The shaft in

stanleyi is slender and evenly wide from end to end (see Fig. 2 in Goodman *et al.*, 2017a)..

ECHOLOCATION:
In Benin, Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype [as "*Neoromicia stanleyi*"].

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 40; FN = 50, BA = 12, a metacentric X chromosome, and an acrocentric Y chromosome, for specimens from Zimbabwe and South Africa.

Protein / allozyme
See Morales *et al.* (1991) for results from nine specimens from South Africa.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats (as "*Neoromicia melckorum*") to be about 62 minutes, and the digestibility rate about 82.3 %.

POPULATION:
Structure and Density
Population size and trends are uncertain due to taxonomic difficulties (Jacobs, 2019a).

Trend
2018: Unknown (Jacobs, 2019a).

PARASITES:
HEMIPTERA
Cimicidae
Kock *et al.* (1998b: 237) mentioned the presence of *Aphrania* cf. *barys* Jordan and Rothschild, 1912.

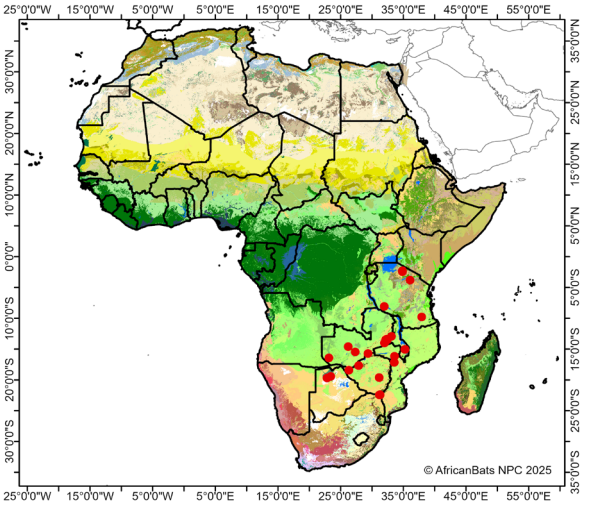

Figure 377. Distribution of *Laephotis stanleyi*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Botswana, Kenya, Malawi, Mozambique, South Africa, Tanzania, Zambia, Zimbabwe.

Laephotis wintoni (Thomas, 1901)

*1901. *Læphotis Wintoni* Thomas, Ann. Mag. nat. Hist., ser 7, 7 (41): 460. Publication date: 1 May 1901. Type locality: Kenya: Kitui [01 22 S 38 01 E, 3 500 ft]. [Goto Description]. Holotype: NHMUK 1901.5.6.5: ♂, skin and skull. Collected by: Dr. Sidney Langford Hinde; collection date: 7 January 1901; original number: S.L.H.64. - Etymology: In honour of Mr W.E. de Winton, "whose labours on the small mammals of Africa all naturalists...have been so constantly indebted for assistance" (Thomas, 1901d: 462). (Current Combination).
1942. *Laephotis wintoni:* Tate, Bull. Am. Mus. Nat. Hist., 80 (4): 279. Publication date: 27 November 1942. (Current Spelling).
1999. *Laephotis cf. wintoni:* P.J. Taylor, S. Afr. J. Zool., 34 (1): 22. (Name Combination).

TAXONOMY:
In a morphometric analysis with specimens of the other *Laephotis* taxa, specimens of *L. wintoni* and *L. namibensis* were not clearly separated (Kearney and Seamark (2005: 85). Unfortunately, specimens from the Western Cape province in South Africa have been identified as both *L. wintoni* (Rautenbach and Nel, 1978b) and *L. namibensis* (Skinner and Smithers, 1990). Specimens from Lesotho and the Free State province in South Africa were assigned to cf. *wintoni* pending clarification of the species distinctions (Kearney and Taylor, 1997). Additional characters, or other systematic techniques will be required to clarify the species distinction. Specimens from KwaZulu-Natal Province in South Africa previously identified as cf. *wintoni* (Kearney and Taylor, 1997) were reassigned to *L. botswanae* (Kearney and Seamark, 2005: 85).

South African specimens were assigned to *L. wintoni* based on multivariate analysis of external and cranial measurements (Rautenbach and Nel, 1978b, Watson, 1990a, Kearney and Taylor, 1997). However, on the basis of post-palatal measurements and morphometric analyses of cranial characters including palatal measurements by Hill (1974a), the specimens assigned to *L. wintoni* by Kearney and Taylor (1997) have now been re-identified as *L. botswanae* (Kearney and Seamark, 2005). Specimens from Algeria Forest in the Western Cape (South Africa) originally described by

Rautenbach and Nel (1978b) as *L. wintoni* were subsequently re-identified as *L. namibensis* in Skinner and Smithers (1990). However, new specimens from Algeria have been referred to as *L. wintoni* (based on Rautenbach and Nel, 1978b) by Jacobs *et al.* (2005). On the basis of morphometric analyses of cranial characters, including palatal measurements, the distinction between *L. wintoni* and *L. namibensis* could not be confirmed by Kearney and Seamark (2005); therefore, pending clarification of the status of *namibensis*, information from Jacobs *et al.* (2005) is mentioned in the profile for *L. namibensis*.

Laephotis namibensis and *L. wintoni* may be conspecific, which would make the former a paler, western race of the latter (Kearney and Seamark, 2005).

No subspecies are currently recognized.

COMMON NAMES:
Afrikaans: Winton se langoorvlermuis, Winton-langoorvlermuis. Chinese: 温氏长耳蝠. Czech: netopýr Wintonův. English: De Winton's Long-eared Bat, Winton's Long-eared Bat. French: Oreillard de De Winton, Chauve-souris à longues oreilles de De Winton, Noctophile de De Winton. German: De Wintons Langohrfledermaus. Italian: Lefòte di Wìnton.

SIMILAR SPECIES:
Not easily distinguished from other *Laephotis*:
Laephotis angolensis - FA shorter (32 - 36 mm). Ears shorter (15 - 18 mm) and narrower. Skull shorter and broader (GLS: 13.7 - 13.8 mm; GWS: 6.7 - 8.1 mm; C-M^3: 4.3 mm).
L. botswanae - FA on average shorter, 36.3 (30 - 39) mm. Skull usually smaller, GLS: 14.6 (14.1 - 15.5) mm; C-M^3: 4.7 (4.5 - 4.9) mm.
L. namibensis - Skull usually longer, GLS: 16.1 - 17.0 mm. Dorsal pelage and wings sometimes creamy-brown (see Geographic Variation).

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) because, although it is seldom recorded, it has a relatively wide distribution, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Schlitter, 2008g; IUCN, 2009; Monadjem and Schlitter, 2017c).

Assessment History
Global
2016: LC ver 3.1 (2001) (Monadjem and Schlitter, 2017c). 2008: LC ver 3.1 (2001) (Schlitter, 2008g; IUCN, 2009). 2004: LC ver 3.1 (2001) (Schlitter, 2004a; Jacobsen *et al.*, 1986). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: VU D2 ver 3.1 (2001) (Avenant *et al.*, 2016a). 2004: VU D2 ver 3.1 (2001), included *L. botswanae* from Hella-Hella and *L. namibensis* from Cederberg (Friedmann and Daly, 2004).

MAJOR THREATS:
There appear to be no major threats to this species (Schlitter, 2008g; IUCN, 2009; Monadjem and Schlitter, 2017c).

CONSERVATION ACTIONS:
Schlitter (2008g) [in IUCN (2009)] and Monadjem and Schlitter (2017c) reports that it has been recorded from the Sehlabathebe National Park in Lesotho, and may be present in additional protected areas. Additional studies into the population abundance and distribution are needed.

GENERAL DISTRIBUTION:
Recorded from Ethiopia in the north of its range, south through parts of Kenya (including Nyeri, Mount Kenya) and Tanzania (Mazumbai Forest Reserve, West Usambara Mountains (Kock and Howell, 1988); Kebebe Farms, Iringa district (Stanley and Kock, 2004), southern Zambia, Lesotho (including Sehlabathebe National Park), and South Africa (the Clarens district in the eastern Free State).

Laephotis wintoni occurs at high altitude (> 1,500 m above sea level) in Lesotho and the Free State (Kearney and Seamark, 2005), where it has been collected from montane grasslands. In Lesotho, it was netted over water (Lynch, 1994).

Specimens recorded from the Western Cape Province in South Africa have also been identified as *L. namibensis*, see the discussion in the generic account. The specimens from Game Valley Estates (Hella Hella) near Richmond, KwaZulu Natal, South Africa (Kearney and Taylor, 1997; Skinner and Chimimba, 2005: 317) are in fact *L. botswanae* (Kearney and Seamark, 2005).

Native: Ethiopia (Kearney and Seamark, 2005: 87; Simmons, 2005: 492; Skinner and Chimimba, 2005: 317); Kenya (Kearney and Seamark, 2005: 87; Simmons, 2005: 492; Skinner and Chimimba, 2005: 317); Lesotho (Lynch and Watson, 1990; Lynch, 1994: 194; Kearney and Seamark, 2005: 87 as *L.* cf. *wintoni*; Skinner and Chimimba, 2005: 317; Monadjem *et al.*, 2010d: 564 as *L* cf. *wintoni*); South Africa (Lynch, 1994; Kearney and

Taylor, 1997; Kearney and Seamark, 2005: 87 as *L.* cf. *wintoni*; Simmons, 2005: 492; Skinner and Chimimba, 2005: 317; Monadjem *et al.*, 2010d: 564 as *L.* cf. *wintoni*); Tanzania (Kock and Howell, 1988; Stanley and Kock, 2004: 174; Simmons, 2005: 492).

BIOGEOGRAPHY:
There are scattered records in the Afromontane Afroalpine and Somalia Masai BZs of Ethiopia and East Africa and records much further south in the Afromontane Afroalpine and Highveld BZs of South Africa.

GEOGRAPHIC VARIATION:
None recorded (Kearney, 2013e: 584).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Laephotis wintoni is a small bat with a mass of around 10 g, without noseleaf and with tail more or less fully enclosed in interfemoral membrane; ears separated, of medium length for a vespertilionid (21 - 21 mm) and of medium relative length (53 - 60% of FA, n= 12). Mid-dorsal hairs ca. 8 mm. Dorsal pelage yellowish-brown to reddish-brown; hairs distinctly bicoloured, basal 6 mm dark brown, terminal 2 mm yellowish-brown or reddish-brown. Ventral pelage with chin yellowish-orange, reddish-brown or pale brown, throat paler, pelvic region cream or white. Hairs (except in pelvic region) blackish-brown with yellowish-orange, reddish-brown, cream or white tips. Hairs in pelvic region pure white. Head fairly flat; naked skin on muzzle and around eyes is dark brown. Buccal pads observed in one ♂. Ears dark brown, roughly triangular but very elongated; tip rounded; inner margins almost meeting on forehead hut not joined. Ears may be held erect above the head or (when resting) held horizontally at right-angles to head. Wings dark brown or blackish-brown; presence or absence of hind-border is not known. Interfemoral membrane paler and more translucent.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32.

Four upper and five lower cheekteeth and two upper incisors on each side. The upper premolar is sharply pointed and rises above the molars.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 378. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1901.5.6.5, holotype of *Laephotis Wintoni* Thomas, 1901.

As in all *Laephotis* spp. with braincase slightly flattened (rises slightly above the rostrum); rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull on average medium-long and wide for the genus (GLS: 15.6 -16.3 mm; GWS: 8.8 - 9.5 mm). Palatal length: 8.1 (7.9 - 8.5) mm, n= 15.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002) as *L.* cf. *wintoni*.

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 7.5 Pa, aspect ratio 5.6 for a wingspan of 27 cm and a wing area of 134 cm^2 and a body mass of 10 g.

SEXUAL DIMORPHISM:
Sexes similar (Monadjem *et al.*, 2010d, Kearney, 2013e: 584).

ECHOLOCATION:
The echolocation call of this species has not been recorded (Monadjem *et al.*, 2010d). However, Thiagavel *et al.* (2017: Suppl.) mention a peak frequency of 23.08 kHz.

MOLECULAR BIOLOGY:
Karyotype
Rautenbach *et al.* (1993) reported 2*n* = 34, FN = 50, BA = 18, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from the Western Cape Province in South Africa, which were identified as *L. wintoni*, but reassigned to *L. namibensis* (Skinner and Smithers, 1990). Rautenbach *et al.* (1993) also obtained the same results for specimens from Namibia identified as *L. namibensis*.

Genetics
See Stadelmann *et al.* (2004b) for the results of a specimen from the Western Cape in South Africa, for a locality that has had the taxa reassigned to *L. namibensis* (Skinner and Smithers, 1990).

HABITAT:
Excluding records from the Western Cape province locality in South Africa that have also been assigned to *L. namibensis* (Skinner and Smithers, 1990), it is a montane species found at high altitudes above 1000 m (Kock and Howell, 1988; Stanley and Kock, 2004: 176; Kearney and Seamark, 2005). *L. wintoni* has been found in East Africa in both forest (62.5 % of specimen records) and savanna (37.5 % of specimen records) biomes (Kock and Howell, 1988; Kearney and Seamark, 2005: 85). Specimens assigned to *L.* cf. *wintoni* from the Free State Province of South Africa and Lesotho are from the grassland biome (Kearney and Seamark, 2005: 85).

HABITS:
In Ethiopia, found at 1700 m, near a large Rift Valley reservoir on the Awash R. surrounded by Acacia woodland that has been extensively degraded to provide open farmland (Largen *et al.*, 1974). In East Africa, recorded from highland and mountainous areas with mosaics of evergreen bushland, secondary Acacia wooded grasslands and farmlands, and forests on the mountains: caught in forests, near forests and in woodlands. In the Free State Province of South Africa, recorded amongst large exotic trees in a drainage line flanked by sandstone cliffs (Watson, 1990a). In Lesotho, recorded from the vicinity of a dam surrounded by a vlei overgrown with medium-height (600 mm) vegetation in Sehlabathebe N. P. (Lynch and Watson, 1990). In Sehlabathebe N. P., there is no significant cover of tall grass, forbs or woody vegetation; the climate is harsh; the topographical relief is fairly uniform, and the altitude is 2,300 - 2,650 m (Kearney, 2013e 584).
See Jacobs *et al.*, 2005).

ROOST:
One individual was found under exfoliating rock (TM) (Kearney, 2013d: 583). Kingdon (1974) (in Altringham, 2011: 143) mentions a bat roosting behind tree bark.

DIET:
A study in the Western Cape province of South Africa found the diet was dominated by tympanate moths in three of four individuals studied, the fourth individual's diet was dominated by beetles (Jacobs *et al.*, 2005). Hemiptera and Tricoptera were also eaten but in much smaller proportions (Jacobs *et al.*, 2005).

Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 68 minutes, and the digestibility rate about 81.4 %.

POPULATION:
Structure and Density
This seems to be an uncommon species, possibly having large population fluctuations. Multiple individuals have been caught in Lesotho and South Africa, however, in East Africa it is known from many localities, but as one or two animals only (Schlitter *pers. comm.* [in Schlitter (2008g) in IUCN (2009)] and Monadjem and Schlitter (2017c)). Rare, but numbers in museum collections are increasing (Kearney, 2013e: 584).

Trend
2016: Unknown (Monadjem and Schlitter, 2017c).
2008: Unknown (Schlitter, 2008g; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
In Lesotho, a pregnant ♀ was collected in November (Lynch, 1994).

VIRUSES:
Bunyaviridae
Phlebovirus
Rift Valley Fever Virus (RVFV)
Oelofsen and Van der Ryst (1999) tested two and four individuals from Clarens, South Africa and Lesotho respectively for RVFV antigen using an enzyme linked immunosorbet assay (ELISA), none tested positive.

Coronaviridae - Coronaviruses
SARS-CoV
Müller *et al.* (2007b) tested between 1986 and 1999, for antibodies to SARS-CoV in serum of one individual from Limpopo Province, South Africa, and found none (0/1).

Rhabdoviridae
Lyssavirus - Rabies related viruses
Rabies

Oelofsen and Smith (1993) tested two and four individuals from Clarens, South Africa and Lesotho respectively using "Trousse Platelia Rage" ELISA kit (Diagnostic Pasteur), none tested positive for antibodies to rabies virus glycoprotein G. Oelofsen and Smith (1993) also tested two and four individuals from Clarens, South Africa and Lesotho respectively by means of the "Rapid rabies enzyme immunodiagnosis" (RREID) test (Diagnostic Pasteur), none were tested positive.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Ethiopia, Kenya, Lesotho, South Africa, Tanzania.

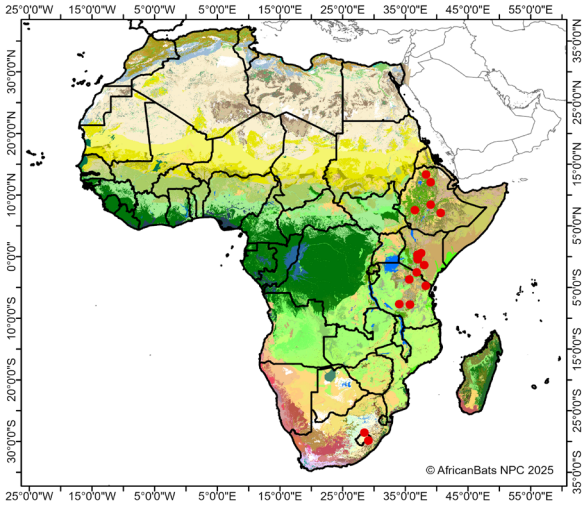

Figure 379. Distribution of *Laephotis wintoni*.

Genus ***Mimetillus*** Thomas, 1904

*1904. *Mimetillus* Thomas, Abstr. Proc. Zool. Soc. Lond., 10: 12. Publication date: 22 November 1904. - Comments: Type species: *Vesperugo (Vesperus) moloneyi* Thomas, 1891. - Etymology: Lanza *et al.* (2015: 361 - 362) indicate that it possibly is derived from the masculine scientific Latin adjective *mimèticus*, meaning "mimetic" and the end of the masculine scientific Latin substantive *(Pipistre)llus*, meaning "bat", which combines to a "bat miming a member of the genus *Pipistrellus* (= *Vesperugo*)". (Current Combination).

? *Mimetillus sp.:*

TAXONOMY:
Pending revision, considered here to be a monotypic genus endemic to tropical Africa including Bioko Island (Happold, 2013da: 585). See Simmons (2005), Cotterill (2001 d) and Monadjem *et al.* (2010d).

Placed in tribe Vespertilionini (Simmons, 2005), but the analyses of the cyt *b* sequences by Monadjem *et al.* (2020a: 1141) indicate that this genus falls outside the Vespertilionini or Pipistrellini tribes.

Currently (Simmons and Cirranello, 2023b) recognized species of the genus *Mimetillus*: ***moloneyi*** (Thomas, 1891).

COMMON NAMES:
Czech: Moloneyovi netopýři. English: Flat-headed Vesper Bats, Mimic Bats, Narrow-winged Bats, Flat-headed Bats. French: Mimétille, Chauve-souris à tête plate. German: Schmalflügel-Fledermäuse. Italian: Mimetìlli.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Diagnostic combination of characters: four upper and five lower cheekteeth and two upper incisors on each side; head conspicuously flattened; ears relatively short and not joined at base; outer margin of ear not reaching mouth; phalanges of third, fourth and fifth fingers very short (third finger shorter than HB); no body pattern; wings not reticulated (Happold, 2013da: 585).

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$. $PM^1/_2$, $M^3/_3$ = 32.

Mimetillus moloneyi (Thomas, 1891)

*1891. *Vesperugo (Vesperus) Moloneyi* Thomas, Ann. Mag. nat. Hist., ser 6, 7 (42): 528, text-fig. Publication date: 1 June 1891. Type locality: Nigeria: Western region: Lagos [06 27 N 03 23 E]. [Goto Description]. Holotype: NHMUK 1891.5.5.2: ad ♂, alcoholic (skull not removed). Collected by: Sir Alfred Moloney. Presented/Donated by: Sir Alfred Moloney. See Thomas (1891a: 529). - Etymology: In honour of Sir Cornelius Alfred Moloney (1848 - 1913), a British civil cervant, collector of the type specimen (see Lanza *et al.*, 2015: 363).

1905. *Mimetillus moloneyi:* Thomas, Proc. zool. Soc. Lond., 1904, II (II): 188. Publication date: 18 April 1905. (Name Combination, Current Combination).

1920. *Mimetillus thomasi* Hinton, Ann. Mag. nat. Hist., ser 9, 6 (32): 240. Publication date: 1 August 1920. Type locality: Zambia: Ndola [12 58 S 28 38 E, 1 400 m]. [Goto Description]. Holotype: NHMUK 1920.11.3.28: ad ♀. Collected by: Captain Guy Chester Shortridge; collection date: 4 October 1919; original number: 481. - Etymology: In honour of Oldfield Thomas.

1933. *Mimetillus berneri* Monard, Bull. Soc. Neuchât. Sci. nat., 57: 49 (for 1932?). Type locality: Angola: South-Central Angola: Vila da Ponte [14 25 S 16 15 E]. Syntype: MHNG 1326.004: ♂, alcoholic (skull not removed).

Collected by: Dr. Albert Monard; collection date: 1928 - 1929. - Comments: Allen (1939a:89) mentions 1932 as year of publication.

1953. *Mimetillus moloneyi berneri:* Ellerman, Morrison-Scott and Hayman, Southern African Mammals 1758 to 1951: a reclassification, 82. Publication date: 23 December 1853. (Name Combination).

1953. *Mimetillus moloneyi moloneyi:* Ellerman, Morrison-Scott and Hayman, Southern African Mammals 1758 to 1951: a reclassification, 82. Publication date: 23 December 1953. (Name Combination).

1953. *Mimetillus moloneyi thomasi:* Ellerman, Morrison-Scott and Hayman, Southern African Mammals 1758 to 1951: a reclassification, 82. Publication date: 23 December 1953. (Name Combination).

TAXONOMY:

Koopman (1993a: 207) included *thomasi* and *berneri*; but see Cotterill (2001c) and Simmons (2005). Monadjem *et al.* (2010d: 444; 2010c: 390) consider *thomasi* to be a separate species.

COMMON NAMES:

Castilian (Spain): Murciélago de cabeza Plana. Chinese: 非洲扁颅蝠. Czech: netopýr Moloneyův. English: Moloney's Flat-headed Vesper Bat, Moloney's Mimic Bat, Moloney's Flat-headed Bat. French: Mimétille de Moloney, Chauve-souris à tête plate de Moloney. German: Moloneys Schmalflügel-Fledermaus, Moloneys Flachkopf-Fledermaus. Italian: Mimetillo di Moloney.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017an).

Assessment History

Global

2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2017an). 2008: LC ver 3.1 (2001) (Jacobs *et al.*, 2008ai; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004ah; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

There appear to be no major threats to this species as a whole (Jacobs *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017an).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008ai) [in IUCN (2009)] and Monadjem *et al.* (2017an) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Additional research into the taxonomy of this species is needed.

GENERAL DISTRIBUTION:

Widespread over much of sub-Saharan Africa. It ranges from Sierra Leone in the west, through West Africa and Central Africa (although seemingly absent from much of the Congo basin), to southern Sudan and western Ethiopia in the east, from here it ranges southwards through East Africa to Zambia and Angola, with the southernmost record from south-central Mozambique. It is found at elevations of up to 2,300 m asl.

Native: Angola; Cameroon; Central African Republic (Lunde *et al.*, 2001: 537); Congo (Bates *et al.*, 2013: 325 - 1st authenticated record); Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 564); Côte d'Ivoire; Equatorial Guinea; Ethiopia; Gabon; Ghana; Guinea (Fahr *et al.*, 2006a; Decher *et al.*, 2016: 266); Kenya (Start, 1969: 223); Liberia (Fahr, 2007a: 104); Mozambique; Nigeria; Sierra Leone; Sudan; Tanzania; Togo; Uganda; Zambia.

DETAILED MORPHOLOGY:

Baculum

Hill and Harrison (1987).

ECHOLOCATION:

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

HABITAT:

Monadjem *et al.* (2016y: 369) recorded this species from forested and disturbed habitats between 400 and 520 m at the Mount Nimba area.

ROOST:

Altringham (2011: 143) [referring to Kingdon (1974)] mentions that this species also roosts behind tree bark.

DIET:

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 83 minutes, and the digestibility rate about 79.2 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

POPULATION:
Structure and Density
Although the species is difficult to catch, it is not considered to be especially rare (Jacobs *et al.*, 2008ai; IUCN, 2009; Monadjem *et al.*, 2017an).

Trend
2016: Unknown (Monadjem *et al.*, 2017an). 2008: Unknown (Jacobs *et al.*, 2008ai; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Krutzsch (2000: 124) indicates that males have enlarged testes in January and June and that females parturate in February/March and in August.

PARASITES:
ACARI
Fain (1959e: 155) described *Notoedres (Notoedres) mimetilli* (Sarcoptidae) from "*Mimetillus thomasi*" from Katanga, DRC, and Fain (1963: 256) reported the same parasite on a *M. moloneyi* from Bio [=Bo?], Sierra-Leone.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mozambique, Nigeria, Sierra Leone, South Sudan, Tanzania, Uganda, Zambia.

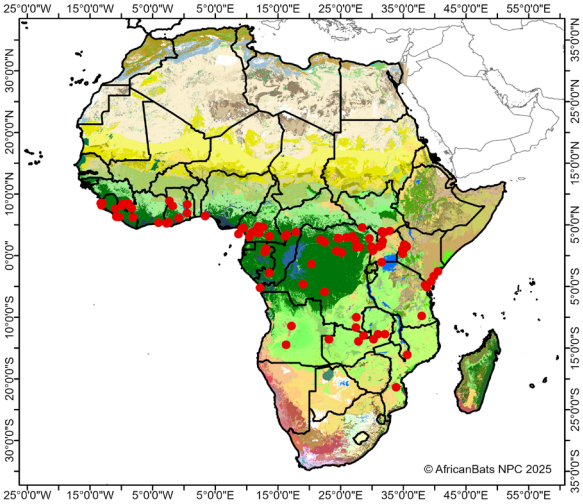

Figure 380. Distribution of *Mimetillus moloneyi*.

Genus ***Neoromicia*** Roberts, 1926

1889. *Vesperus:* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (1): 6. Publication date: March 1889. - Comments: In part. Not of not Keyserling and Blasius (1839). Monadjem *et al.* (2020a: 1127) mention "*Vesperugo* Bocage, 1889", but Bocage (1889a: 7) only uses this genus name in combination with *pipistrellus* and *Kuhli* (and possibly *tenuipinnis*, neither of which is currently assigned to *Neoromicia*. On page 6, he described "*Vesperus guineensis*", which is currently included in *Neoromicia*. Bocage (1889b: 17-18) mentions the following *Vesperus* species: *capensis* and *bicolor*, which again are not in *Neoromicia*.
1901. *Vespertilio:* Thomas, Ann. Mag. nat. Hist., ser 7, 7 (37): 32. Publication date: 1 January 1901. - Comments: In part. Not of Linnaeus, 1758 (see Monadjem *et al.*, 2020a: 1127).
1911. *Eptesicus:* G.M. Allen, Bull. Mus. comp. Zool., 54 (9): 321. Publication date: December 1911. - Comments: In part. Not of Rafinesque, 1820 (see Monadjem *et al.*, 2020a: 1127).
*1926. *Neoromicia* Roberts, Ann. Transv. Mus., 11: 245. Publication date: 14 September 1926 [Goto Description]. - Comments: Type species: *Eptesicus zuluensis* Roberts, 1924. - Etymology: From the Greek prefix "*νεο*" (nèo), meaning "new" and the feminine scientific Latin substantive *Romicia*, which in turn is a feminine scientific Latin substantive almost surely deriving from the Greek substantive "*ῥόμιξα*" (rhómiksa), corresponding to the masculine Latin substantive *rùmex* (genitive *rùmicis*), meaning "dock", a plant with spear-shaped leaves. *Neoromicia calcarata,* the type species of the genus, is really provided of a well-developed calcar, i.e. of a well-developed uropatagial spur (see Lanza *et al.*, 2015: 380). - ZooBank: 7173CFF6-F27B-44D7-948E-23FC40080224.
1930. *Pipistrellus:* Zammarano, Le colonie Italiane di diretto dominio. Fauna e caccia, 147. - Comments: In part. Not of Kaup, 1829 (see Monadjem *et al.*, 2020a: 1127).
1956. *Ephesicus:* Theodor, Parasitology, 46: 391. - Comments: used in combination with the species *tenuipinnis*, and therefore synonym of *Neoromicia*, not of *Eptesicus*. (Lapsus).
1987. *Nycterikaupius* Menu, Palaeovert., 17 (3): 108, pl 4, fig 1. Publication date: 15 November 1987 [Goto Description]. - Comments: In part. The species assigned to this genus by Menu (1987: 109) are currently (sensu Monadjem *et al.*, 2020a: 1140) included in the genera *Laephotis, Neoromicia, Pipistrellus* and *Pseudoromicia*.
1995. *Scabifer:* Peterson, Eger and Mitchell, Faune de Madagascar, Chiroptères, 84: 95. (Lapsus).
2000. *Pipestrellus:* Nwoha, Caxton-Martins and Baxter-Grillo, Folia Morphol., 59 (3): 154. Publication date: 6 July 2000. (Lapsus).
2003. *Neuromicia:* Avery, Avery and Colahan, Navors. nas. Mus., 19 (1): 8. Publication date: April 2003. (Lapsus).
2007. *Neromicia:* Schneider and Jorge, Ostrich, 78 (3): 656. (Lapsus).
2013. *Epseticus:* Bitty, Kadjo, Gonéndélé, Okon and Kouassi, Int. J. Biol. Chem. Sci., 7 (4): 1684. Publication date: August 2013. (Lapsus).
2013. *Necroromicia:* Fenton, Koedoe, 55 (1): 1140 (p3). Publication date: 19 March 2013. (Lapsus).
2015. *Neoromycia:* Thies and Lewis, Occ. Pap. Mus. Texas Tech Univ., 330: 7. Publication date: 10 February 2015. (Lapsus).

2020. *Neomoricia:* Motayo, Oluwasemowo and Akinduti, PeerJ, 8 (e10434): 7. Publication date: 26 November 2020. (Lapsus).
2020. *Neoremicia:* Lacroix, Vidal, Keita, Thaurignac, Esteban, De Nys, Diallo, Toure, Goumou, Soumah, Povogui, Koivogui, Monemou, Raulino, Nkuba, Foulongne, Delaporte, Ayouba and Peeters, Viruses, 12 (855): 2. Publication date: 5 August 2020. (Lapsus).
2020. *Neormicia:* Motayo, Oluwasemowo and Akinduti, PeerJ, 8 (e10434): 4. Publication date: 26 November 2020. (Lapsus).
2020. *Neoromicia cf. guineensisa:* Yu, Csorba, Huang, Li, Liu, Quan, Wang, Shi, Wu and Li, Zool. Res. (China), 42 (1): Suppl. Publication date: 18 December 2020. (Lapsus).
? *Neoromicia sp. IVK-2011*
? *Neoromicia sp.:*

Taxonomy:

Considered a subgenus of *Eptesicus* by Koopman (1993a: 201); considered a subgenus of *Pipistrellus* by Grubb *et al.* (1998: 85) and Hill and Harrison (1987: 248), but considered a valid genus by Volleth *et al.* (2001: 25), Simmons (2005). See also Riccucci and Lanza (2008) for a discussion on the gender of this genus name.

Helbig *et al.* (2010: 168) suggest that *Neoromicia* is actually a para- or polyphyletic group.

Without any further explication, Taylor (2019a: 282, 283) placed all *Neoromicia* species in the genus *Laephotis*, but in their revision of the East African pipistrellus-like bats, Monadjem *et al.* (2020a: 1114, 1127) recognized *Neoromicia* back as a valid genus, containing only *zuluensis* and allied species.

Currently (Simmons and Cirranello, 2023b) recognized pecies of the genus *Neoromicia*: ***anchietae*** (Seabra, 1900), ***bemainy*** (Goodman, Rakotondramanana, Ramasindrazana, Kearney, Monadjem, Schoeman, Taylor, Naughton and Appleton, 2015); ***guineensis*** (Bocage, 1889); ***hlandezi*** Taylor, Strydom, Richards, Markotter, Toussaint, Kearney, Cotterill, Howard, Weier, Keith, Neef, Mamba, Magagula and Monadjem, 2022; ***somalica*** (Thomas, 1901); ***zuluensis*** (Roberts, 1924).

Common Names:

Czech: banánoví netopýři. English: Neoromicia Pipistrelle Bats. Italian: Neoromìcie. Ukrainian: Неоромиція [= Neoromitsiya]

Palaeontological or archaeological records:

Avery (2007: 619) reported on the presence of *Neoromicia* sp. in Pleistocene deposits at Wonderwerk Cave, South Africa.

General description of external morphology:

Tragus: Monadjem *et al.* (2013c: 204) present a line drawing of the tragi of specimen DNSM 13225 (identified as *N.* sp. 1) from Mount Nimba, Liberia.

Detailed morphology:

Baculum

The shaft tip of the baculum was bulbous and lobed in all the *Neoromicia* species from Liberia examined (Monadjem *et al.*, 2013c: 197).

Echolocation:

Kofoky *et al.* (2009: 382) reported the calls potentially from *N. melckorum* and *N. matroka*, which had steep FM followed by a shallow QFM pulse at a low duty cycle.

Predators:

Goodman *et al.* (2015c: 78) found the remains of five *Pipistrellus/Neoromicia* sp. individuals in pellets of Bat Hawk *Macheiramphus alcinus* Bonaparte, 1850 in western central Madagascar.

Parasites:

DIPTERA

Nycteribiidae

Dick *et al.* (2023: 74) mentioned *Basilia (Basilia) robusta* Theodor, 1956 was found on bats belonging to this genus.

Viruses:

Circoviridae

Squirrel associated cyclovirus 1 was reported from a bat in the DRC by Vidovszky *et al.* (2023: Suppl.)

Coronaviridae

None of the 34 Kenyan *Neoromicia* sp. tested by Tao *et al.* (2017: Suppl.) was positive for CoV.

South African *Neoromicia* bats were infected by viruses of the subgenus *Merbecovirus* (Motayo *et al.*, 2020: 4)..

Geldenhuys *et al.* (2018: 5) investigated fecal, rectal and intestinal swaps of 58 *Neoromicia* (*N. capensis, N. zuluensis, N. nana* and *N.* cf. *helios*) specimens collected over an eight-year period (2007 - 2015) in northeastern RSA. In these, they found the following virus families: ssRNA viruses: *Orthomyxoviridae* (30.49 %), *Picornaviridae* (22.56 %), *Bunyaviridae* (10.98 %), *Coronaviridae* (9.15 %), *Virgaviridae* (2.44 %), *Caliciviridae* (2.44 %), *Tymoviridae* (2.44 %), *Flaviviridae* (1.83 %), *Rhabdoviridae* (1.22 %) *Solemoviridae* (0.61 %), and unclassified (15.9

%); ssDNA viruses: *Microviridae* (86 %), *Circoviridae* (8 %), *Parvoviridae* (6 %), *Inoviridae* (0.9 %), and *Anelloviridae* (0.05 %); dsDNA viruses: *Herpesviridae*(48 %), *Caudoviridae* (26.7 %), *Adenoviridae* (17 %), *Papillomaviridae* (2.7 %), *Ampullaviridae* (1.8 %), *Iridoviridae* (0.9 %), *Phycodnaviridae* (0.9 %), *Baculoviridae* (0.6 %), *Polydnaviridae* (0.6 %), *Nimaviridae* (0.3 %), and unclassified (0.3 %). One of the *Ciroviridae* (genus *Cyclovirus*) was found to be a new species: *Neoromicia*-associated cyclovirus 1 strain 19681/RSA (or NeoCycloV-1), for which the closest relative was retrieved from human stool (Geldenhuys *et al.*, 2018: 10). Furthermore, they (p. 13) reported the a novel *Neoromicia* picornavirus sequence (BatPicV/NeoC21877/RSA), which should be the first bat picornavirus from an insectivorous bat genus in Africa.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, Guinea, Kenya, Liberia.

Neoromicia aff. guineensis Bocage, 1889

2016. *Neoromicia sp. (aff. guineensis):* Kruskop, Benda, Vasenkov and Lavrenchenko, Lynx, 47: 62. (Name Combination).
? *Neoromicia cf. guineensisa DMR-2017* (Lapsus).

TAXONOMY:
Although very similar to *N. guineensis* morphologically, preliminary molecular genetic analyses by Kruskop *et al.* (2016: 62) indicated that a number of animals differed from other Ethiopian specimens belonging to *N. guineensis, N.* cf. *zuluensis* and *N. somalica*. Further comparisons with specimens from other areas from Africa will be required to assess the taxonomic status of these specimens.

CONSERVATION STATUS:
Global Justification
Not assessed

Assessment History
Global
Not assessed

Regional
None known.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ethiopia, South Sudan.

Neoromicia anchietae (Seabra, 1900)

1900. *V[esperugo] Anchietæ:* Bocage, Bull. Mus. natn. Hist. nat., Paris, 6: 164. (Name Combination, Alternate Spelling).
*1900. *Vesperugo Anchieta* Seabra, J. Sci. mat. phys. nat., ser 2, 6 (21): 26. Publication date: August 1900. Type locality: Angola: Cahata [12 20 S 14 50 E]. [Goto Description]. Paratype: MNHN ZM-MO-1900-538: ad ♀, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta. Number 211 in Rode (1941: 246). Syntype: NHMUK 1906.1.3.1: ad ♀, skull and alcoholic. - Etymology: This species is named after Mr Anchieta, a Portuguese national, who was a prolific collector of zoology material in Angola in the 1860's and who has numerous reptiles, birds and mammals named after him (Taylor, 2005).
1935. *Pipistrellus anchietae:* Monard, Arq. Mus. Bocage, 6: 31. (Name Combination, Current Spelling).
1953. *Pipistrellus (Pipistrellus) anchietai:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 78. (Name Combination, Alternate Spelling).
1965. *Pipistrellus anchietai:* Koopman, Am. Mus. Novit., 2219: 30. (Name Combination).
1987. *[Attalepharca] anchietae:* Menu, Palaeovert., 17 (3): 126. (Name Combination).
1987. *Pipistrellus (Hypsugo) anchietae:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 273. (Name Combination).
1993. *Pipistrellus (Hypsugo) anchietai:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 219. (Name Combination).
1994. *H[ypsugo] anchietae:* Heller, Volleth and Kock, Senckenb. biol., 74 (1/2): 1. (Name Combination).
2001. *P[ipistrellus] (Hypsugo) anchieta:* Kock, Senckenb. biol., 81 (1/2): 279. (Name Combination).
2002. *Hypsugo anchietae:* Kearney, Volleth, Contrafatto and Taylor. (Name Combination).
2017. *Hypsugo anehietai:* Gunnell, Smith and Smith, PLoS ONE, 12 (3): Suppl. Publication date: 8 March 2017. (Lapsus).
2019. *L[aephotis] anchietae:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2020. *Laephotis anchietae:* Simmons and Cirranello, BatNames.org.
2020. *Neoromicia anchietae:* Weier, Keith, Neef, Parker and Taylor, Diversity, 12 (188): 5. Publication date: 11 May 2020. (Name Combination, Current Combination).
? *Hypsugo cf. anchietae:*
? *Pipistrellus (Hypsugo) anchieta:* (Name Combination, Alternate Spelling).

TAXONOMY:



Figure 381. *Neoromicia anchietae* (ECJS-119/2009) caught in the Okavango, Botswana.

The oldest name for this species may be *bicolor*; see Koopman (1975: 404). Koopman (1994: 114) mentions this species as *P. bicolor* in the subgenus *Pipistrellus*. Incorrect original spelling as *anchieta*, corrected to *anchietae* by Seabra (1900b: 120).

Based on the morphology of the penis, Fasel *et al.* (2020: 1) suggest that *anchietae* should be placed in the genus *Neoromicia* rather than in *Hypsugo*.

Simmons and Cirranello (2020) transferred *anchietae* to the genus *Laephotis*, but Monadjem *et al.* (2020a: 1126) transferred it to *Neoromicia*.

COMMON NAMES:

Afrikaans: Anchieta-vlermuis. Czech: netopýr Anchietův. English: Anchieta's Pipistrelle, Anchieta's Bat, Miombo pipistrelle. French: Vespère d'Anchieta, Pipistrelle du Miombo, Pipistrelle d'Anchieta. German: Anchietas Zwergfledermaus, Anchietas Pipistrelle.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008ap; IUCN, 2009; Monadjem *et al.*, 2017bf).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as "*Pipistrellus anchietae*"] (Monadjem *et al.*, 2017bf). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus anchietae*"] (Jacobs *et al.*, 2008ap; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004aq; IUCN, 2004). 1996: VU [assessed as "*Pipistrellus anchietai*"] (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016i). 2004: NT ver 3.1 (2001) [assessed as "*Pipistrellus anchietae*"] (Friedmann and Daly, 2004).

MAJOR THREATS:

There appear to be no major threats to this species, although further research is needed to confirm this (Jacobs *et al.*, 2008ap; IUCN, 2009; Monadjem *et al.*, 2017bf).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008ap) [in IUCN (2009)] and Monadjem *et al.* (2017bf) report that it is present in a number of protected areas in Zimbabwe and South Africa. Further studies are needed into the distribution, natural history and possible threats to this species.

GENERAL DISTRIBUTION:

Neoromicia anchietae is largely a southern African species which formerly was considered to range from Angola in the west, through southern Democratic Republic of the Congo, and from here south into Zambia, Zimbabwe, and eastern South Africa. It could be more widespread in southern Africa than is currently understood (Skinner and Chimimba, 2005). However, as pointed out by Taylor *et al.* (2022) the Angolan population is genetically and morphologically distinct from the eastern population, which led Palmeirim *et al.* (2023: 313) to conclude that *Neoromicia anchietae* is an endemic (or possibly near-endemic) to the Angolan Central Escarpment. Eastwards, its range might extend to western Zambia.

The specimens previously reported from Madagascar are now attributed to *N. bemainty*.

The record from South Sudan (USNM 586793) seems odd and its identity doesn't seem to be confirmed by any recent review, but it currently (April 2024) is still mentioned as "*Hypsugo anchietae*" in the USNM online catalogue.

South of 8° S, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 987,832 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 563; Taylor *et al.*, 2018b: 60); Botswana (Monadjem *et al.*, 2010d: 563); Congo (The Democratic Republic of the);

Eswatini (Monadjem *et al.*, 2010d: 563, Monadjem *et al.*, 2021: 5); Mozambique (Monadjem *et al.*, 2010d: 563); South Africa (Koopman, 1994: 114; Kearney and Taylor, 1997: 54; Monadjem *et al.*, 2007c as *H.* cf. *anchietae*; Monadjem *et al.*, 2010d: 563); Zambia (Ansell, 1973; Monadjem *et al.*, 2010d: 563); Zimbabwe (Monadjem *et al.*, 2010d: 563).

Presence uncertain: Namibia (Cotterill, 2004a: 261).

DETAILED MORPHOLOGY:
Penis
According to Fasel *et al.* (2020: 1394), the penises of "*Hypsugo anchietae*" and *Neoromicia zuluensis* are relatively similar, but the one from *anchietae* has longer hairs (more than 50 % of the diameter of the penis) immediately after the flexure.

Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002).

FUNCTIONAL MORPHOLOGY:
Amador *et al.* (2019: Suppl.) [referring to Schoeman and Jacobs (2008)] mention a wing loading value of 6.8 Pa, aspect ratio 5.4 for a wingspan of 22 cm and a wing area of 87 cm^2 and a body mass of 6 g.

ECHOLOCATION:
Schoeman and Waddington (2011: 291) mention a peak frequency of 55.9 ± 0.3 kHz and a duration of 2.1 ± 0.1 ms for specimens from Durban, South Africa.

Weier *et al.* (2020: Suppl.) reported on 18 *Neoromicia anchietae* calls from the Okavango River Basin with the following characteristics: F_{max}: 60.37 ± 3.51 kHz, F_{min}: 52.48 ± 12.57 kHz, F_{knee}: 57.93 ± 0.59 kHz, F_{char}: 56.67 ± 1.14 kHz, slope: 13.75 ± 15.14 OPS, duration: 4.66 ± 1.75 ms.

125 calls of 8 bats were reported by Moir (2020: 29-30) and Moir *et al.* (2021a: 371) from southern KwaZulu-Natal and Eastern Cape (RSA): F_{max}: 87.09 ± 8.74 (74.02 - 92.60) kHz, F_{min}: 46.06 ± 1.26 (44.46 - 47.95) kHz, F_{char}: 46.63 ± 1.29 (44.83 - 48.38) kHz, F_{knee}: 50.5 ± 2.08 (46.88 - 52.85) kHz, and duration: 2.73 ± 0.32 (2.16 - 3.16) ms.

Taylor-Boyd *et al.* (2025: 116) report the following values for 16 calls from Zambian bats: Interpulse interval: 82.0 ± 20.5 (59.2 - 31.0) ms; F_{max}: 48.8 ± 3.1 (44.6 - 56.2) kHz; Start slope: -22.6 ± 3.3 (-16.3 - -27.6) kHz/ms; End slope: -5.7 ± 2.3 (-0.9 - -9.5) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.4 - 0.6) ms.

MOLECULAR BIOLOGY:
Karyotypic
Rautenbach *et al.* (1993) and Kearney *et al.* (2002) both reported 2*n* = 26, FN = 32, BA = 8, a submetacentric X chromosome, and an acrocentric Y chromosome, for specimens from South Africa.

HABITAT:
In southern Africa, the species primarily occurs in Savanna (85 %) and Coastal mosaic (10 %) habitats (Cooper-Bohannon *et al.*, 2016: Table S2).

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 86 minutes, and the digestibility rate about 78.8 %.

POPULATION:
Structure and Density
It is a locally common species in southern Africa. Very few specimens are currently known from Madagascar (Jacobs *et al.*, 2008ap; IUCN, 2009; Monadjem *et al.*, 2017bf).

Trend
2016: Unknown (Monadjem *et al.*, 2017bf). 2008: Unknown (Jacobs *et al.*, 2008ap; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter.

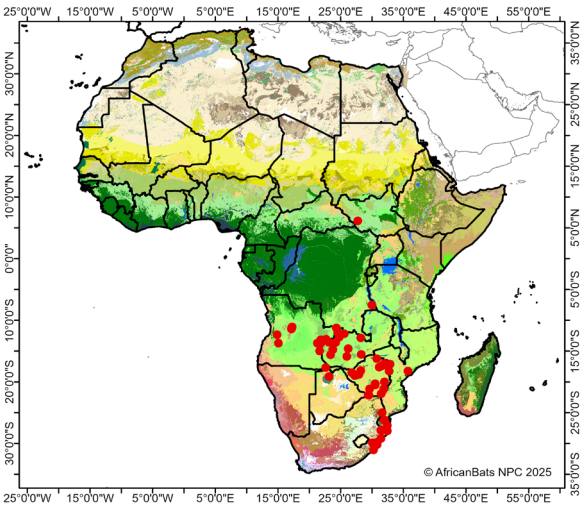

Figure 382. Distribution of *Neoromicia anchietae*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Angola, Botswana, Congo (Democratic Republic of the), Eswatini, Ethiopia, Mozambique, South Africa, South Sudan, Zambia, Zimbabwe.

Neoromicia bemainty (Goodman, Rakotondramanana, Ramasindrazana, Kearney, Monadjem, Schoeman, Taylor, Naughton and Appleton, 2015)

*2015. *Hypsugo bemainty* Goodman, Rakotondramanana, Ramasindrazana, Kearney, Monadjem, Schoeman, Taylor, Naughton and Appleton, Zool. J. Linn. Soc., 173 (4): 992, 1008, figs 9 - 12. Type locality: Madagascar: Province de Toliara: 60 km N Morondava, along the Kirindy River: Kirindy Forest (CNFEREF) [20°4'29.1"S, 44°40'14.4"E, 45 m].
2020. *Neoromicia bemainty:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1140. Publication date: 10 September 2020. (Name Combination, Current Combination).
? *Hypsugo anchietae:* (Name Combination).

TAXONOMY:
Originally included in the genus *Hypsugo* but transferred to *Laephotis* by Simmons and Cirranello (2020). However, based on cyt *b* sequence analyses, Monadjem *et al.* (2020a: 1120, 1140) transferred it again to *Neoromicia*.

COMMON NAMES:
English: Kirindy serotine, Kirindy Pipistrelle, Dark Madagascar pipistrelle. French: Pipistrelle sombre de Madagascar. German: Kirindy-Zwergfledermaus.

CONSERVATION STATUS:
Global Justification
This species is known from several different portions of western dry deciduous forests of Madagascar, where, based on frequency of capture, it appears to be relatively common (Goodman *et al.*, 2015b). It has been found within and at the edge of several protected areas. This species is known from relatively intact dry deciduous forest, as well in degraded habitats, in both cases often netted over water pools, and it is presumed not to be strictly forest-dependent. As it is difficult to separate in the hand from other sympatrically occurring vesper bats known from western Madagascar, it is presumed to have a broader geographic distribution than currently documented (Goodman, 2017a).

Assessment History
Global
2016: LC ver 3.1 (2001) (Goodman, 2017a).

Regional
Endemic to Madagascar see global status.

MAJOR THREATS:
Goodman (2017a) report that the forested habitats in the region of Madagascar are under considerable pressure associated with logging for wood products and clearing for swidden (slash-and-burn) agriculture (Zinner *et al.*, 2014). It is presumed that these habitat modifications have an impact on this species, but as it is known to not be strictly forest dependent, it is difficult to assess if these pressures form a major threat.

CONSERVATION ACTIONS:
Goodman (2017a) report that this species is known to occur in the general vicinity of the Kirindy Forest north of Morondava, which is part of the Menabe Antimena (Kirindy CNFEREF) protected area; the Zombitse-Vohibasia National Park; the Kirindy Mitea National Park; and Amoron'i Onilahy (Sept Lacs) protected area (Goodman *et al.*, 2015b; Goodman, 2017a).

GENERAL DISTRIBUTION:
This species is recorded from Madagascar, where it was collected from four localities in the centre-west and south-west (Kirindy Forest [CFPF]; Sept Lacs; Parc National de Kirindy-Mitea; Parc National de Zombitse-Vohibasia), where it occurs in dry and degraded forests (Bates *et al.*, 2006: 319; Garbutt, 2022: 100).

Native: Madagascar (Bates *et al.*, 2006: 319, as *Hypsugo anchietae*).

HABITAT:
Ravelomanantsoa *et al.* (2019: 111) captured this bat in a marshy zone near Ambereny.

DIET:
Rakotondramanana *et al.* (2015: 77) reported the following volume percentages present in the diet of *N. bemainty*: Coleoptera: 14.1 ± 12.56; Hymenoptera: 12.0 ± 14.60; Lepidoptera: 18.6 ± 20.27; Isoptera: 52.0 ± 33.78; Homoptera: 2.2 ± 3.59; Arachnida: 0.5 ± 1.73; Orthoptera: 0.5 ± 1.73. Expressed as frequency percentages, the values are: Coleoptera: 61.7 ± 37.62; Hymenoptera: 53.3 ± 47.74; Lepidoptera: 58.3 ± 48.59; Isoptera: 80.0 ± 39.08; Homoptera: 13.3 ± 23.09; Arachnida: 6.7 ± 23.09; Orthoptera: 6.7 ± 23.09.

PREDATORS:
Razakaratrimo *et al.* (2019: 107) mention the bat hawk (*Macheiramphus alcinus anderssoni* (Gurney, 1866)) as predator.

POPULATION:
Population not known but presumably substantial as it has been captured at several different geographically separate sites and in degraded

habitats that have been modified by human actions (Goodman, 2017a).

Trend:- 2016: Unknown (Goodman, 2017a).

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Madagascar.

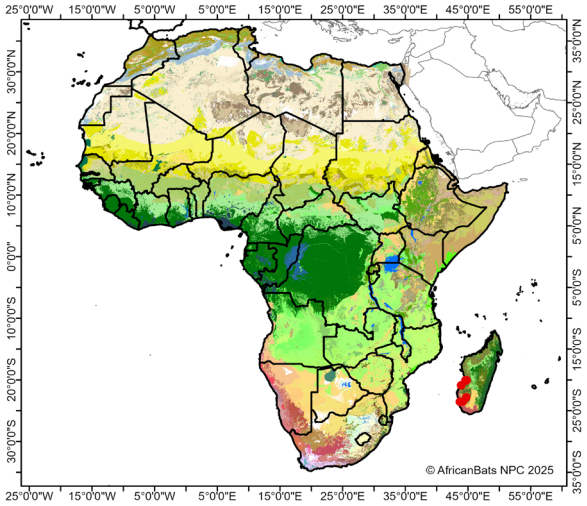

Figure 383. Distribution of *Neoromicia bemainty*.

Neoromicia guineensis (Bocage, 1889)

*1889. *Vesperus guineensis* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (1): 6. Publication date: March 1889. Type locality: Guinea-Bissau: Bissau (island) [11 52 N 15 39 W]. [Goto Description]. - Comments: Bocage (1889a: 7) mentions 2 ♀♀; sent from Bissau in 1879 by Mr. Rodrigo da Costa. - Etymology: From the feminine scientific Latin *guineènsis*, meaning "inhabitnig Guinea", referring to the provenance of the type specimen (Guinea-Bissau) (see Lanza *et al.*, 2015: 403).

1897. *Vesperugo (Vesperus) guineensis:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 110. (Name Combination).

1916. *Eptesicus rectitragus* Wettstein, Anz. kais. Akad. Wiss., Wien, 53: 191. Publication date: 1916. Type locality: Sudan: S Kordofan, N edge of Nuba Mountains: Dilling [12 02 N 29 39 E, 660 m]. [Goto Description]. Holotype: NMW 8411: juv ♂. Collected by: Otto Ritter von Westersheim Wettstein; collection date: 20 March 1914; original number: AM 96/2. - Comments: Wettstein (1916: 189) mentions Prof. Dr. Franz Werner as collector.

1923. *Eptesicus guineensis:* de Beaux, Atti Soc. ital. Sci. nat., 62: 98. (Name Combination).

1975. *Eptesicus (Eptesicus) guineensis:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 406. (Name Combination).

1987. *Pipistrellus (Neoromicia) guineensis:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).

1993. *Eptesicus (Neoromicia) guineensis:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 202. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] g[uineensis] guineensis:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] g[uineensis] rectitragus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1995. *Pipistrellus guineensis:* Koopman, Kofron and Chapman, Am. Mus. Novit., 3148: 11. (Name Combination).

2006. *Neoromicia guineensis:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 133 - 134. (Name Combination, Current Combination).

2007. *Eptesicus quineensis:* Lameed, Biodiversity, 8 (4): 8. (Lapsus).

2011. *N[eoromicia] guineenesis:* Benda, Al-Jumaily, Reiter and Nasher, Hystrix, It. J. Mamm., (ns) 22 (1): 41. Publication date: July 2011. (Lapsus).

2019. *L[aephotis] guineensis:* M. Taylor, Bats: An illustrated guide to all species, 284. Publication date: 11 April 2019. (Name Combination).

? *Eptesicus guineensis rectitragus:* (Name Combination).

? *Neoromicia guineensis guineensis:* (Name Combination).

? *Neoromicia guineensis rectitragus:* (Name Combination).

TAXONOMY:
This species is called *pusillus* by Hayman and Hill (1971); but see Koopman (1975: 406, 407). Mentioned in the genus *Pipistrellus* by Koopman (1994: 117).

COMMON NAMES:
Czech: netopýr savanový. English: Guinean Pipistrelle Bat, Tiny Serotine, Guinea Serotine. French: Sérotine de Guinée, Sérotine minuscule, Pipistrelle de Guinée. German: Guinea-Zwergfledermaus, Guinea-Pipistrelle. Italian: Pipistrèllo guineàno.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008l; IUCN, 2009; Monadjem and Fahr, 2017e).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Neoromicia guineensis*] (Monadjem and Fahr, 2017e). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus guineensis*"] (Fahr, 2008l; Bocage, 1889c). 2004: LC ver 3.1 (2001) (Fahr, 2004g; IUCN, 2004). 1996: LR/nt (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Fahr, 2008l; IUCN, 2009; Monadjem and Fahr, 2017e).

CONSERVATION ACTIONS:
Fahr (2008l) [in IUCN (2009)] and Monadjem and Fahr (2017e) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas.

GENERAL DISTRIBUTION:
Neoromicia guineensis is widely distributed in West and Central Africa, ranging into East Africa. Western distribution ranges from Senegal and Gambia to Ghana, Burkina Faso, and Benin. Recorded as far east as the border between Ethiopia and Somalia, and in Yemen. The southernmost records are from Congo and the DRC (close to the border areas with Angola).

Specimens reported from Tanzania might pertain to *N. somalica*, see Koopman (1994: 117)).

The specimen from Port Said (Egypt - ZMB 54952) was collected by Gustav Schrader. However (see appendix 4d), Schrader was both a collector and natural history dealer based in Port Said, who collected in Egypt, but also in Asia Minor, Ethiopia and Somaliland. Chances are that this specimen was rather collected in Ethiopia, which would fit the general distribution area.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Burkina Faso (Kock *et al.*, 2002b: 89; Kangoyé *et al.*, 2015a: 620); Cameroon; Central African Republic; Chad (Kock *et al.*, 2002b: 89); Congo (The Democratic Republic of the); Côte d'Ivoire; Ethiopia; Gambia (Kock *et al.*, 2002b: 89); Ghana; Guinea; Guinea-Bissau (Bocage, 1889a; Seabra, 1900a; Monard, 1939; Veiga-Ferreira, 1949;; Rainho and Ranco, 2001; Kock *et al.*, 2002b: 89); Liberia (Monadjem and Fahr, 2007: 47); Nigeria; Senegal; Sudan; Togo; Uganda; Yemen (Entwistle and Corp, 1997a: 40).

Bates *et al.* (2013: 339) rejected the presence of *N. guineensis* in the Republic of Congo as Van Cakenberghe and Happold (2013k: 625) only mark a locality on the map without providing further data.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Benda *et al.* (2011b: 41).

Brain
Amrein *et al.* (2007) from specimens collected from Bénin reported that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus was found to be absent. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream.

SEXUAL DIMORPHISM:
In Burkina Faso, Kangoyé *et al.* (2015a: 620) found that females have higher average values than males for both body (except Ear and 3ph2) and cranial measurements.

ECHOLOCATION:
Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype:
Rainho *et al.* (2023: 40) reported 2*n*=26, FNa=46 and 12 pairs of autosomes (10 large-to-medium-sized metacentric pairs, one small metacentric and one small acrocentric pair). The X chromosome is a medium-sized subtelocentric.

DIET:
For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 62 minutes, and the digestibility rate about 82.3 %.

POPULATION:
Structure and Density
This species is relatively common (Fahr, 2008l; IUCN, 2009; Monadjem and Fahr, 2017e).

Trend
2016: Unknown (Monadjem and Fahr, 2017e). 2008: Unknown (Fahr, 2008l; IUCN, 2009).

PARASITES:
HEMIPTERA
Cimicidae

Szentiványi *et al.* (2022: 12) reported *Aphrania recta* from Senegales *Neoromicia* cf. *guineensis*.

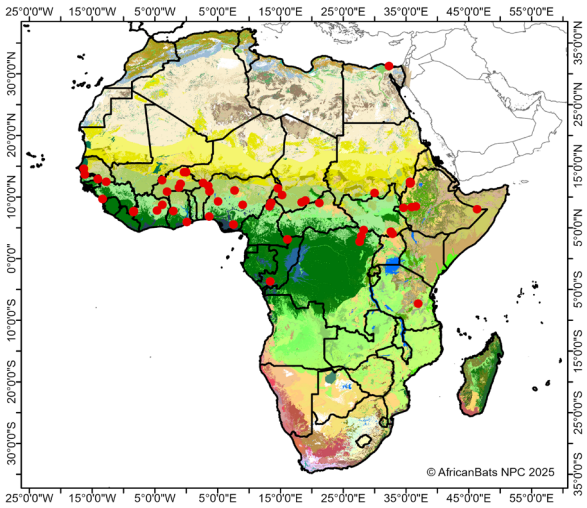

Figure 384. Distribution of *Neoromicia guineensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Ethiopia, Ghana, Guinea, Kenya, Nigeria, Senegal, South Sudan, Sudan, Tanzania, The Gambia.

Neoromicia hlandzeni Taylor, Strydom, Richards, Markotter, Toussaint, Kearney, Cotterill, Howard, Weier, Keith, Neef, Mamba, Magagula and Monadjem, 2022

*2022. *Neoromicia hlandzeni* Taylor, Strydom, Richards, Markotter, Toussaint, Kearney, Cotterill, Howard, Weier, Keith, Neef, Mamba, Magagula and Monadjem, Zool. J. Linn. Soc., 196 (4): 1578, 1583, figs 5-7. Publication date: 7 October 2022. Type locality: Eswatini: Siweni Riparian Site [26 10 48 S 032 02 55 E, 110 m]. Holotype: DNSM 8423: ad ♂, skull and alcoholic. Collection date: 5 September 2005; original number: AM-2066. Paratype: DNSM 8422: ad ♂, skull and alcoholic. Collection date: 6 September 2005. Paratype: TM 47718: ad ♂, skull and alcoholic. Collected by: Dr. Ara Monadjem; collection date: 26 September 2005; original number: AM-2073. - Etymology: eHlandzeni means the 'lowveld' or wilderness in the SiSwati language indicating the specific lowveld (low-lying savanna) habitat of the new species Taylor *et al.* (2022: 1584). (Current Combination).

COMMON NAMES:
English: Lowveld serotine

CONSERVATION STATUS:
Global Justification
Currently not been globally assessed hence no justification.

Assessment History
Global
No assessment known, hence no history of assessment to report.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Eswatini, South Africa, Zimbabwe (Taylor *et al.* (2022: 1586).

ECHOLOCATION:
Taylor *et al.* (2022: 1586) mention the following parameters: F_{max}: 87.09 ± 8.74 kHz, F_{min}: 46.06 ± 1.26 kHz, F_{char}: 46.63 ± 1.29 kHz, F_{knee}: 50.5 ± 2.08 kHz and duration: 2.73 ± 0.32 ms.

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2023c: 47, 49) mention 2*n* = 26, FNa = 32. The X chromosome is metacentric or submetacentric and the Y chromosome is an acrocentric.

HABITAT:
This species is apparently associated with coastal and scarp forests (Eastern Cape and KwaZulu-Natal, RSA), lowveld savannas (Eswatini) and well wooded riparian areas (Zimbabwe) (Taylor *et al.*, 2022: 1586).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Eswatini, South Africa.

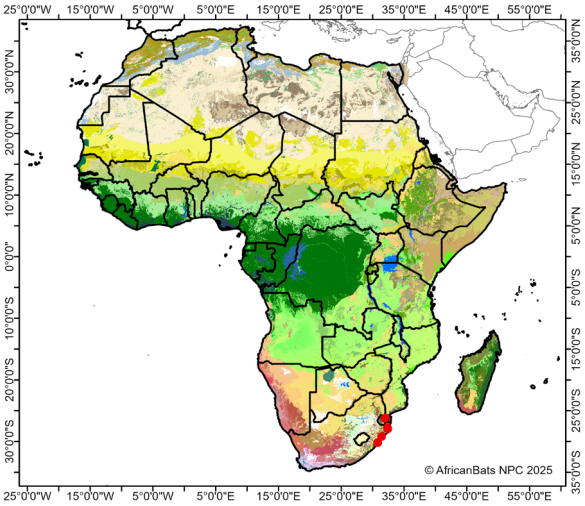

Figure 385. Distribution of *Neoromicia hlandzeni*.

Neoromicia humbloti (A. Milne-Edwards, 1881)

*1881. *Vesperus Humbloti* A. Milne-Edwards, C. R. séances Acad. Sci., Paris, 91: 1035. Publication date: 1881. Type locality: Madagascar: "Madagascar". [Goto Description]. Syntype: MNHN ZM-MO-1986-1074: juv, skull and alcoholic. 1 ad ♀, 2 ad ♂♂, 1 ad? ♂, 2 imm ♀♀, 3 imm ♂♂. Syntype: MNHN ZM-MO-1986-1075: juv, skull and alcoholic. Syntype: MNHN ZM-MO-1986-1076: juv, alcoholic (skull not removed). Syntype: MNHN ZM-MO-1986-1077. Syntype: MNHN ZM-MO-1986-1078. Syntype: MNHN ZM-MO-1986-1079. Syntype: MNHN ZM-MO-1986-1080. Syntype: MNHN ZM-MO-1986-1081. Syntype: MNHN ZM-MO-1986-1082. - Comments: The label on the type specimen mentions: "between Foulepoint and Lake Alaoutr".

1897. *Vesperugo (Vesperus) humbloti:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 110. (Name Combination).

1939. *Eptesicus humbloti:* G.M. Allen, Bull. Mus. comp. Zool., 83: 85. (Name Combination).

1994. *P[ipistrellus (Neoromicia] s[omalicus] humbloti:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

2006. *E[ptesicus] humblotii:* Hoofer, Van den Bussche and Horáček, J. Mamm., 87 (5): 991. Publication date: October 2006. (Lapsus).

2006. *Neoromicia humbloti:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 135. (Name Combination).

2012. *Vespertilio humbloti:* Goodman, Taylor, Ratrimomanarivo and Hoofer, Zootaxa, 25: 25. (Name Combination).

TAXONOMY:

The status of *humbloti* cannot be validated (see Peterson *et al.*, 1995: 104). It is sometimes mentioned as synonym of *somalicus* Thomas, 1901. However, if this is correctly assigned to that form, then *humbloti* A. Milne-Edwards, 1881 should be the valid name for what is now known as *Laephotis somalicus*.

We consider *humbloti* to be an island species, allied to *L. somalicus* Thomas, 1901, but differing from it on specific level. The relation with *L. malagasyensis* Peterson, Eger and Mitchell, 1975 still needs to be evaluated.

Goodman *et al.* (2015a: 1004-1005) studied the type series of *Vesperus humbloti* and concluded that these specimens should be assigned to *Pipistrellus hesperidus* (Temminck, 1840), pending further confirmation based on bacular structure or molecular genetics.

CONSERVATION STATUS:

Global Justification

Assessment History

Global

Not assessed (IUCN, 2004).

GENERAL DISTRIBUTION:

Native: Madagascar.

POPULATION:

Structure and Density

Unknown.

Trend

Not assessed.

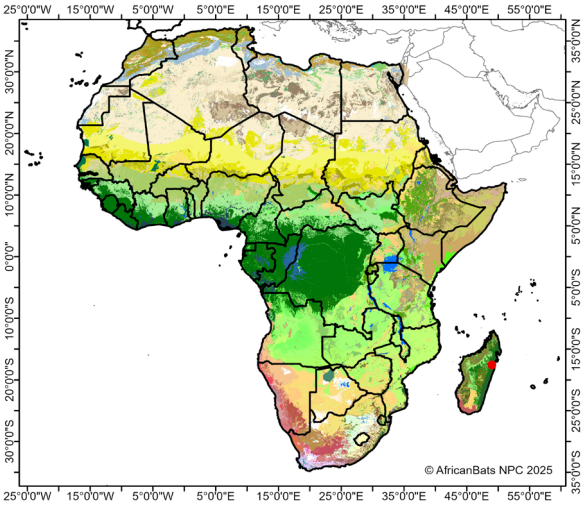

Figure 386. Distribution of *Neoromicia humbloti*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Madagascar.

Neoromicia somalica (Thomas, 1901)

*1901. *Vespertilio minutus somalicus* Thomas, Ann. Mag. nat. Hist., ser 7, 8 (43): 32. Publication date: 1 July 1901. Type locality: Somalia: Northwest province: Hargeisa [09 33 N 44 04 E, 3 500 ft]. [Goto Description]. Holotype: NHMUK 1898.6.9.1: ad, skin and skull. Collected by: R. McDonald Hawker Esq. Collection date: 14 November 1897; original number: RH5. - Etymology: From the masculine scientific Latin adjective *somàlicus*, meaning "inhabiting Somalia", referring to the provenance of the type specimen (see Lanza *et al.*, 2015: 447).

1907. *Vespertilio somalicus:* Matschie, Liste der von Herrn V.B. Schillings gesammelten Säugetier-Arten, 534. (Name Combination).

1911. *Eptesicus minutus somalicus:* G.M. Allen, Bull. Mus. comp. Zool., 54 (9): 326. (Name Combination).

1916. *Eptesicus ugandæ* Hollister, Smiths. Misc. Coll., 66 (1) (2406): 3. Publication date: 10 February 1916. Type locality: South Sudan: [formerly in Uganda]: between Nimule and Gondokoro: Ledgus: Thorn *et al.* (2009: 54-6) indicate that Ledgus was situated within the Uganda protectorate at the time the taxon was described. Currently, this locality is in the Central Equatoria province of South Sudan (see also Fisher and Ludwig, 2015: 80). [04 11 N 31 32 E]. [Goto Description]. Holotype: USNM 166520: ad ♀, skull and alcoholic. Collected by: John Alden Loring; collection date: 15 February 1910; original number: 9022. - Comments: Type locality might be in Uganda rather than Sudan as originally mentioned.

1918. *Eptesicus capensis somalicus:* Hollister, Bull. U.S. natl. Mus., 99: 92. (Name Combination).

1930. *P[ipistrellus] minutus somalicus:* Zammarano, Le colonie Italiane, 147. (Name Combination).

1962. *E[ptesicus] somalicus:* Rosevear, Mammalia, 26 (4): 457. (Name Combination).

1965. *[Eptesicus somalicus] ugandae:* Koopman, Am. Mus. Novit., 2219: 14. (Name Combination).

1969. *Eptesicus somalicus ugandae:* Kock, Abh. Senckenberg. naturforsch. Ges., 521: 175. (Name Combination).

1971. *Eptesicus (Eptesicus) somalicus somalicus:* Hayman and Hill, Mammals of Africa: Chiroptera, 44. (Name Combination).

1971. *Eptesicus (Eptesicus) somalicus ugandae:* Hayman and Hill, Mammals of Africa: Chiroptera, 44. (Name Combination).

1971. *Eptesicus (Eptesicus) somalicus:* Hayman and Hill, Mammals of Africa: Chiroptera, 44. (Name Combination).

1971. *Eptesicus somalicus somalicus:* Hill and Morris, Bull. Br. Mus. (nat. Hist.) Zool., 21 (2): 42. (Name Combination).

1987. *Nycterikaupius somalicus:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination).

1987. *Pipistrellus (Neoromicia) somalicus:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).

1993. *Eptesicus (Neoromicia) somalicus:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 203. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] s[omalicus] somalicus:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] s[omalicus] ugandae:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1995. *P[ipistrellus] somalicus:* Barratt, Bruford, Burland, Jones, Racey and Wayne, Symp. zool. Soc. Lond., 67: 380. (Name Combination).

1995. *P[ipistrellus] somalius:* Burland, Jones, Racey and Wayne, Symp. zool. Soc. Lond., 67: 379. (Lapsus).

1995. *Pipistrellus somalicus:* Koopman, Kofron and Chapman, Am. Mus. Novit., 3148: 11. (Name Combination).

2003. *Neoromicia somalicus:* Hoofer and Van Den Bussche, Acta Chiropt., 5 (Suppl): 19. (Name Combination, Alternate Spelling).

2004. *N[eoromicia] s[omalicus] somalicus:* Goodman and Ranivo, Mamm. biol., 69 (6): 434. (Name Combination).

2008. *N[eoromicia] somalica:* Riccucci and Lanza, Hystrix, It. J. Mamm., (ns) 19 (2): 176. - Comments: Riccucci and Lanza (2008: 176) indicate that the genus *Neoromicia* is feminine, therefore the spelling of the species ending must also be feminine according to Art. 31.2 of the ICZN (1999). (Name Combination).

2010. *Neoromicia somalica:* Decher, Norris and Fahr, Mammalia, 74 (2): 173. Publication date: 13 Aoril 2010. (Current Combination).

2013. *Neoromicia cf. somalica:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. (Name Combination).
2019. *L[aephotis] somalica:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2020. *Laephotis somalicus:* Simmons and Cirranello, BatNames.org. (Current Spelling).
? *Eptesicus somalicus:* (Name Combination).
? *Neoromicia cf. somalica JA-2016a*
? *Neoromicia somalicus somalicus:* (Name Combination, Alternate Spelling).
? *Neoromicia somalicus ugandae:* (Name Combination, Alternate Spelling).
? *Neoromicia somalicus vansoni:* (Name Combination, Alternate Spelling).

TAXONOMY:

Koopman (1993a: 203) included *zuluensis*; see Koopman (1975: 404, 405), but see Peterson *et al.* (1995), Simmons (2005). Mentioned in the genus *Pipistrellus* by Koopman (1994: 117). The subspecific allocations of West African and Tanzanian populations are uncertain (Koopman, 1994: 117).

Riccucci and Lanza (2008) indicated that the genus *Neoromicia* is feminine, therefore the ending of the species name *somalicus* must be *somalica*.

Helbig *et al.* (2010: 168) suggest transferring *somalica* to the genus *Laephotis*. However, this was rejected by Monadjem *et al.* (2020a: 1120, 1140).

COMMON NAMES:

Afrikaans: Somali-dakvlermuis. Chinese: 索马里伏翼. Czech: netopýr somálský. English: Somali Serotine, Somali Pipistrelle Bat, Somalian Pipistrelle Bat, Somali Serotine Bat. French: Sérotine de Somalie, Pipistrelle de Somalie. German: Somalia-Zwergfledermaus, Somalia-Pipistrelle. Italian: Pipistrèllo sòmalo.

CONSERVATION STATUS:

Global Justification

Although this species is known mainly from patchy records from a large area, it is listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, tolerance of a broad range of habitats, presumed large overall population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs, 2008g; IUCN, 2009; Monadjem and Jacobs, 2017d).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Neoromicia somalica*] (Monadjem and Jacobs, 2017d). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus somalicus*"] (Jacobs, 2008g; IUCN, 2009). 2004: LC ver 3.1 (2001) [assessed as "*Neoromicia somalicus*"] (Jacobs, 2004c; IUCN, 2004). 1996: LR/lc [assessed as "*Eptesicus somalicus*"] (Baillie and Groombridge, 1996).

Regional

None known.

MAJOR THREATS:

There appear to be no major threats to this species as a whole (Jacobs, 2008g; IUCN, 2009; Monadjem and Jacobs, 2017d).

CONSERVATION ACTIONS:

Jacobs (2008g) [in IUCN (2009)] and Monadjem and Jacobs (2017d) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected area, although it seems likely to occur in some East African parks. Further studies are needed into the taxonomy, distribution, natural history and threats to this species.

GENERAL DISTRIBUTION:

Neoromicia somalica has been recorded over much of West, Central and East Africa. It ranges from Guinea Bissau in the west, to Sudan, Eritrea and Somalia in the east, being found as far south as Tanzania and southern Democratic Republic of the Congo adjacent to the border with northern Angola, Zambia, and Zimbabwe.

Happold and Happold (1997b: 825) record *N. somalica* in Malawi, with reservations.

Specimens from southern Africa might possibly represent *Neoromicia zuluensis*, since the distinction between the two species (*zuluensis* and *somalica*) has not been made throughout the literature.

Earlier records from Madagascar are now assigned to *Laephotis malagasyensis*.

Native: Benin; Botswana; Burkina Faso (Kangoyé *et al.*, 2015a: 621); Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the); Côte d'Ivoire; Eritrea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Ghana; Guinea (Decher *et al.*, 2016: 273); Guinea-Bissau (Veiga-Ferreira, 1949; Lopes and Crawford-Cabral, 1992; Koopman, 1993a; Rainho and Ranco, 2001:64); Kenya; Liberia; Malawi (Happold and Happold, 1997b: 825); Namibia;

Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62); Zambia (Benda *et al.*, 2022: 292); Zimbabwe (Cotterill, 2004a: 261).

Bates *et al.* (2013: 339) reject the presence of *N. somalica* in the Republic of Congo as Van Cakenberghe and Happold (2013q: 654) only marked a locality on their map, but did not provide further details.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) line drawing of tragi of specimen DNSM 12612 from Mount Nimba, Liberia.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

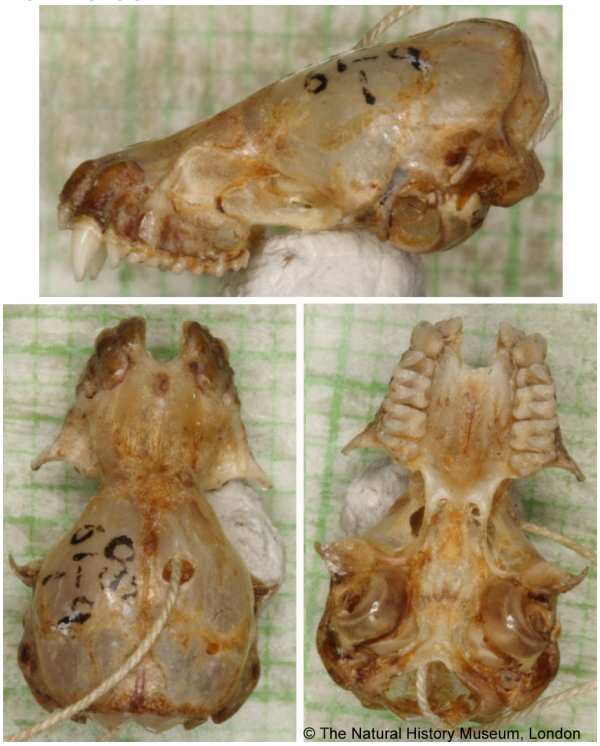

Figure 387. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1898.6.9.1, holotype of *Vespertilio minutus somalicus* Thomas, 1901.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987).

ECHOLOCATION:
Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

MOLECULAR BIOLOGY:
Karyotype
McBee *et al.* (1987) reported 2*n* = 26, FN = 48, BA = 24, a subtelocentric X chromosome, and an acrocentric Y chromosome.

From Senegal, Koubínová *et al.* (2013: 3) report the following karyotype for 13 ♂♂ and 7 ♀♀: 2*n*: 28, FNa = 50, FN = 54, X = metacentric, Y = submetacentric. There is one additional pair of acrocentric autosomes as compared to specimens from Cameroon. Koubínová *et al.* (2013: 10) assign these Senegalese specimens to "*Neoromicia* cf. *somalica*".

Genetics
See Hoofer and Van Den Bussche (2003) for the results of a specimen from Kenya.

HABITAT:
Monadjem *et al.* (2016y: 370) recorded this species from an urban environment in the Mount Nimba area, whereas it is otherwise known from savanna areas.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 51 minutes, and the digestibility rate about 84.5 %.

POPULATION:
Structure and Density
Little information is available on the population abundance or size of this species. It may be locally rare, or at least rarely recorded (Jacobs, 2008g; IUCN, 2009; Monadjem and Jacobs, 2017d).

Trend
2016: Unknown (Monadjem and Jacobs, 2017d).
2008: Unknown (Jacobs, 2008g; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
The litter size of this species is more than one (polytocy, see Garbino *et al.*, 2021: Suppl.)

PARASITES:
PROTOZOA
Kassahun *et al.* (2015: 168) examined 6 Ethiopian specimens and found two of them (from Aba-Roba) to be infected by *Leishmania* parasites (see also Azami-Conesa *et al.*, 2021: Suppl.; de Souza *et al.*, 2023: 5).

INSECTA
Siphonaptera
Hastriter (2016: 16) reported *Lagaropsylla consularis* Smit, 1957 from a *N. somalica* specimen from Maji Moto, Kenya.

VIRUSES:
Coronaviridae
Lane *et al.* (2022: 221) found Eidolon bat coronavirus in *Neoromicia* cf. *somalica* specimens from Ethiopia.

Rhabdoviridae

Stuchin *et al.* (2018: 345) referred to reports of this species being infected by Rabies lyssavirus.

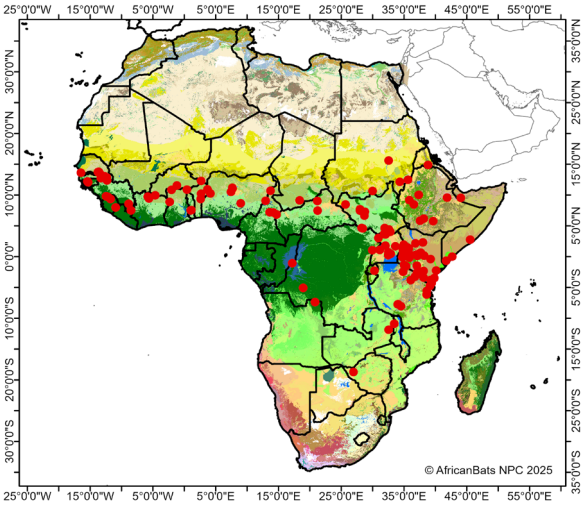

Figure 388. Distribution of *Neoromicia somalica*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Côte d'Ivoire, Eritrea, Eswatini, Ethiopia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Neoromicia zuluensis (Roberts, 1924)

*1924. *Eptesicus zuluensis* Roberts, Ann. Transv. Mus., 10: 60, text-fig 1. Publication date: 31 January 1924. Type locality: South Africa: KwaZulu-Natal: White Umfolosi Game Reserve [28 19 S 31 50 E]. [Goto Description]. Holotype: TM 3024: ad ♀, skin and skull. Collected by: Austin Roberts; collection date: 29 June 1922; original number: 14. [Second label has G.M. Allen as collector]; note: shot at dusk.

1926. *[Neoromicia] zuluensis:* Roberts, Ann. Transv. Mus., 11: 245. (Name Combination).

1932. *Neoromicia vansoni* Roberts, Ann. Transv. Mus., 15 (1): 15. Publication date: 1 October 1932. Type locality: Botswana: Zweizwe Waterhole [18 36 00 S 24 22 00 E]. [Goto Description]. Holotype: TM 6553: ad ♀, skin and skull. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 7 July [June on label] 1930; original number: 882.

1934. *Neoromicia pusilla vansoni:* Shortridge, Mammals of South West Africa, 59. (Name Combination).

1939. *Eptesicus vansoni:* G.M. Allen, Bull. Mus. comp. Zool., 83: 92.

1951. *Neoromicia zuluensis vansoni:* Roberts, Mammals of South Africa, 85. (Name Combination).

1951. *Neoromicia zuluensis zuluensis:* Roberts, Mammals of South Africa, 84. (Name Combination).

1953. *Eptesicus (Eptesicus) zuluensis vansoni:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1953. *Eptesicus (Eptesicus) zuluensis zuluensis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1953. *Eptesicus (Eptesicus) zuluensis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1962. *[Eptesicus zuluensis] zuluensis:* Meester, Ann. Transv. Mus., 24 (2/3): 242. (Name Combination).

1970. *Eptesicus zuluensis vansoni:* Roer, Bijdr. Dierk., 40 (1): 71. (Name Combination).

1978. *Eptesicus somalicus zuluensis:* Ansell, Mammals of Zambia, 25. (Name Combination).

1984. *Eptesicus (Eptesicus) somalicus zuluensis:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch., 244. (Name Combination).

1987. *Pipistrellus (Neoromicia) zuluensis:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).

1988. *P[ipistrellus] zuluensis:* Thorn, Mammalia, 52 (2): ???. (Name Combination).

1992. *Eptesicus zulensis:* Freitas, Bogo and Christoff, Z. Säugetierk., 57: 331. (Lapsus).

1994. *P[ipistrellus (Neoromicia)] s[omalicus] zuluensis:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

2001. *Neoromicia zuluensis:* Volleth, Bronner, Göpfert, Heller, von Helversen and Yong, Chromosome Res., 9 (1): 44. (Name Combination, Current Combination).

2017. *Neoromicia zuluensisin:* Han, Wen, Zhao, Liu, Luo, Zhou, Qin, Zhu, Liu, Qi, Li, Yu and Yu, Zoonoses Public Health, 64 (5): 643. Publication date: 1 April 2017. (Lapsus).

2019. *L[aephotis] zuluensis:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).

2019. *Laephotis zuluensis:* M. Taylor, Bats: An illustrated guide to all species, 284. Publication date: 11 April 2019. (Name Combination).

2020. *Neromicia zuluensis:* Monadjem, Richards, Decher, Hutterer, Mamba, Guyton, Naskrecki, Markotter, Wipfler, Kropff and Dalton, Zool. J. Linn. Soc., 121 (2): Suppl(for 2021). Publication date: 4 September 2020. (Lapsus).

TAXONOMY:



Figure 389. A female *Neoromicia zuluensis* (TM 48097) caught at Lapalala Wilderness Area, Limpopo Province, South Africa.

Bronner *et al.* (2003) state that although Ellerman *et al.* (1953) and Hayman and Hill (1971) recognised "*Eptesicus (= Neoromicia) zuluensis*" as a distinct species, Koopman (1975, 1982, 1993a), Meester *et al.* (1986) and Corbet and Hill (1992) treated it as a subspecies of "*Eptesicus* (= *Pipistrellus*) *somalicus*". Rautenbach *et al.* (1993) confirmed its distinctness from the latter on the grounds of interspecific chromosomal differences.

As a separate species by many authors, e.g., Volleth *et al.* (2001: 44), who assigned it to the genus *Neoromicia*.

Simmons and Cirranello (2020) included this species in the genus *Laephotis*, but this was rejected by Monadjem *et al.* (2020a: 1126, 1140) based on analyses of cyt *b* sequences.

COMMON NAMES:

Afrikaans: Aalwyndakvlermuis, Aalwynvlermuis. Chinese: 祖鲁伏翼. Czech: netopýr zuluský. English: Zulu Pipistrelle Bat, Aloe Bat, Aloe Serotine, Aloe Serotine Bat, Zulu Serotine Bat. French: Sérotine des aloes, Pipistrelle zouloue. German: Zulu-Zwergfledermaus, Zulu-Pipistrelle.

ETYMOLOGY OF COMMON NAME:

Roberts (1924) collected the original specimen at his camp and records in his description of the species that it was the Cape serotine bat, (currently *Laephotis capensis*), that he found in an aloe. He used the name aloe bat and it has remained associated with *N. zuluensis* (Taylor, 2005).

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs and Cotterill, 2008b; IUCN, 2009; Monadjem *et al.*, 2017ad).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as *Neoromicia zuluensis*] (Monadjem *et al.*, 2017ad). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus zuluensis*"] (Jacobs and Cotterill, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs and Cotterill, 2004b; IUCN, 2004). 2000: LR/nt [assessed as "*Eptesicus zuluensis*"] (Hilton-Taylor, 2000).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016n). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004). 1986: Indeterminate (Smithers, 1986).

MAJOR THREATS:

There appear to be no major threats to this species as a whole (Jacobs and Cotterill, 2008b; IUCN, 2009; Monadjem *et al.*, 2017ad).

CONSERVATION ACTIONS:

Jacobs and Cotterill (2008b) [in IUCN (2009)] and Monadjem *et al.* (2017ad) report that it seems probable that this adaptable species is present within a number of protected areas. It has been recorded from Kruger National Park, South Africa. No direct conservation measures are currently needed for the species as a whole.

GENERAL DISTRIBUTION:

Neoromicia zuluensis is widespread in East and southern Africa. The eastern distribution ranges from Ethiopia and South Sudan to Uganda and Kenya. The southern range extends from Zambia and southern parts of the Democratic Republic of the Congo to southern South Africa, and from eastern Angola to central Zambia and Zimbabwe. In the RSA, the species' distribution is linked with land use/land cover (Babiker Salata, 2012: 50).

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,198,714 km^2.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d:570; Taylor *et al.*, 2018b: 60); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 570); Congo (The Democratic Republic of the); Eswatini (Monadjem *et al.*, 2010d: 570, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 153; 2011: 54); Kenya; Malawi (Ansell and Dowsett, 1988: 42); Mozambique (Monadjem *et al.*, 2010d: 570; Monadjem *et al.*, 2010c: 384); Namibia (Monadjem *et al.*, 2010d: 570); South Africa

(Monadjem *et al.*, 2010d: 570); Sudan; Uganda; Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 570); Zimbabwe (Monadjem *et al.*, 2010d: 570).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 390. Clockwise from top lateral, ventral and dorsal skull images of TM 3024, holotype of *Eptesicus zuluensis* Roberts, 1924.

DETAILED MORPHOLOGY:

Baculum

Hill and Harrison (1987) and Kearney *et al.* (2002).

FUNCTIONAL MORPHOLOGY:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 5.7 Pa, aspect ratio 6.4 for a wingspan of 23 cm and a wing area of 69 cm^2 and a body mass of 4 g.

ECHOLOCATION:

In Waterberg, South Africa, Taylor *et al.* (2013b: 17) recorded the following parameters for 5 calls: F_{max}: 73.8 ± 14.93 (59.1 - 92.8) kHz, F_{min}: 48.1 ± 1.94 (45.7 - 50.5) kHz, F_{knee}: 51.3 ± 2.85 (48.4 - 55.8) kHz, F_{char}: 49.0 ± 1.81 (46.3 - 51.2) kHz, duration: 2.4 ± 0.52 (1.7 - 3.0) ms.

At Farm Welgevonden, South Africa, Taylor *et al.* (2013a: 556) report a F_{knee} value of 51 (48 - 56) kHz.

Linden *et al.* (2014: 40) reported the following parameters from the Soutpansberg range (RSA): F_{min}: 46 - 50 kHz, F_{char}: 46 - 51 kHz, F_{knee}: 48 - 56 kHz, slope: 487 - 867 OPS, duration: 2 - 3 ms. 20 calls were recorded by Parker and Bernard (2018: 57) in the Mapungubwe National Park (RSA): F_{char}: 48.11 ± 1.17 kHz, F_{max}: 63.23 ± 4.44 kHz, F_{min}: 47.70 ± 1.36 kHz, F_{knee}: 52.09 ± 2.33 kHz, duration: 4.91 ± 1.36 ms, at 7.47 ± 2.12 calls/sec.

At Telperion Nature Reserve (RSA), Kearney *et al.* (2019: 37) recorded a release call (6 pulses) with the following characteristics: F_{char}: 45.89 ± 0.43 (45.45 - 46.51) kHz, slope at start of call: 52.41 ± 16.85 (31.71 - 68.40), time between start of call and F_{char}: 3.43 ± 0.84 (2.26 - 4.83) ms and duration: 3.82 ± 0.58 (3.13 - 4.83) ms. From the same locality, De Jong *et al.* (2025: 322) reported the following parameters for 29 calls from 2 *Neoromicia zuluensis* : F_{char}: 45.93 ± 1.28 kHz, F_{knee}: 48.87 ± 1.98 kHz, F_{min}: 45.74 ± 1.31 kHz, F_{max}: 84.90 ± 15.01 kHz, Bandwidth: 39.15 ± 15.53 kHz, Duration: 2.82 ± 0.60 ms. 20 calls from 4 males had the following values: F_{char}: 45.42 ± 0.99 kHz, F_{knee}: 48.92 ± 2.55 kHz, F_{min}: 45.18 ± 1.02 kHz, F_{max}: 72.57 ± 15.74 kHz, Bandwidth: 27.40 ± 15.67 kHz, Duration: 2.78 ± 0.50 ms.

From the MalaMala Game Reserve (KNP, RSA), Gumede *et al.* (2025: Appendix S1) reported F_{char}: 48.11 ± 1.17 kHz, F_{max}: 63.23 ± 4.44 kHz, F_{min}: 47.70 ± 1.36 kHz.

From Swaziland, the following parameters were reported by Monadjem *et al.* (2017c: 179): F_{min}: 46.1 ± 2.82 (39.9 - 45.3) kHz, F_{knee}: 46.6 ± 2.91 (43.3 - 48.5) kHz, F_c: 43.6 ± 3.10 (40.1 - 45.9) kHz and duration: 3.7 ± 0.67 (3.0 - 4.2) ms.

12 calls from the Okavango River Basin reported by Weier *et al.* (2020: Suppl.) had the following characteristics: F_{max}: 54.17 ± 3.34 kHz, F_{min}: 49.65 ± 0.96 kHz, F_{knee}: 50.65 ± 1.40 kHz, F_{char}: 50.14 ± 0.88 kHz, slope: 8.43 ± 16.98 OPS, duration: 3.59 ± 1.28 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 99 calls of 9 bats: F_{max}: 61.2 ± 8.6 kHz, F_{min}: 46.65 ± 5.2 kHz, F_{knee}: 49.86 ± 2.26 kHz, F_{char}: 48.41 ± 1.76 kHz, slope: -238.88 ± 3564.48 OPS, duration: 3.74 ± 1.5 ms. 15 calls recorded at the Venetia mine by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 3.87 ± 0.79 ms, F_{min}: 44.34 ± 3.87 kHz, F_{max}: 52.77 ± 2.90 kHz, F_{knee}: 48.53 ± 0.84 kHz and F:47.31± 0.66 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 27 *Neoromicia zuluensis* calls from the Kruger Park (RSA): F_{min}: 46 ± 1.2

(43.9 48.7) kHz, Duration: 3.7 ± 0.7 (2.6 4.9) ms, F_{max}: 58.2 ± 7.9 (32.7 69.7) kHz, F_{knee}: 48.1 ± 1.4 (45.3 51.3) kHz, F_{char}: 46.7 ± 1.3 (44.4 49.3) kHz.

79 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 46 - 51 kHz, F_{max}: 59 - 93 kHz, F_{char}: 46 - 51 kHz, F_{knee}: 48 - 56 kHz and duration 2 - 34 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 55) reported F_{char}: 48.11 ± 1.17 kHz, F_{max}: 63.23 ± 4.44 kHz and F_{min}: 47.70 ± 1.36 kHz.

Taylor-Boyd *et al.* (2025: 116) report the following values for 12 calls from Zambia: Interpulse interval: 83.6 ± 24.3 (46.3 - 137.0) ms; F_{max}: 52.8 ± 4.0 (45.3 - 57.9) kHz; Start slope: -29.1 ± 12.7 (-18.0 - -8.2) kHz/ms; End slope: -2.7 ± 2.3 (-0.6 - 0.9) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.3 - 0.8) ms.

Molecular Biology:

Karyotype

Both Rautenbach *et al.* (1993) and Kearney *et al.* (2002) recorded 2*n* = 28, FN = 48, BA = 22, and a subtelocentric X chromosome. However, as can been seen from Figure 9 in Kearney *et al.* (2002), the FN number was incorrectly reported and should be FN = 50, and BA = 24. Rautenbach *et al.* (1993) also reported an acrocentric Y chromosome. GTG-bands identified three Robertsonian fusion chromosomes (7/11, 8/9, 10,12), considered as distinguishing characters for the genus *Neoromicia* Kearney *et al.* (2002).

Protein / allozyme

See Morales *et al.* (1991) for results from three specimens from South Africa.

Habitat:

In southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) found that *N. zuluensis* is primarily present in Savanna (81 %) and SW arid (10 %) habitats. In the northern Namib Desert, the activities of this species are related to water quality

Diet:

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 56 minutes, and the digestibility rate about 83.5 %.

Predators:

Malan *et al.* (2022: 167) reported one individual found in a pellet from a bat hawk (*Macheiramphus alcinus* Bonaparte, 1850.

Population:

Structure and Density

In general, this is a locally uncommon species (Jacobs and Cotterill, 2008b; IUCN, 2009; Monadjem *et al.*, 2017ad).

Trends

2016: Unknown (Monadjem *et al.*, 2017ad).
2008: Unknown (Jacobs and Cotterill, 2008b; IUCN, 2009).

Reproduction and Ontogeny:

In Malawi, births occurred early in the wet season (Happold and Happold, 1990b: 568).

Monadjem *et al.* (2010d) [in Weier *et al.* (2018: Suppl.)] mentioned births from late November to early December.

Parasites:

PROTOZOA

Harris *et al.* (2018: 2, 3) reported the presence of *Hepatozoon* sp. from a *Neoromicia zuluensis* from Louis Trichardt, in the Limpopo province (RSA).

HEMIPTERA

Cimicidae

Kock *et al.* (1998b: 237) mentioned *Aphrania* cf. *barys* Jordan and Rothschild, 1912 on bats from Namibia.

Viruses:

Coronaviridae - Coronaviruses

The report of a new virus by Ithete *et al.* (2013: 1697) that was closely related to Middle East respiratory syndrome (MERS)-CoV, the host was incorrectly identified and is related to *Laephotis capensis*.

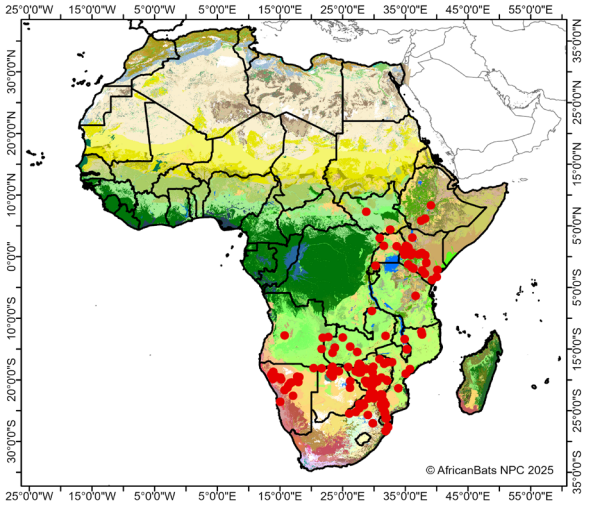

Figure 391. Distribution of *Neoromicia zuluensis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Angola, Botswana, Eswatini, Ethiopia, Kenya, Malawi, Mozambique, Namibia, Rwanda, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Genus ***Nycticeinops*** Hill & Harrison, 1987

*1987. *Nycticeinops* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 254. - Comments: Type species: *Nycticejus schlieffeni* Peters, 1859. - Etymology: Lanza *et al.* (2015: 364) mention the following: "masculin scientific Latin substantive made up of the masculine scientific Latin substantive *Nycticeius* (Nicticèius) and the feminine Greek substantive "*ὄφις*" (ópsis) 'aspect, appearance', referring to the likeness of the genus *Nycticeinops* to the genus *Nycticeius*, The etymology proposed by Hill and Harrison (1987) is imperfect". (Current Spelling).

2005. *Nycteceinops:* Eick, Jacobs and Matthee, Mol. Biol. Evol., 22 (9): 1871. Publication date: 1 June 2005. (Lapsus).

*2019. *Parahypsugo* Hutterer, Decher, Monadjem and Astrin, Acta Chiropt., 21 (1): 7. Publication date: 5 October 2019. - Etymology: From the Greek prefix *para* (meaning beside or near), combined with the existing genus name *Hypsugo*, emphasizing the close genetic and morphological relationships between the two genera (see Hutterer *et al.*, 2019 7).

? *Nycticeinops sp.*

TAXONOMY:
Bronner *et al.* (2003) state that the genus *Nycticeius* has long been considered to comprise two species: *N. humeralis*, from North America, and *N. schlieffenii* from Africa and Arabia. Koopman (1978) found these species so similar that he retained them in the same genus, a treatment disputed by Kitchener and Caputi (1985). Hill and Harrison (1987) demonstrated consistent differences between these species in baculum morphology and proposed the allocation of *schlieffeni* to the distinct genus *Nycticeinops*. Extensive karyotypic differences between the American *humeralis* (2*n* = 46 and FN = 48; Baker and Patton, 1967; Bickham, 1979) and East African *schlieffeni* (2*n* = 34 and FN = 52) provide additional evidence that the two species are not congeneric (Ruedas *et al.*, 1990) and *mt*DNA sequence divergence data strongly support their allocation to distinct genera (Hoofer and Van Den Bussche, 2001). However, Rautenbach *et al.* (1993) report an intermediate karyotype of 2*n* = 42 and FN = 50 for *schlieffeni* from South Africa. This not only suggests the existence of two species in Africa, but also casts some doubt on the karyotypic basis for generic distinction between these forms. We nevertheless recognise these as distinct genera owing to clearcut differences in bacular and *mt*DNA properties.

Meester *et al.* (1986) state that *Scoteinus* Dobson, 1875 has frequently been included in this genus for the species *schlieffenii*, either as a subgenus (Ellerman *et al.*, 1953; Hayman and Hill, 1971), or as a synonym (Rosevear, 1965). Allen (1939a) and Roberts (1951) regard *Scoteinus* as a valid genus, which includes *schlieffenii*. However, Sinha and Chakraborty (1971) place *Nycticeius emarginatus* (Dobson, 1871), the type species of *Scoteinus*, in the distinct Indo-Malayan genus *Scotomanes*, and Koopman (1975, 1978) accordingly regards *schlieffenii* as a *Nycticeius sensu stricto*.

Currently (Simmons and Cirranello, 2023b) recognized extant species of the genus *Nycticeinops*: ***macrocephalus*** (Hutterer and Kerbis Peterhans,2020); ***schlieffenii*** (Peters, 1859). Addtionally there is also the extinct ***†serengetiensis*** Gunnell, Butler, Greenwood and Simmons, 2015.

COMMON NAMES:
Czech: Schlieffenovi netopýři. English: Twilight bats. French: Nycticeinops. German: Abendfledermäuse. Italian: Nitticèinopi, Nicticèinopi.

GEOGRAPHIC VARIATION:
Volleth *et al.* (2023c: 50) point to the importance of the Dahomey gap in this genus. One example is the pair *happoldorum/grandidieri*, where the prior occurs in the west and the latter in the east. They also point out that the baculum of *N. happoldorum* is twice as large as that of *N. grandidieri*. This is also the case for a second species pair: *crassulus/bellieri*, with *crassulus* having the larger baculum. These morphological differences are also supported by molecular results.

PARASITES:
ARACHNIDA
Macronyssidae
Orlova *et al.* (2024: 154) [referring to Zumpt, 1961] mentioned *Nycticeinops* sp. as host for *Chelanyssus aethiopicus* (Hirst, 1921).

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Nycticeinops 'incertae-sedis'

2013. *Nycticeinops cf. schlieffenii:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. (Name Combination).

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

Nycticeinops macrocephalus (Hutterer and Kerbis Peterhans, 2020)

*2013. *Hypsugo cf. eisentrauti:* Kerbis Peterhans, Fahr, Huhndorf, Kaleme, Plumptre, Marks and Kizungu, Bonn. Zool. Bull., 62 (2): 189. Publication date: November 2013. (Current Combination).
2020. *Nycticeinops macrocephalus:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1140. Publication date: 10 September 2020. (Current Combination).
*2020. *Parahypsugo macrocephalus* Hutterer and Kerbis Peterhans, Lynx, NS 50: 53, figs 1, 2A, 3. Publication date: February 2020. Type locality: Congo (Democratic Republic of the): Sud-Kivu province: Misotschi-Kabogo Highlands: Kabobo Forest: 4 km SW Talama [04 59 29 S 29 04 49 E, 1950 m]. Holotype: FMNH 195086: ad ♀, skin and skeleton and skull. Collection date: 17 February 2007; original number: MHH 845. Paratype: SMF 79444: ad ♂, skin and skull. Collected by: Klaus-Gerhard Heller and Marianne Volleth; collection date: 28 March 1990; original number: 339. - Etymology: The name is derived from the Greek "μακρος" (Latinised to macros), meaning large and "κεφαλή" (Latinised to cephale), meaning head.

TAXONOMY:
As already indicated by Van Cakenberghe and Happold (2013i: 622) *eisentrauti* records from the DRC, Uganda, Kenya and Somalia do not resemble closely to the holotype and paratype of "*Pipistrellus] eisentrauti*" to be considered respresentatives of this species. Kerbis Peterhans *et al.* (2013: 189) therefore assigned these tentatively to "*H[ypsugo]* cf. *eisentrauti*", indicating that they could represent a yet undescribed species. Hutterer and Kerbis Peterhans (2020: 53) formally described this species, but also indicated that the specimens from Somalia and Kenya still need to be examined, as they might possibly represent yet another species.

Based on the morphological similarities with *happoldorum*, Monadjem *et al.* (2020a: 1140, 1141) placed this species in the genus *Nycticeinops*.

COMMON NAMES:
English: Large Headed Pipistrelle.

CONSERVATION STATUS:
Global Justification
Not assessed.

Assessment History
Global
Not assessed.

Regional
None known.

GENERAL DISTRIBUTION:
Native: Congo (The Democratic Republic of the), Rwanda

Presence uncertain: Kenya; Somalia; Uganda

DETAILED MORPHOLOGY:
Baculum
Heller *et al.* (1994: 2) (as "*Hypsugo eisentrauti*").

MOLECULAR BIOLOGY:
Karyotype
Volleth *et al.* (2001) reported 2*n* = 42, FN = 58, BA = 18, a metacentric X and a dot-like Y chromosome for a male "*Hypsugo eisentrauti*" specimen from Rwanda, which is currently considered to be the paratype of *Parahypsugo macrocephalus*.

Genetics
Volleth *et al.* (2023c: 37) reported that the cyt b sequence of the paratype was 98.4 % similar to that of a *Nyctinceinops eisentrauti* specimen from Cameroon.

POPULATION:
Structure and Density
Unknown.

Trend
Not assessed.

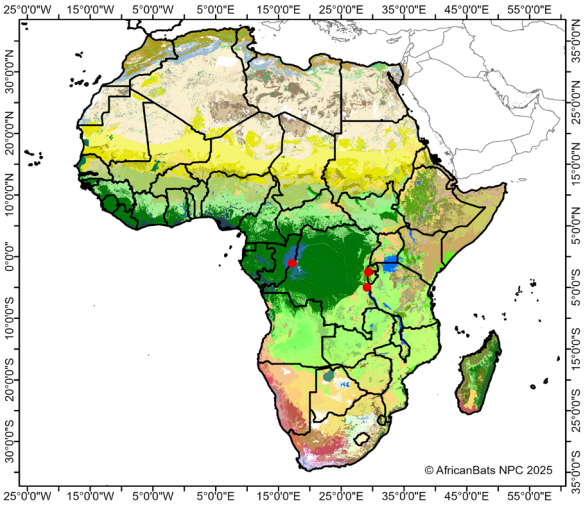

Figure 392. Distribution of *Nycticeinops macrocephalus*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Congo (Democratic Republic of the), Rwanda.

Nycticeinops schlieffenii (Peters, 1859)

*1859. *Nycticejus Schlieffenii* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, p 224. Type locality: Egypt: Cairo [30 03 N 31 15 E]. [Goto Description]. Holotype: ZMB 585: ad ♂, alcoholic and cranium only (no mandibula). Collected by: Graf Afred von Schlieffen. See Turni and Kock (2008: 53). - Comments: Allen (1939a: 97) mentioned 1860 as year of publication, Kock (1969a: 186) mentions 1859. The publication covers a meeting held on 28 February 1859. - Etymology: In honour of the collector Count Wilhelm von Schlieffen-Schlieffenburg (Smithers, 1983: 111). Johnston (2006: 3) mentions Schlieffen-Schlieffiennburg. Lanza *et al.* (2015: 366) [referring to Beolens *et al.* (2009)] mention Graf Wilhelm Schlieffen von Schlieffenberg (1833 - ?).

1877. *N[ycticejus] adovanus* Heuglin, Reise in Nordost Afrika, 2: 34. Publication date: 1877. Type locality: Ethiopia: Tigre province: As(s)am river: Adowa [14 10 N 38 54 E, 1 900 m]. [Goto Description].

1887. *Scotophilus minimus* Noack, Zool. Jb. Syst., 2 (2): 280, pl 10, fig 36 - 37. Publication date: 7 May 1887. Type locality: Congo (Democratic Republic of the): (formerly indicated as in Democratic Republic of the Congo): Marungu: Qua Mpala [06 45 00 S 29 31 00 E, 774 m]. [Goto Description]. - Comments: Kock (1969a: 187), Meester *et al.* (1986: 62) situate Qua Mpala in the Democratic Republic of the Congo, not in Tanzania. Noack (1887: 280) refers to the type specimen as a female with separate skull.

1905. *Scotophilus schliefferri:* Schwann, Novit. Zool., 12 (1): 1. (Lapsus).

1908. *Scoteinus schlieffeni albiventer* Thomas and Wroughton, Proc. zool. Soc. Lond., 1908, III: 540. Publication date: 30 October 1908. Type locality: Sudan: Northern province: Naikhala. Holotype: NHMUK 1904.11.3.4: ad ♂. Collected by: Nathanial Charles Rothschild; collection date: 13 February 1904; original number: 73. Presented/Donated by: Nathanial Charles Rothschild.

1908. *Scoteinus schlieffeni australis* Thomas and Wroughton, Proc. zool. Soc. Lond., 1908, III: 539. Publication date: 30 October 1908. Type locality: Mozambique: 120 km SW Inhambane: Coguno [24 23 S 34 32 E]. [Goto Description]. Holotype: NHMUK 1906.11.8.19: ad ♂. Collected by: Captain Claude Henry Baxter Grant; collection date: 5 August 1906. - Comments: Considered a valid subspecies of *Nycticeius schlieffeni* by Taylor (1998: 56).

1908. *Scoteinus schlieffeni bedouin* Thomas and Wroughton, Proc. zool. Soc. Lond., 1908, III: 540. Publication date: 30 October 1908. Type locality: : Jemen, Aden, Lahej. - Comments: Extrelimital.

1911. *Nycticeius africanus* G.M. Allen, Bull. Mus. comp. Zool., 54 (6): 328. Publication date: December 1911. Type locality: Kenya: Northern Guaso Nyiro: Meru River: effluent of northern Guaso Nyiro [=Ewaso Ngiro] [00 03 N 37 39 E]. [Goto Description]. Holotype: MCZ 8272: ♂, skin and skull. Collected by: Glover Morrill Allen; collection date: 11 August 1909; original number: 113. See Allen (1911: 328); Helgen and McFadden (2001: 147). - Comments: Thorn *et al.* (2009: 57) mention 00 29 N 37 40 E as coordinates for the type locality.

1916. *Scotoecus cinnamomeus* Wettstein, Anz. kais. Akad. Wiss., Wien, 53: 191. Publication date: 1916. Type locality: Sudan: Kordofan province: Nubbaka [=En Nabbaka] [12 35 N 29 55 E]. [Goto Description]. - Comments: Thorn *et al.* (2009: 57) mention 12 47 N 30 46 E as coordinates for the type locality. Type specimen: ♀, collected by Prof. Dr. Franz Werner, collection date 17 March 1914. Two cotypes [= paratypes], 1 ♀ from Nubbaka, collection date 17 March 1914; 1 ♀ from Dilling, collection date: 20 March 1914 (see Wettstein, 1916: 191).

1926. *Scoteinus schleiffeni:* Cabrera and Ruxton, Ann. Mag. nat. Hist., ser 9, 17 (103): 594. Publication date: 1 May 1926. (Lapsus).

1932. *Scoteinus schlieffeni fitzsimonsi* Roberts, Ann. Transv. Mus., 15 (1): 17. Publication date: 1 October 1932. Type locality: Botswana: N Bechuanaland, Ngamiland,: Tsotsoroga Pan [18 40 S 24 25 E]. [Goto Description]. Holotype: TM 6550: ad ♂, skin and skull. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 19 June 1930; original number: 833. . Cotype: TM 6551: ad ♂, skin and skull. Collected by: The Vernay-Lang Kalahari Expedition 1930; collection date: 19 June 1930; original number: 830.

1987. *Nycticeinops schlieffenii:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (4): 275. Publication date: 30 July 1987. (Name Combination, Current Combination).

2005. *Nycteceinops schlieffeni:* Eick, Jacobs and Matthee, Mol. Biol. Evol., 22 (9): 1871. Publication date: 1 June 2005. (Lapsus).

2010. *Nycticeinops schlieffeni:* Monadjem, Taylor, Cotterill and Schoeman, Bats of Southern and Central Africa. A biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, 486. (Alternate Spelling).
2011. *Nycticeius schlieffini:* Altringham, Bats, 215. (Lapsus).
2012. *Nycticeinops schilieffeni:* Manga Mongombe, Master's thesis. University of Maroua, Cameroon, 12. - Comments: . (Lapsus).
2013. *Nycticeinops cf. schlieffenii:* Koubínová, Irwin, Hulva, Koubek and Zima, Front. Zool., 10: 5. - Comments: Koubínová *et al.* (2013: 7) found differences in diploid chromosome number and/or in chromosome morphology between the populations from Senegal and other regions in Africa. (Name Combination).
2016. *Nycticeius schleifeni:* Mikula, Morelli, Lučan, Jones and Tryjanowski, Mammal Rev.. Publication date: 20 January 2016. (Lapsus).
2020. *Nycticeinops cf. schlieffeni:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans, and Patterson, B. D., Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Name Combination, Alternate Spelling).
? *Nycticeinops cf. schlieffeni TD-2020*
? *Nycticeinops schlieffeni albiventer:* (Name Combination).
? *Nycticeinops schlieffeni fitzsimonsi:* (Name Combination).
? *Nycticeinops schlieffeni schlieffeni:* (Name Combination).
? *Nycticeius (Scoteinus) schleiffenii:* (Name Combination).
? *Nycticeius schlieffeni australis:* (Name Combination).
? *Nycticeius schlieffeni:* (Alternate Spelling).
? *Nycticeius schlieffenii:* (Name Combination).

TAXONOMY:



Figure 393. A female *Nycticeinops schlieffenii* (TM 48141) caught at Makalali-GR, Limpopo, South Africa.

Includes *cinnamomeus*; see Koopman (1975: 412 - 413). Assigned to the genus *Nycticeinops* by Harrison and Bates (1991: 94) and Hutson *et al.* (2001: 29), which is considered a subgenus of *Nycticeius* by Pavlinov *et al.* (1995: 116).

Based on COI sequences, Volleth *et al.* (2023c: 37) assigned specimens from Ethiopia, Senegal, Somalia an Burkina Faso to *Nycticeinops schlieffenii*, but animals from South Africa - which showed only 88.6 % similarity - are assigned to *Nycticeinops* cf. *schlieffenii*.

COMMON NAMES:

Afrikaans: Schlieffen se vlermuis, Schlieffen-vlermuis, Klein dakvlermuis. Chinese: 施氏墓蝠. Czech: netopýr Schlieffenův, netopýr krátkouchý. Dutch: Schlieffens vleermuis. English: Schlieffen's Bat, Schlieffen's Twilight Bat. French: Nycticeinops de Schlieffen, Chauve-souris du crépuscule, Chauve-souris de Schlieffen. German: Schlieffens Abendfledermaus. Italian: Nitticèinope di Schlieffen, Nicticèinope di Schlieffen. Kiluba (DRC): Kasusu. Malawian: Liputiputi, Ndemiya, Namzeze. Portuguese: Morcego de Schlieffens.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Butler and Greenwood (1965) found material in the early Pleistocene at Olduvai, which they referred to as "cf *Nycticeius* (*Scoteinus*) *schlieffeni* (Peters)" (see Butler (1978).

CONSERVATION STATUS:

Global Justification

Widespread and rather common, with no major threats. Assessed as Least Concern LC ver 3.1 (2001) (Jacobs *et al.*, 2008b; IUCN, 2009).

Assessment History

Global

2008: LC ver 3.1 (2001) [as *Nycticeinops schlieffeni*] (Jacobs *et al.*, 2008b; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et al.*, 2004am; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional

South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016o). 2004: LC ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:

None known (Jacobs *et al.*, 2008b; IUCN, 2009).

CONSERVATION ACTIONS:

Jacobs *et al.* (2008b; IUCN, 2009).

GENERAL DISTRIBUTION:

Distribution is split into two: one range in W Africa (including N Senegal, S Mauritania, Burkina Faso, Togo, Benin, and Nigeria), and one covering much of E and S Africa (as far south as NE Swaziland). The species is absent from much of the Horn of Africa, NE Ethiopia, E Tanzania, and NE Mozambique. There is a smaller central

African range in NE Democratic Republic of the Congo (DRC). There are also records from Niger, Central African Republic (CAR), and the Nile delta in Egypt.

The record on Madagascar is for three specimens in the Paris Museum (ZM-MO-1985-1036, ZM-MO-1985-1037, ZM-MO-1985-1038) which are currently (November 2021) also in the online catalogue mentioned as "*schlieffeni*".

For southern Africa, Cooper-Bohannon *et al.* (2016: Table S2) calculated a potential distribution area of 1,003,159 km^2. Babiker Salata (2012: 50) indicated that the distribution in the RSA is mostly affected by the annual mean temperature.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 570; Taylor *et al.*, 2018b: 63); Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Archer, 1977; Monadjem *et al.*, 2010d: 570); Burkina Faso (Kangoyé *et al.*, 2015a: 621); Cameroon; Central African Republic; Chad; Congo (The Democratic Republic of the) (Noack, 1887; Hayman *et al.*, 1966; Monadjem *et al.*, 2010d: 570); Djibouti (Pearch *et al.*, 2001: 388); Egypt; Eritrea; Eswatini (Monadjem *et al.*, 2010d: 571, Monadjem *et al.*, 2021: 5); Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Ghana; Kenya; Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 570); Mali (Meinig, 2000: 105); Mauritania (Allegrini *et al.*, 2011: 3); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 570; Monadjem *et al.*, 2010c: 384); Namibia (Monadjem *et al.*, 2010d: 571); Niger; Nigeria; Saudi Arabia; Senegal; Somalia; South Africa (Monadjem *et al.*, 2010d: 571); Sudan; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62); Yemen (Benda *et al.*, 2011b: 41); Zambia (Ansell, 1978; Monadjem *et al.*, 2010d: 571); Zimbabwe (Monadjem *et al.*, 2010d: 571).

Geographic variation:

Koubínová *et al.* (2013: 9) indicate that *N. schlieffenii* is distributed in three areas in Africa: West, East, and South (respectively represented by Senegal, Somalia, and South Africa in their study) and found that the West and East areas differed in karyotype from the South, and that West and East differed in their *S12* gene.

General description of cranial and dental morphology:

Scott *et al.* (2012: 2943) report that the mandibular symphyse is fully fused in *N. schlieffenii*.

Detailed morphology:

Penis

The penis of *Nycticeinops schlieffenii* was the largest of the six pipistrelloid species examined by Fasel *et al.* (2020: 1394). In flaccid state, it was at least 5.8 mm in length (in the other species it was 5.3 mm at most). The prepuce is covered by long, mostly anteriorly directed hairs.

Baculum

Hill and Harrison (1987) and Kearney *et al.* (2002).

Vomeronasal complex

In this species, the VNC is bar-shaped in cross section (Smith *et al.*, 2024: 9).

Functional morphology:

Amador *et al.* (2019: Suppl.) [referring to Norberg and Rayner (1987)] mention a wing loading value of 6.7 Pa, aspect ratio 6.9 for a wingspan of 22 cm and a wing area of 73 cm^2 and a body mass of 5 g.

Sexual dimorphism:

In Burkina Faso, Kangoyé *et al.* (2015a: 621) found the average body (except Tragus and 3ph3) and cranial (except CM) measurements in females to be larger than in males.

Echolocation:

See Taylor (1999b) and Taylor *et al.* (2005).

From Maroua, Cameroon, Manga Mongombe (2012: 79) reported a FM call type for 1 call and the following parameters: F_{max}: 51.3 kHz, F_{min}: 40.0 kHz, F_{mean}: 45.7 kHz, F_{knee}: 51.3 kHZ, F_{char}: 41.0 kHz, and duration: 0.91 ms.

In Swaziland, Monadjem *et al.* (2017c: 179) recorded F_{min}: 40.1 ± 1.48 (38.7 - 42.4) kHz, F_{knee}: 43.4 ± 1.67 (41.7 - 45.4) kHz, F_c: 40.3 ± 1.29 (39.2 - 42.4) kHz and duration: 3.1 ± 0.64 (2.4 - 4.0) ms. They could detect the calls up to a distance of 15 m.

Weier *et al.* (2020: Suppl.) reported on 25 calls from the Okavango River Basin with the following characteristics: F_{max}: 45.39 ± 3.35 kHz, F_{min}: 39.87 ± 7.35 kHz, F_{knee}: 42.20 ± 0.48 kHz, F_{char}: 41.84 ± 0.60 kHz, slope: 6.66 ± 13.38 OPS, duration: 4.42 ± 1.75 ms.

Luo *et al.* (2019a: Supp.) reported the following data (Hand released bats): F_{peak}: 42.5 kHz, F_{start}: NA kHz, F_{end}: NA kHz, Band width: NA kHz, and duration: 3.5 ms.

In the Limpopo province (RSA), Weier *et al.* (2021: 7) reported the following characteristics for 104 calls of 7 bats: F_{max}: 50.27 ± 9.84 kHz, F_{min}: 40.2 ± 5.93 kHz, F_{knee}: 42.86 ± 0.75 kHz, F_{char}:

41.61 ± 1.35 kHz, slope: -708.66 ± 5655.95 OPS, duration: 3.98 ± 2.13 ms. 15 calls recorded at the Venatia mine by Cory-Toussaint and Taylor (2022: Table S1) had a duration of 3.62 ± 1.17 ms, F_{min}: 38.49 ± 4.40 kHz, F_{max}: 49.89 ± 3.83 kHz, F_{knee}: 44.62 ± 0.69 kHz and F_{char}: 42.45 ± 0.43 kHz.

Brinkley *et al.* (2021: Table S1) mention the following parameters for 1 *Nycticeinops schlieffeni* call from the Kruger Park (RSA): F_{min}: 40.1 kHz, Duration: 3.9 ms, F_{max}: 42.8 kHz, F_{knee}: 42.2 kHz, F_{char}: 42.1 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype.

26 pulses recorded by Taylor *et al.* (2020a: 77) at Venetia Limpopo Nature Reserve and Mapungubwe National Park (RSA) had F_{min}: 42 kHz, F_{max}: 50 kHz, F_{char}: 41 kHz, F_{knee}: 44 kHz and duration 2 ms.

Along the Chobe River (Botswana/Namibia), Parker and Bernard (2023: 55) reported F_{char}: 42.10 ± 0.30 kHz, F_{max}: 42.80 ± 1.30 kHz and F_{min}: 40.10 ± 1.50 kHz.

In Zambia, Taylor-Boyd *et al.* (2025: 116) report the following values for 8 calls: Interpulse interval: 80.8 ± 39.0 (50.5 - 162.0) ms; F_{max}: 48.5 ± 4.5 (43.4 - 57.2) kHz; Start slope: -29.1 ± 9.8 (-24.1 - -7.7) kHz/ms; End slope: -5.7 ± 3.4 (-1.1 - -7.1) kHz/ms; Ledge duration: 0.5 ± 0.1 (0.3 - 0.6) ms.

Molecular Biology:

Karyotype

Ruedas *et al.* (1990) reported 2*n* = 34, FN = 52, and BA = 20, for specimens from Somalia, whereas Rautenbach *et al.* (1993) reported 2*n* = 42, FN = 50, and BA = 10, for specimens from South Africa. However, both Ruedas *et al.* (1990) and Rautenbach *et al.* (1993) reported submetacentric X, and acrocentric Y chromosomes. Unfortunately, Rautenbach *et al.* (1993) do not identify the actual voucher specimens associated with the work, since further work should be done to ascertain whether this variation is an indication of two distinct species.

From Senegal, Koubínová *et al.* (2013: 3) report the following karyotype for 4 ♂♂ and 1 ♀: 2*n* = 34, Fna = 52, FN = 56, X = metacentric, Y = dot-like. They also found a 5.56 - 5.91 % difference in the *12S* gene as compared with conspecifics from other areas available in GenBank.

Volleth *et al.* (2023c: 44) reported 2*n*=34, FNa = 50 and nine meta- to submetacentric and seven acrocentric autosomal pairs. The X chromosomes is a medium-sized metacentric.

Genetics

See Hoofer and Van Den Bussche (2003).

Habitat:

In southern Africa, it primarily occurs in Savanna habitats (86 %; Cooper-Bohannon *et al.*, 2016: Tabls S2). However, Marsden *et al.* (2023: 7) indicate that this species can inhabit cities, although they possess no obvious advantageous characteristics for urban life.

Diet:

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 62 minutes, and the digestibility rate about 82.4 %.

Predators:

Nyffeler and Knörnschild (2013: 4) refer to Happold *et al.* (1988: 369) for one of two records of an identified African bat becoming entangled in a spider's web (the other being *Neoromicia nana*).

Mikula *et al.* (2016: Supplemental data) and Malan *et al.* (2022: 167) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator.

Population:

Structure and Density

Rather common (Jacobs *et al.*, 2008b; IUCN, 2009).

Trend

2008: Unknown (Jacobs *et al.*, 2008b; IUCN, 2009).

Reproduction and Ontogeny:

van der Merwe and Rautenbach (1987: 41) reported that in *N. schlieffenii* spermatogenesis occurs over a 10-month period with the first signs of spermatozoa in the epididymides by the end of April. From the end of April until the beginning of September, they found spermatozoa in the epididymides. Copulation begins during June (early winter in Transvaal) and the females have spermatozoa in the uterine horns from then until the end of August (late winter) when ovulation occurs. *N. schlieffenii* is seasonally monoestrous and most of the births occur in November.

In Malawi, Happold and Happold (1990b: 567) reported births early in the wet season.

Garbino *et al.* (2021: Suppl.) mention that this species has more than one young per litter. van der Merwe and Rautenbach (1986: 48; 1990:

540) reported that "*Nycticeius schlieffeniii*" commonly gives birth to twins and occasionally even triplets. For 11 females, they found an average of 3.1 corpora lutea and 2.8 foetuses.

PARASITES:

HEMIPTERA

Cimicidae

Aphrania recta Ferris and Usinger, 1957 recorded 35 miles east of Kordofan, Sudan (Haeselbarth *et al.*, 1966: 11).

Szentiványi *et al.* (2022: 12) reported *Aphrania recta* Ferris and Usinger, 1957 from Mauritania.

DIPTERA

Nycteribiidae

Dick *et al.* (2023: 73) mentioned *Basilia (Basilia) ansifera* Theodor, 1956 has been found on *Nycticeinops schlieffenii*:

SYPHONAPTERA

Ischnopsyllidae

Lagaropsylla consularis Smit, 1957. Traditional host being Molossid Bats, but has been recorded from this taxa (Haeselbarth *et al.*, 1966: 1990). *Lagaropsylla idea* Smit, 1957, of which the primary host are molossids but recorded from this taxon (Haeselbarth *et al.*, 1966: 190).

Hastriter (2016: 18) reported the flea *Lagaropsylla idae* Smit, 1957 from a *N. schlieffenii* specimen from Majo Moto, Kenya.

VIRUSES:

Rhabdoviridae

Viljoen *et al.* (2023a: 1) reported the coding-complete sequence of a lyssavirus, provisionally designated Phala bat lyssavirus (PBLV) in a bat from South Africa.

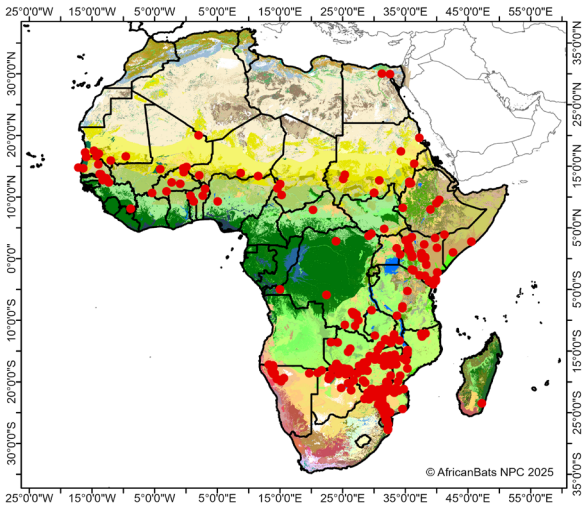

Figure 394. Distribution of *Nycticeinops schlieffenii*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:

"Africa", Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Côte d'Ivoire, Egypt, Eswatini, Ethiopia, Ghana, Guinea, Kenya, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Senegal, Somalia, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

†*Nycticeinops serengetiensis* Gunnell, Butler, Greenwood and Simmons, 2015

*2015. *Nycticeinops serengetiensis* Gunnell, Butler, Greenwood and Simmons, Am. Mus. Novit., 3846: 1, 17, figs 9C-H, 10. Publication date: 16 December 2015. - Etymology: Named for the famed Serengeti region in northern Tanzania where Olduvai Gorge is located (Gunnell *et al.* (2015a: 18).

SIMILAR SPECIES:

The teeth of *N. serengetiensis* are on average 20 % larger than those of *N. schlieffeni*.

PALAEONTOLOGICAL OR ARCHAEOLOGICAL RECORDS:

Timeframe:

Pleistocene (Brown *et al.*, 2019: Suppl.).

Genus ***Pseudoromicia*** Monadjem, Patterson, Webala and Demos, 2020

1872. *Vesperus:* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 263.

1878. *Vesperugo:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 183. Publication date: 15 June 1878. - Comments: In part. Not of Keyserling and Blasius, 1839 (see Monadjem *et al.*, 2020a: 1127, 1138).

1897. *Eptesicus:* Matschie, Arch. Naturg., 63 (1): 84. Publication date: October 1897. - Comments: In part. Not of Rafinesque, 1820 (see Monadjem *et al.*, 2020a: 1127).

1900. *Vespertilio:* Miller, Proc. Wash. Acad. Sci., 2: 649. Publication date: 28 December 1900. - Comments: Not of Linnaeus, 1758. Monadjem *et al.* (2020a: 1132) mentions it "in part", but Miller (1900: 649) only mentions one species.

1987. *Nycterikaupius* Menu, Palaeovert., 17 (3): 108, pl 4, fig 1. Publication date: 15 November 1987 [Goto Description]. - Comments: In part. The species assigned to this genus by Menu (1987: 109) are currently (sensu Monadjem *et al.*, 2020a: 1140) included in the genera *Laephotis, Neoromicia, Pipistrellus* and *Pseudoromicia*.

2002. *Neoromicia:* Kearney, Volleth, Contrafatto and Taylor, Acta Chiropt., 4 (1): 58. - Comments: In part. Not of Roberts, 1926 (see Monadjem *et al.*, 2020a: 1132).
*2020. *Pseudoromicia* Monadjem, Patterson, Webala and Demos, in: Monadjem et al., Zool. J. Linn. Soc., 191 (4): 1120, 1132. Publication date: 10 September 2020. - Etymology: From the Greek ψευδο, meaning false and the genus *Romicia* Gray, 1838, in turn derived from the Ancient Greek ρόμιξα, meaning a javelin or huntingspear (Monadjem *et al.*, 2020a: 1132).
2023. *Pseudoroemecia:* Dick, Verrett, Webala and Patterson, ZooKeys, 1169: 74. Publication date: 13 July 2023. (Lapsus).
? *Pseudoromicia sp. Tanzania*

TAXONOMY:
Currently (Simmons and Cirranello, 2023b) recognized species of *Pseudoromicia*: ***brunnea*** (Thomas, 1880); ***isabella*** (Decher, Hutterer and Monadjem, 2016); ***kityoi*** (Monadjem, Kerbis Peterhans, Nalikka, Waswa, Demos and Patterson, 2020); ***mbamminkom*** Grunwald, Demos, Nguéagni, Tchamba, Monadjem, Webala, Kerbis Peterhans, Patterson and Ruedas, 2023; ***nyanza*** (Monadjem, Patterson, Webala and Demos, 2020); ***principis*** Juste, Torrent, Méndez-Rodríguez, Howard, García-Mudarra, Nogueras and Ibáñez, 2023; ***rendalli*** (Thomas, 1889); ***roseveari*** (Monadjem, Richards, Taylor and Stoffberg, 2013); ***tenuipinnis*** (Peters, 1872).

MOLECULAR BIOLOGY:
Genetics
Cytogenetic data examined by Volleth *et al.* (2023c: 50) point to a closer relationship between *P. brunnea* and *P. tenuipinnis* compared to *P. rendalli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Tanzania.

Pseudoromicia brunnea (Thomas, 1880)

*1880. *Vesperugo (Vesperus) brunneus* Thomas, Ann. Mag. nat. Hist., ser 5, 6 (32): 165, 1 text-fig. Publication date: 1 August 1880. Type locality: Nigeria: Eastern region: Calabar [04 56 N 08 22 E]. Holotype: NHMUK 1880.7.21.7: ad ♀, skull and alcoholic. Collected by: Dr. A. Robb. Presented/Donated by: Dr. J.A. Smith. - Comments: Allen (1939a: 84), Grubb *et al.* (1998: 86) mentioned "Old Calabar, West Africa" as type locality.
1880. *Vesperugo brunneus:* Dobson, Report 50th Meeting British Association Advancement Science, 1880: 185. - Comments: (redescription of type). (Name Combination).
1939. *Eptesicus brunneus:* G.M. Allen, Bull. Mus. comp. Zool., 83: 84. (Name Combination).
1971. *Eptesicus [(Eptesicus)] brunneus:* Hayman and Hill, Mammals of Africa: Chiroptera, 44. (Name Combination).
1987. *Nycterikaupius brunneus:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination).
1987. *Pipistrellus (Neoromicia) brunneus:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).
1989. *P[ipistrellus] brunneus:* Koopman, Am. Mus. Novit., 2946: 10. - Comments: (This might be a lapsus, since Koopman used *Eptesicus brunneus* on page 7). (Name Combination, Lapsus).
1993. *Eptesicus (Neoromicia) brunneus:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 201. (Name Combination).
1995. *Pipistrellus brunneus:* Koopman, Kofron and Chapman, Am. Mus. Novit., 3148: 11. (Name Combination).
2003. *? (Hypsugo) brunneus:* Hoofer and Van Den Bussche, Acta Chiropt., 5 (Suppl): 38. (Name Combination).
2008. *N[eoromicia] brunnea:* Riccucci and Lanza, Hystrix, It. J. Mamm., (ns) 19 (2): 176. - Comments: Riccucci and Lanza (2008: 176) indicate that the genus *Neoromicia* is feminine, therefore the spelling of the species ending must also be feminine according to Art. 31.2 of the ICZN (1999). (Name Combination).
2013. *Neoromicia bruneus:* Juste, Benda, Garcia-Mudarra and Ibáñez, Zool. Scr., 42 (5): 455. Publication date: September 2013. (Lapsus).
2019. *L[aephotis] brunnea:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2020. *Laephotis brunneus:* Simmons and Cirranello, BatNames.org. (Current Combination).
2020. *Pseudoromicia brunnea:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Current Combination).
? *Neoromicia brunnea:* (Name Combination).
? *Neoromicia brunneus:* (Name Combination).

TAXONOMY:
Mentioned in the genus *Pipistrellus* by Koopman (1994: 117). Included (as "*(Hypsugo) brunneus*") in a separate, unnamed genus by Hoofer and Van Den Bussche (2003: 38).

Helbig *et al.* (2010: 168) suggest that *brunneus* needs to be transferred to a genus that needs to be newly created or resurrected from the current synonymy.

Riccucci and Lanza (2008) indicate that the genus *Neoromicia* is feminine, therefore the species name *brunneus* must be corrected into *brunnea*. This suffix change is still valid after its transfer to the genus *Pseudoromicia* by

Monadjem *et al.* (2020a: 1140) as a result of their analyses of cyt *b* sequences.

COMMON NAMES:
Czech: netopýr kalabarský. English: Brown Pipistrelle Bat, Dark-brown Pipistrelle Bat, Dark-brown Serotine. French: Sérotine brune d'Afrique, Sérotine brun-noire. German: Dunkelbraune Zwergfledermaus, Dunkelbraune Pipistrelle.

CONSERVATION STATUS:
Global Justification
Listed as Near Threatened (NT ver 3.1 (2001)) as its global population is suspected to have declined by ca 25% over the past 10 years (two generations) and will likely continue to decline at a similar rate over the next 5 years (one generation; generation length: 5 years) making it close to qualifying as threatened under criterion A4c. Its extent of occurrence (EOO), area of occupancy (AOO), and habitat is projected to continue to decline due to continuing threats from forest loss and degradation for agricultural use (Cooper-Bohannon and Fahr, 2020).

Assessment History
Global
2019: NT A4c ver 3.1 (2001) [assessed as "*Neoromicia brunnea*"] (Cooper-Bohannon and Fahr, 2020). 2008: NT ver 3.1 (2001) [assessed as "*Pipistrellus brunneus*"] (Fahr, 2008f; IUCN, 2009). 2004: NT ver 3.1 (2001) [assessed as "*Neoromicia brunneus*"] (Fahr, 2004k; IUCN, 2004). 1996: LR/nt [assessed as "*Eptesicus brunneus*"] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
This species is threatened by deforestation resulting from logging operations, and the conversion of its habitat to agricultural use (Fahr, 2008f; IUCN, 2009; Cooper-Bohannon and Fahr, 2020).

CONSERVATION ACTIONS:
Fahr (2008f) [in IUCN (2009)] there appear to be no conservation measures in place for this species. There is a need to establish and manage suitable protected areas for this species. Cooper-Bohannon and Fahr (2020) report that this species has been recorded from several protected areas including Tai and Comoe National Parks in Ivory Coast and East Nimba Nature Reserve in Liberia. However, due to its habitat specificity, there is a need to establish and manage further suitable protected areas for this species. There is a need for further research to better understand the species distribution and ecology (particularly roosting and foraging requirements) and to identify important areas for this species. Other research needs include: population size and trend data, ecology (i.e. diet, reproduction, roosting requirement) and significant threats (Cooper-Bohannon and Fahr, 2020).

GENERAL DISTRIBUTION:
Pseudoromicia brunnea is known from a few widespread localities in West and Central Africa. It ranges from Sierra Leone in the west, to Congo in the east. The distribution is believed to be patchy, as surveys have generally been unable to locate this species outside of its known range.

Native: Cameroon; Congo (Bates *et al.*, 2013: 325 - 1st authenticated record); Côte d'Ivoire; Equatorial Guinea (Bioko); Gabon; Ghana; Liberia; Nigeria; Sierra Leone.

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) present a line drawing of the tragi of specimen DNSM 13229 from Mount Nimba, Liberia.

DETAILED MORPHOLOGY:
Baculum
The basal lobes in the lateral view were broadest near the shaft base, tapering to a rounded end and were flattened at the bottom, giving them a 'shoe-like' appearance (Monadjem *et al.*, 2013c: 197). Line drawing of dorsal and ventral bacula of specimen DNSM 13229 from Mount Nimba, Liberia are shown in Monadjem *et al.* (2013c: 204).

MOLECULAR BIOLOGY:
Karyotype
McBee *et al.* (1987) reported 2*n*=36, FN=50, BA = 16, a submetacentric X chromosome and an acrocentric Y chromosome.

Volleth *et al.* (2023c: 41) reported 2*n*=36, FNa=50 and seven large to medium meta- to submetacentric, one small submetacentric, and nine small acrocentric autosomal pairs. The X chromosome is a medium-sized submetacentric and the Y chromosome a small bi-armed one;

GENETICS
See Hoofer and Van Den Bussche (2003).

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:



Figure 395. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1880.7.21.7, holotype of *Vesperugo* (*Vesperus*) *brunneus* Thomas, 1880.

HABITAT:
Monadjem *et al.* (2016y: 369) recorded this species from forested habitats between 400 and 520 m altitude in the Mount Nimba area.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 86 minutes, and the digestibility rate about 78.8 %.

POPULATION:
Structure and Density
Although there are limited data available on the global population for this species (Fahr, 2008f; IUCN, 2009), it is suspected to be declining, but currently not at a rate for it to be designated as threatened. It has a very wide distribution and probably occurs across the Upper Guinea region wherever forest patches remain. However, it is never caught in large numbers (usually in ones and twos) and it is not clear if this reflects its social organisation or reflects its population densities (Cooper-Bohannon and Fahr, 2020).

Trend
2019: Decreasing (Cooper-Bohannon and Fahr, 2020). 2008: Decreasing (Fahr, 2008f; IUCN, 2009).

PARASITES:
DIPTERA
Nycteribiidae
Tripselia echinata Theodor 1957 from Old Calabar, Nigeria (Haeselbarth *et al.*, 1966: 113).

VIRUSES:
Rhabdoviridae
Cameron *et al.* (2021: 2) reported a new rhabdovirus from a "*Neoromicia brunnea*" captured in the Republic of Congo.

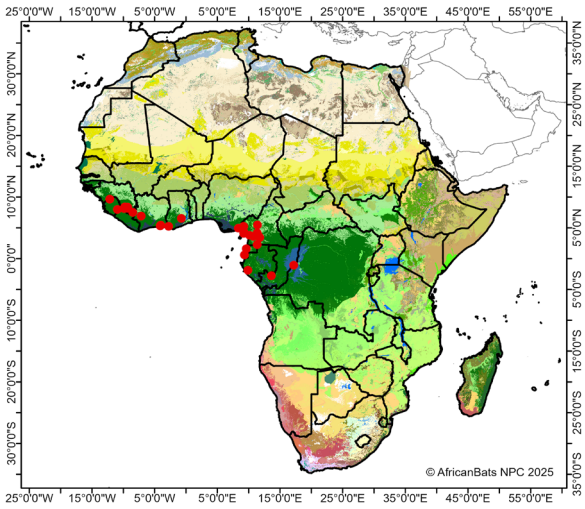

Figure 396. Distribution of *Pseudoromicia brunnea*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Liberia, Nigeria, Sierra Leone.

Pseudoromicia isabella (Decher, Hutterer and Monadjem, 2016)

2013. *Neoromicia cf. rendalli:* Monadjem, Richards, Taylor and Stoffberg, Zool. J. Linn. Soc., 167 (1): 194. Publication date: 18 January 2013. (Name Combination).

*2016. *Neoromicia isabella* Decher, Hutterer and Monadjem, in: Decher et al., Acta Chiropt., 17 (2): 260, 101967, figs 4,6,7B-C, 8 (for 2015). Publication date: 27 January 2016. Type locality: Guinea: Macenta Province: Simandou Range: Foko Confluence [08 29 48.62 N 08 54 48.22 W, 765 m]. Holotype: ZFMK MAM-2008.0292: ad ♂, skull and alcoholic. Collected by: Jan Decher; collection date: 7 March 2008; original number: JD 650. COI sequence GenBank nr. KT598187 (see Decher *et al.*, 2016: 267). Paratype: ZFMK MAM-2008.0291: ad ♀, alcoholic (skull not removed). Collected by: Jan Decher; collection date: 7 March 2008; original number: JD 647. - Etymology: "The species epithet refers (as a noun in apposition) to the 'Isabella' colouration (sensu Ridgeway, 1912) of the dorsal fur of this bat, and also recalls the name of Jan Decher's daughter Isabelle." (see Decher *et al.*, 2016: 267). - ZooBank: 5F782E04-64B5-40EA-8315-92A56DAE3EA8.

2019. *L[aephotis] isabella:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).

2020. *Pseudoromicia isabella:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Current Combination).
? *Neoromicia cf. rendalli SaSt-2013*

TAXONOMY:
Originally described in the genus *Neoromicia*, but transferred to *Laephotis* by Taylor (2019a: 283). However, based on cyt *b* sequence analyses, Monadjem *et al.* (2020a: 1125) transferred this species to the genus *Pseudoromicia*, although the indicate that the single sequence was on a long branch from the other species assigned to this genus.

COMMON NAMES:
English: Isabelline White-winged Serotine. German: Isabell-Weissflügel Serotine.

CONSERVATION STATUS:
Global Justification
This species is listed as Data Deficient (DD ver 3.1 (2001)) because this species so far is only known from two specimens in the Simandou Range of Guinea, and one specimen from Mount Nimba, Liberia, both areas threatened by iron ore mining (Decher *et al.*, 2017). There is inadequate information to make an assessment of risk of extinction based on distribution or population status (Decher *et al.*, 2017).

Assessment History
Global
2016: DD ver 3.1 (2001) (Decher *et al.*, 2017).

Regional
None known.

MAJOR THREATS:
This species is threatened by deforestation from conversion of its habitat to agricultural use and due to mining activities (Decher *et al.*, 2017).

CONSERVATION ACTIONS:
Decher *et al.* (2017) report that the single known Guinea locality is part of the Forêt Classée du Pic de Fon (Forest Reserve) but also inside an iron ore mining concession. The Liberia site is highly degraded, but is close to East Nimba Nature Reserve, where the species may also occur.

POPULATION:
There is not enough information about population abundance of this species (Decher *et al.*, 2017).

Trend:- 2016: Unknown (Decher *et al.*, 2017).

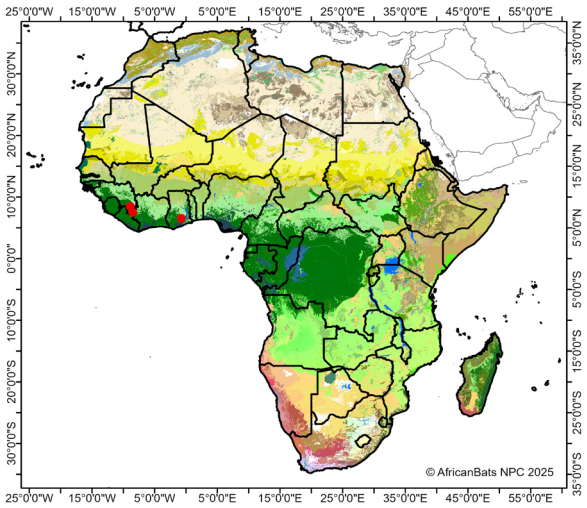

Figure 397. Distribution of *Pseudoromicia isabella*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Ghana, Guinea, Liberia.

Pseudoromicia kityoi Monadjem, Kerbis Peterhans, Nalikka, Waswa, Demos and Patterson, 2020

*2020. *Pseudoromicia kityoi* Monadjem, Kerbis Peterhans, Nalikka, Waswa, Demos and Patterson, in: Monadjem et al., Zool. J. Linn. Soc., 191 (4): 1120 1133, figs 5B, 9. Publication date: 10 September 2020. Type locality: Uganda: Central region: Mukono District: Mabira Forest Reserve, 0.79 km NE Nagojje Station [00 26 42 N 32 53 20 E, 1130 m]. Holotype: FMNH 223211: ad ♂, skull and alcoholic and tissue. Collected by: Betty Nalikka and Sadic Babyesiza Waswa; collection date: 19 October 2012; original number: JCK-7436. Paratype: FMNH 223555: ad ♂. Collected by: Julian C. Kerbis Peterhans; collection date: 19 October 2012; original number: JCK-7434. - Etymology: In honour of Dr. Robert M. Kityo, mammalogist, mentor and longserving curator at the Museum of Zoology, Makerere University, in recognition of his valuable contributions to bats and small mammal research in the region (see Monadjem *et al.*, 2020a: 1133). (Current Combination).

COMMON NAMES:
English: Kityo's serotine

CONSERVATION STATUS:
Monadjem *et al.* (2020a; 1136) suggest assigning "Data Deficient" status to this species.

GENERAL DISTRIBUTION:
Monadjem *et al.* (2020a: 1136) suggest that this species is also present in the Congo Basin forest patches in Uganda (e.g., Semliki, Kibale, Kashyoha-Kitomi) and Kenya (Kakamega),

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Uganda.

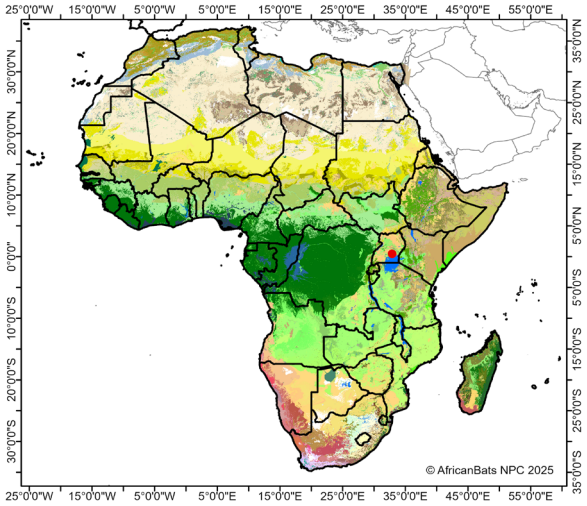

Figure 398. Distribution of *Pseudoromicia kityoi*.

Pseudoromicia mbamminkom Grunwald, Demos, Nguéagni, Tchamba, Monadjem, Webala, Kerbis Peterhans, Patterson and Ruedas, 2023

*2023. *Pseudoromicia mbamminkom* Grunwald, Demos, Nguéagni, Tchamba, Monadjem, Webala, Kerbis Peterhans, Patterson and Ruedas, Syst. Biod., 21 (1), 2156002: 6, 7, figs 7 - 13. Publication date: 18 January 2023. Type locality: Cameroon: Centre region: NW slope of Mount Mbam Minkom: near the village of Nkolakie (also spelled Nkolakié) [03 58 09 N 011 22 50 E, 785 m]. Holotype: FMNH 240714: ad ♀, skull and alcoholic. Collected by: Amanda L. Grunwald, Yvette Nguéagni and Luis A. Ruedas; collection date: 14 August 2019; original number: ALG 23. not pregnant nor lactating. - Etymology: A noun in apposition, referring to the type locality (Grunwald *et al.*, 2023: 7).

COMMON NAMES:
English: Mbam Minkom Serotine

CONSERVATION STATUS:
Grunwald *et al.* (2023: 14) suggest an IUCN status of "Data Deficient", but also indicate that "*P. mbamminkom* may be facing a higher risk of extinction in the wild than its IUCN designation of DD would suggest."

GENERAL DISTRIBUTION:
Only known from the type locality.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32 (Grunwald *et al.*, 2023: 9).

ECHOLOCATION:
From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 22 calls of 1 bat: F_{peak}: 41.6 ± 2.4 (36.0 - 42.9) kHz, F_{min}: 34.2 ± 0.8 (33.5 - 36.8) kHz, F_{max}: 58.4 ± 1.5 (55.6 - 68.4) kHz, duration: 2.5 ± 0.3 (2.0 - 2.9) ms.

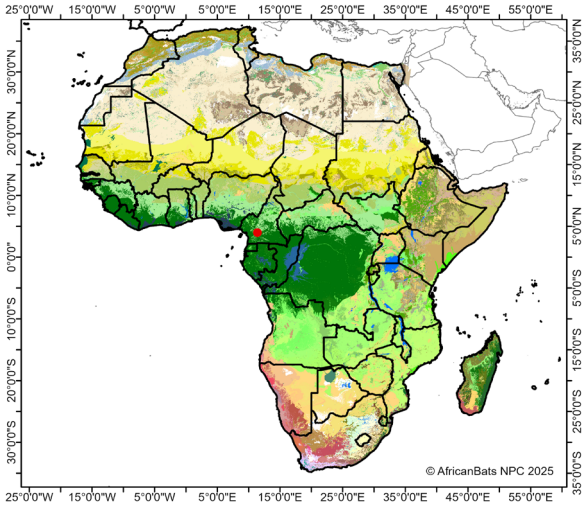

Figure 399. Distribution of *Pseudoromicia mbamminkom*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Cameroon.

Pseudoromicia nyanza Monadjem, Patterson, Webala and Demos, 2020

2012. *Neoromicia tenuipinnis:* Patterson and Webala, Field. Life Earth Sc., 6: 43. Publication date: 29 November 2012. - Comments: See Monadjem *et al.* (2020a: 1136), who also assigned the *tenuipinnis* specimens referred to by Musila *et al.* (2019b: 127) and Rydell *et al.* (2019: 150) to this species.

*2020. *Pseudoromicia nyanza* Monadjem, Patterson, Webala and Demos, in: Monadjem et al., Zool. J. Linn. Soc., 191 (4): 1120, 1136, figs 8B,10. Publication date: 10 September 2020. Type locality: Kenya: Kisumu county (formerly Nyanza province): Kisumu Impala Sanctuary, State Lodge Campsite [00 06 34 S 34 44 46 E, 1130 m]. Holotype: FMNH 215626: ad ♂, skull and alcoholic and tissue. Collected by: Bruce D. Patterson, Paul W. Webala and Carl W. Dick; collection date: 8 January 2021; original number: BDP-5719. Paratype: FMNH 215625: ♀. Collected by: Bruce D. Patterson; collection date: 8 January 2012; original number: BDP-5697. Paratype: FMNH 215627: ♀. Collected by: Bruce D. Patterson; collection date: 8 January 2012; original number: BDP_5721. Paratype: FMNH 215628: ♀. Collected by: Bruce D. Patterson; collection date: 8 January 2012; original number: BDP-5722. Paratype: FMNH 215629: ♀. Collected by: Bruce D. Patterson; collection date: 8 January 2012; original number: BDP-5723. - Etymology: The name refers to the region where it was found: former Nyanza province, which in turn is a Bantu word, meaning a large body of water (see Monadjem *et al.*, 2020a: 1137). (Current Combination).

2025. *Pseudoromlcia cf. nyanza:* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, Zool. J. Linn. Soc., 204 (2): 5, 7. Publication date: 13 June 2025. (Name Combination).

COMMON NAMES:
English: Nyanza serotine

CONSERVATION STATUS:
Monadjem *et al.* (2020a: 1138) suggest assigning this species to the "Least Concern" category.

GENERAL DISTRIBUTION:
Monadjem *et al.* (2020a: 1138) report it from western Kenya, and possibly eastern Uganda.

Benda *et al.* (2025: 99) mention that Monadjem *et al.* (2024) assigned 55 eastern African *Pseudoromicia tenuipinnis* specimens to *P. nyanza* This would result in *P. nyanza* being distributed from NW DRC, SW Ethiopia, central Kenya, N Tanzania, and W Burundi.

ECHOLOCATION:
The type specimen's echolocated calls had a peak frequency (start and end frequencies) of 40.4 kHz (56.4 - 39.3 kHz). The peak frequency of 16 other specimens from the type locality was 40.4 ± 0.84 (55.1 ± 7.91 to 39.5 ± 0.68) kHz (Monadjem *et al.*, 2020a: 1138).

PARASITES:
DIPTERA
Nycteribiidae
Dick *et al.* (2023: 74) found *Basilia (Basilia) robusta* Theodor, 1956 on *Pseudoromicia nyanza*:from Kisumu Impala Sanctuary (Kenya).

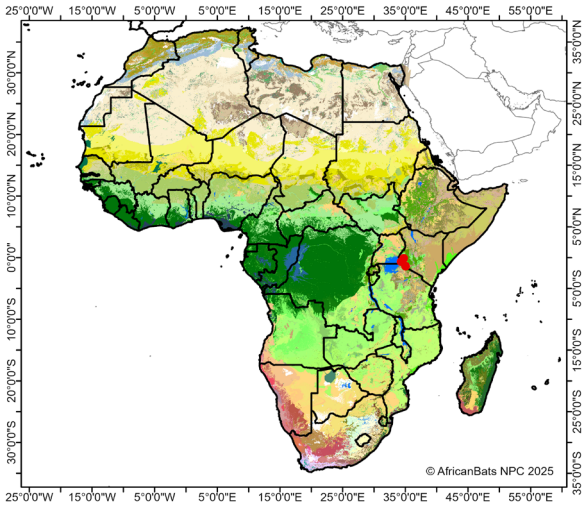

Figure 400. Distribution of *Pseudoromicia nyanza*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
Kenya.

Pseudoromicia principis Juste, Torrent, Méndez-Rodríguez, Howard, García-Mudarra, Nogueras and Ibáñez, 2023

*2023. *Pseudoromicia principis* Juste, Torrent, Méndez-Rodríguez, Howard, García-Mudarra, Nogueras and Ibáñez, J. Mamm., 104 (2): 365, 366, figs 3 - 5, 6A, 6Bc, 6Ce,6Dh, 7. Publication date: 11 January 2023. Type locality: São Tomé and Príncipe: Santo António: Río Papagaio [01 40 00 N 07 25 00 E, 0 m]. Holotype: EBD 17475M: ad ♀, skin and skeleton and skull. Collected by: Carlos J. Ibáñez Uargui and Javier Juste; collection date: 26 March 1988; original number: B6718. Paratype: EBD 17358M: sad ♂, skull and alcoholic. Collected by: Carlos J. Ibáñez Uargui and Javier Juste; collection date: 30 March 1988. Paratype: EBD 29604M: ad ♀, skull and alcoholic. Collection date: 3 November 1992. Paratype: EBD 29605M: ad ♀, skull and alcoholic. Collection date: 3 November 1992. Paratype: EBD 29606M: ad ♀, skull and alcoholic. Collection date: 12 November 1992. Paratype: EBD 29607M: ad ♂, skull and alcoholic. Collection date: 12 November 1992. - Etymology: In reference to the island where the type locality is situated (see Juste *et al.*, 2023: 9).

COMMON NAMES:
English: Principe's Pipistrelle

CONSERVATION STATUS:
Juste *et al.* (2023: 9) suggest to list this species as "Data Deficient" since hardly anything is known about its ecological requirements.

GENERAL DISTRIBUTION:
This species is restricted to the island of Príncipe in the Gulf of Guinea.

DENTAL FORMULA:
The permanent dental formula is as follows: $I^2/_3$, $C^1/_1$, $PM^1/_2$, $M^3/_3$ = 32 (Juste *et al.*, 2023: 7).

DETAILED MORPHOLOGY:
Juste *et al.* (2023: 9) indicate that *P. principis* is the smallest member of the genus, with skull dimensions not overlapping with any other *Pseudoromicia* species.

ECHOLOCATION:
Forty calls analysed by Juste *et al.* (2023: 8) had the following characteristics: F_{start}: 55.47 ± 8.43 (44.75 - 74.05) kHz; F_{end} : 44.71 ± 1.44 (41.92 - 47.83) kHz; F_{peak}: 45.69 ± 1.26 (43.9 - 48.3) kHz; Duration: 5.82 ± 1.39 (5.32 - 9.41) ms; Inter-pulse interval: 90.55 ± 8.89 (72 - 114.7) ms.

HABITAT:
Palmeirim *et al.* (2025: 6, 9) indicated that *Pseudoromicia principis* is an edge forager, which they found in all of the land-use cover types they sampled (old-regrowth forests, secondary regrowth forests, agricultural areas and urban/bare soil areas).

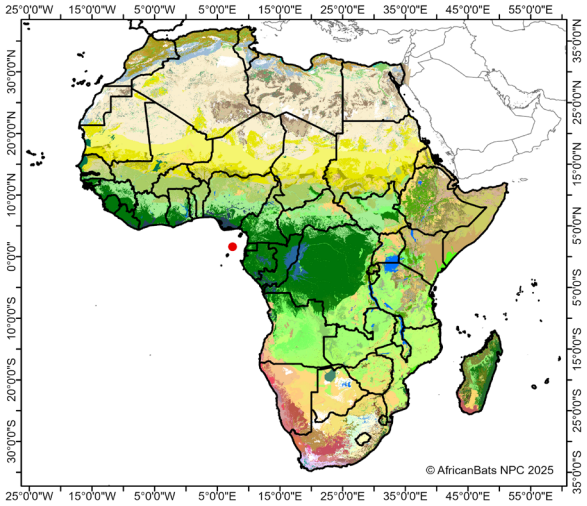

Figure 401. Distribution of *Pseudoromicia principis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
São Tomé and Príncipe.

Pseudoromicia rendalli (Thomas, 1889)

*1889. *Vesperugo (Vesperus) Rendalli* Thomas, Ann. Mag. nat. Hist., ser 6, 3 (16): 362, fig 1. Publication date: 1 April 1889. Type locality: The Gambia: Bathurst [=Banjul] [13 28 N 16 39 W]. [Goto Description]. Holotype: NHMUK 1889.3.2.3: ad ♂, skull and alcoholic. Collected by: Dr. Percy John Rendall. See Thomas (1889: 26-7). - Etymology: In honour of Dr. Percy Rendall (1861 - 1948), an English zoologist and the collector of the type specimen (see Thomas, 1889: 364; Smithers, 1983: 102; Taylor, 2005; Lanza *et al.*, 2015: 428).

1897. *Vesperugo (Eptesicus) rendalli:* Thomas, Proc. zool. Soc. Lond., 1896, IV: 791. Publication date: April 1897. (Name Combination).

1899. *Vesperugo Rendalli:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc VI: 1280. (Name Combination).

1911. *Eptesicus phasma* G.M. Allen, Bull. Mus. comp. Zool., 54 (6): 327. Publication date: December 1911. Type locality: Kenya: Northern Guaso Nyiro: Meru River: effluent of northern Guaso Nyiro [=Ewaso Ngiro] [00 03 N 37 39 E]. [Goto Description]. Holotype: MCZ 8279: ad ♂, skin and skull. Collected by: Glover Morrill Allen; collection date: 6 August 1909; original number: 94. See Allen (1911: 327). - Comments: Coordinates of the type locality mentioned as 00 31 N 37 40 E by Thorn *et al.* (2009: 56). The MCZ also has a small series of paratypes (see Helgen and McFadden, 2001: 14).

1917. *Eptesicus faradjius* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 444. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 49045: ad ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 21 February 1911; original number: 1914. Topotype: AMNH 49044: ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49048: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49049: ♀, skin only. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49051: ♂, skin only. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49052: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49053: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49054: ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. Topotype: AMNH 49055: ♀, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition. - Comments: The museum label mentions 1414 as original number.

1926. *Eptesicus rendalli:* Cabrera and Ruxton, Ann. Mag. nat. Hist., ser 9, 17 (103): ???. Publication date: 1 May 1926. (Name Combination).

1953. *Eptesicus (Eptesicus) rendalli:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1965. *E[ptesicus rendalli] phasma:* Koopman, Am. Mus. Novit., 2219: 14. (Name Combination).

1965. *Eptesicus rendalli faradjius:* Koopman, Am. Mus. Novit., 2219: 14. (Name Combination).

1968. *Eptesicus rendalli phasma:* Funaioli and Lanza, Mon. Zool. ital., (NS) 2 (Suppl): 200. (Name Combination).

1975. *E[ptesicus (Eptesicus)] r[endalli] phasma:* Koopman, Bull. Am. Mus. Nat. Hist., 154 (4): 409. (Name Combination).

1984. *Eptesicus (Eptesicus) rendalli phasma:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1984. *Eptesicus (Eptesicus) rendalli rendalli:* Anciaux de Faveaux, Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. (Name Combination).
1987. *Nycterikaupius rendalli:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination).
1987. *Pipistrellus (Neoromicia) rendalli:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).
1992. *Eptesicus rendallii:* Rautenbach and Fenton, Z. Säugetierk., 57: 113. (Lapsus).
1993. *Eptesicus (Neoromicia) rendalli:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 203. (Name Combination).
1994. *E[ptesicus (Neoromicia)] r[endalli] phasma:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).
1994. *E[ptesicus (Neoromicia)] r[endalli] rendalli:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).
1995. *Pipistrellus rendalli:* Koopman, Kofron and Chapman, Am. Mus. Novit., 3148: 11. (Name Combination).
2002. *Neoromicia rendalli:* Kearney, Volleth, Contrafatto and Taylor, Acta Chiropt., 4 (1): 58. (Name Combination).
2002. *Pipistrellus r[endalli] phasma:* Kock, Barnett, Fahr and Emms, Acta Chiropt., 4 (1): ???. (Name Combination).
2003. *? (Hypsugo) rendalli:* Hoofer and Van Den Bussche, Acta Chiropt., 5 (Suppl): 38. (Name Combination).
2008. *Vesperus hösemanni* Turni and Kock, Zootaxa, 1869: 82. - Comments: Turni and Kock (2008: 82) mention this name as a label name, introduced by Matschie, on ZMB 10096 from Tanzania, Lake Tanganyika, Ujiji, an adult male, skull and alcoholic, and tentatively linked it to "*Neoromicia* cf. *tenuipinnis*". Since this name has not been published before, Turni and Kock should be considered the authors. Monadjem *et al.* (2010d: 477) considered it a synonym of "*Neoromicia rendalli*".
2017. *Neromicia cf. rendalli:* Reardon and Schoeman, Acta Chiropt., 19 (2): Suppl. Publication date: December 2017. (Lapsus).
2019. *L[aephotis] rendalli:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).
2020. *Pseudoromicia rendalli:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Current Combination).
? *Neoromicia rendalli faradjius:* (Name Combination).
? *Neoromicia rendalli phasma:* (Name Combination).
? *Neoromicia rendalli rendalli:* (Name Combination).
? *Neoromicia rueppellii:* (Alternate Spelling).
? *Pipistrellus (Neoromicia) rendalli rendalli:* (Name Combination).

TAXONOMY:



Figure 402. *Pseudoromicia rendallii* (ECJS-44/2009), caught at Chitabe, Okavango, Botswana.

Mentioned in the genus *Pipistrellus* by Koopman (1994: 117). Volleth *et al.* (2001: 44) assigned this species to the genus *Neoromicia*. Reviewed by Kock *et al.* (2002b: 89). Included (as (*Hypsugo*) *rendalli*) in a separate, unnamed genus by Hoofer and Van Den Bussche (2003: 38).

Helbig *et al.* (2010: 168) suggest that *rendalli* needs to be transferred to a genus that needs to be newly created or resurrected from the current synonymy. The species was transferred to the genus *Leaphotis* by Taylor (2019a: 283), but subsequently transferred again to *Pseudoromicia* by Monadjem *et al.* (2020a: 1132) based on analyses of cyt-*b* sequences.

COMMON NAMES:

Afrikaans: Rendall se dakvlermuis, Rendal-dakvlermuis. Chinese: 任氏伏翼. Czech: netopýr Rendallův. English: Rendall's Serotine, Rendall's Serotine Bat, Rendall's Pipistrelle Bat, Rendall's Pipistrelle. French: Serotine de Rendall, Pipistrelle de Rendall. German: Rendalls Zwergfledermaus, Rendalls Pipistrelle. Italian: Pipistrèllo di Rèndall. Portuguese: Morcego caseiro de Rendall.

CONSERVATION STATUS:

Global Justification

Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Jacobs *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017ct).

Assessment History

Global

2016: LC ver 3.1 (2001) [assessed as "*Neoromicia rendalli*"] (Monadjem *et al.*, 2017ct). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus rendalli*"] (Jacobs *et al.*, 2008w; IUCN, 2009). 2004: LC ver 3.1 (2001) (Jacobs *et*

al., 2004ad; IUCN, 2004). 1996: LR/lc (Baillie and Groombridge, 1996).

Regional
South Africa: 2016: LC ver 3.1 (2001) (Monadjem *et al.*, 2016ab). 2004: CR B2ab(iii) ver 3.1 (2001) (Friedmann and Daly, 2004).

MAJOR THREATS:
In general, there appear to be no major threats to this species. In some parts of its range, this species is threatened by the conversion of its habitat to agricultural use (Jacobs *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017ct).

CONSERVATION ACTIONS:
Jacobs *et al.* (2008w) [in IUCN (2009)] and Monadjem *et al.* (2017ct) report that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas. Further research is needed into the distribution of this patchily recorded species.

GENERAL DISTRIBUTION:
Pseudoromicia rendalli has been widely, but patchily, recorded over much of sub-Saharan Africa. It ranges from Senegal in the west, through West and Central Africa to Somalia in the east, and as far south as eastern South Africa.

Native: Benin (Capo-Chichi *et al.*, 2004: 163); Botswana (Archer, 1975; Monadjem *et al.*, 2010d: 569); Burkina Faso (Kangoyé *et al.*, 2012: 6026; 2015a: 621); Cameroon; Central African Republic; Chad; Congo; Congo (The Democratic Republic of the) (Hayman *et al.*, 1966; Gallagher and Harrison, 1977; Monadjem *et al.*, 2010d: 569); Gambia; Ghana; Kenya; Liberia (Fahr, 2007a: 104); Malawi (Happold *et al.*, 1988; Monadjem *et al.*, 2010d: 569); Mali (Meinig, 2000: 105); Mozambique (Smithers and Lobão Tello, 1976; Monadjem *et al.*, 2010d: 569; Monadjem *et al.*, 2010c: 384); Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; South Africa [KwaZulu Natal] (Kearney and Taylor, 1997: 54; Monadjem *et al.*, 2010d: 569); Sudan; Tanzania; Togo; Uganda; Zambia (Ansell, 1969; Ansell, 1974; Cotterill, 2004a: 261; Monadjem *et al.*, 2010d: 569); Zimbabwe (Monadjem *et al.*, 2010d: 569).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) line drawing of tragi of specimen DNSM 12619 referred to as "*L[aephotis] cf. rendalli*" from Mount Nimba, Liberia.

GENERAL DESCRIPTION OF CRANIAL AND DENTAL MORPHOLOGY:

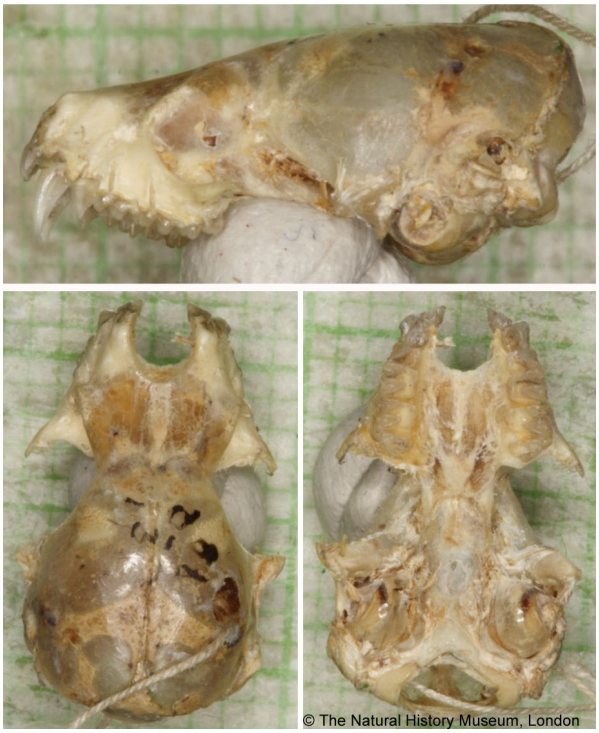

Figure 403. Clockwise from top lateral, ventral and dorsal skull images of NHMUK 1889.3.2.3, holotype of *Vesperugo* (*Vesperus*) *rendalli* Thomas, 1889.

In their study on the reversibility of the mandibular symphyseal fusion, Scott *et al.* (2012: 2943) report that this symphysis is unfused, with smooth surfaces.

DETAILED MORPHOLOGY:
Baculum
Hill and Harrison (1987) and Kearney *et al.* (2002). The baculum of *L[aephotis]* cf. *rendalli* was longer in total length (2.97 mm). The angle of shaft curvature, measured from mid-shaft to the shaft base, was more acute in *N. tenuipinnis* (43°) than in *L.* cf. *rendalli* (58°) (Monadjem *et al.*, 2013c: 197). Line drawing of the dorsal and ventral view of the baculum of specimen DNSM 12619 from Mount Nimba, Liberia referred to as *N.* cf. *rendalli* are shown in Monadjem *et al.* (2013c: 204).

Brain
Amrein *et al.* (2007), from specimens collected from Benin, reported that proliferating cells, detected with Ki-67 and MCM2, in the subgranular layer of the dentate gyrus was found to be absent. Amrein *et al.* (2007) also reported moderate to ample proliferating cells (Ki-67 positive cells) and migrating young neurons (DCX positive cells) in the rostral migratory stream. Amrein *et al.* (2007) furthermore detected few DCX positive cells in the rostral migratory stream and the olfactory bulb.

ECHOLOCATION:
Musila *et al.* (2018c: 43) [referring to Van Cakenberghe and Happold (2013p: 646)] mention a starting frequency of up to 76 kHz and an ending frequency of 42 - 44 kHz.

Roemer *et al.* (2021: Suppl.) categorized the bat's call as a FMd-QCF (Frequency modulation downward - quasi-constant frequency) sonotype [as "*Neoromicia rendalli*"].

MOLECULAR BIOLOGY:
Karyotype
McBee *et al.* (1987), Rautenbach and Fenton (1992) and Kearney *et al.* (2002) all recorded 2*n* = 38, FN = 50, BA = 14, and a submetacentic X chromosome. Rautenbach and Fenton (1992) and Kearney *et al.* (2002) also recorded an acrocentric Y chromosome. GTG-bands identified three Robertsonian fusion chromosomes (7/11, 8/9, 10,12), considered as distinguishing characters for the genus *Neoromicia* Kearney *et al.* (2002).
In Senegal, Koubínová *et al.* (2013: 3) found a very similar karyotype, although they mention the Y chromosome as dot-like and presumably acrocentric.

Genetics
See Hoofer and Van Den Bussche (2003).

ROOST:
In Malawi, Happold and Happold (2023: 160) reported these bats to roost in the fronds of *Hyphaene* palms and in a cotton plant, but in the DRC they were also found in the dense foliage of low bushes and trees, and in huts and houses, where they have been found in groups of up to six animals.

DIET:
Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time for these bats to be about 70 minutes, and the digestibility rate about 81.0 %.

POPULATION:
Structure and Density
This appears to be a locally rare species, usually occurring as moderately small colonies of several individuals up to a few dozen animals (Jacobs *et al.*, 2008w; IUCN, 2009; Monadjem *et al.*, 2017ct).

Trend
2016: Unknown (Monadjem *et al.*, 2017ct). 2008: Unknown (Jacobs *et al.*, 2008w; IUCN, 2009).

REPRODUCTION AND ONTOGENY:
Garbino *et al.* (2021: Suppl.) report this species as being polytocous (more than one young per litter).

PARASITES:
ARACHNIDA
Spinturnicidae
Orlova *et al.* (2024: 152) mentioned this species as host for *Spinturnix faini* Benoit, 1959.

DIPTERA
Nycteribiidae
Basilia ansifera Theodor, 1956 mainly a West African species, reaching Lake Victoria in the east and Lake Nyasa in the south, nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110). *Basilia bouvieri* (Falcoz, 1924) from Tanzania, Sudan, Senegal and Sierra Leone (Haeselbarth *et al.*, 1966: 111, host referred to as "*Eptesicus phasma*") (see also Dick *et al.*, 2023)..

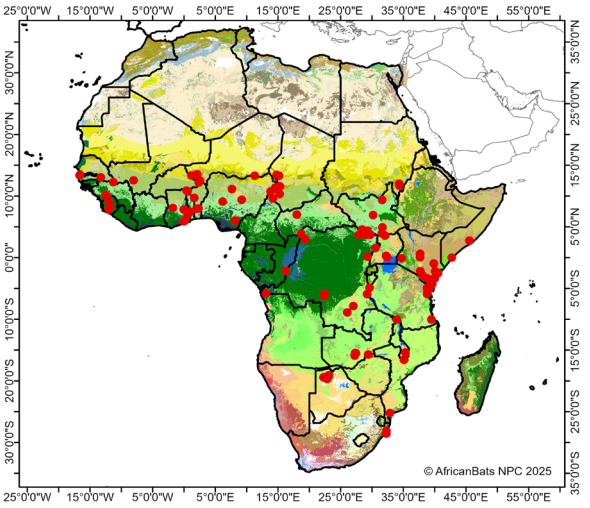

Figure 404. Distribution of *Pseudoromicia rendalli*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS:
"Africa", Benin, Botswana, Cameroon, Central African Republic, Chad, Congo (Democratic Republic of the), Ghana, Guinea, Kenya, Malawi, Mali, Mozambique, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, The Gambia, Togo, Uganda, Zambia, Zimbabwe.

Pseudoromicia roseveari (Monadjem, Richards, Taylor and Stoffberg, 2013)

*2013. *Neoromicia roseveari* Monadjem, Richards, Taylor and Stoffberg, Zool. J. Linn. Soc., 167 (1): 191, 197, figs 4 - 7. Publication date: 18 January 2013. Type locality: Liberia: Nimba province: Yiti River [07 29 N 08 35 W]. Holotype: DNSM 12617: ad ♂, skull and alcoholic. Collected by: Dr. Ara Monadjem; collection date: 23 December 2010; original number: AM2010_12_23_1. Paratype: DNSM 13226: ad ♂. Collected by: Dr. Ara

Monadjem; collection date: 23 December 2011; original number: AM2011_12_23_03. - Etymology: In honour of Donovan Reginald Rosevear who made a significant contribution to West African bat research in the 20th century, culminating in his book 'The bats of West Africa' (see Monadjem *et al.*, 2013c: 201).

2019. *L[aephotis] roseveari:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).

2020. *Pseudoromicia roseveari:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1123. Publication date: 10 September 2020. (Current Combination).

TAXONOMY:

In the original description, Monadjem *et al.* (2013c) distinguish "*Neoromicia roseveari*" from other similar taxa on molecular grounds, craniodental morphology, and baculum structure.

The species was transferred to the genus *Laephotis* by Taylor (2019a: 283), but Monadjem *et al.* (2020a: 1132) moved it to the genus *Pseudoromicia* based on the results of their cyt *b* sequence analyses.

COMMON NAMES:

German: Rosevears Zwergfledermaus.

CONSERVATION STATUS:

Global Justification

Monadjem (2017e) listed as Endangered (EN B1ab(i,ii,iii)+2ab(i,ii,iii)) because, as currently known, it has an extent of occurrence (EOO) less than 5,000 km^2 and an area of occupancy (AOO) of less than 500 km^2, it is only known from just two populations (estimated to represent two locations), and both populations are under increasing threat of deforestation through logging, mining and slash-and-burn agriculture.

Assessment History

Global

2016: EN B1ab(i,ii,iii)+2ab(i,ii,iii) ver 3.1 (2001) [assessed as *Neoromicia roseveari*] (Monadjem, 2017e).

Regional

None known.

MAJOR THREATS:

The only two populations known are under increasing threat of deforestation through logging, mining and slash-and-burn agriculture (Monadjem, 2017e). This is also the case for the Cameroonian population (Grunwald *et al.*, 2025: 304).

CONSERVATION ACTIONS:

Monadjem (2017e) report that there are currently no known conservation actions for this species. It occurs in the East Nimba Nature Reserve. Ensuring the long-term protection of this reserve may be critical to the survival of this species since the Simandou Range currently has no protected areas and furthermore is being developed for mining.

GENERAL DISTRIBUTION:

Native: Cameroon (1st record: Grunwald *et al.*, 2025: 281); Côte d'Ivoire; Guinea (Decher *et al.*, 2016: 273), Liberia

ECHOLOCATION:

From the Mbam Minkom Massif (Cameroon), Werb *et al.* (2024: 287) reported the following for 20 calls of 2 bats: F_{peak}: 39.9 ± 2.6 (35.7 - 55.3) kHz, F_{min}: 37.9 ± 1.2 (34.8 - 38.8) kHz, F_{max}: 53.1 ± 6.1 (41.2 - 72.8) kHz, duration: 2.0 ± 0.3 (1.6 - 2.4) ms.

HABITAT:

This species has only been recorded in forested habitats at the base of Mount Nimba (Monadjem *et al.*, 2016y: 370). In Cameroon it was captured in intact or minimally disturbed forest (Grunwald *et al.*, 2025: 304).

POPULATION:

Structure and Density

Monadjem (2017e) report that just six specimens of this bat have ever been collected making it impossible to define the size of its population. At Mt Nimba, Liberia, four specimens were collected alongside 11 individuals of the closely related *Pseudoromicia brunnea*.

Trend

2016: Unknown (Monadjem, 2017e).

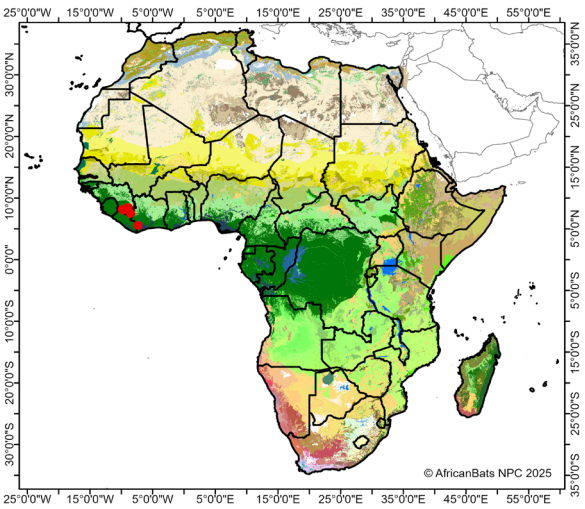

Figure 405. Distribution of *Pseudoromicia roseveari*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: Côte d'Ivoire, Guinea, Liberia.

Pseudoromicia tenuipinnis (Peters, 1872)

*1872. *Vesperus tenuipinnis* Peters, Monatsb. k. preuss. Akad. Wiss. Berlin, 263. Publication date: 1872. Type locality: Guinea: "Guinea". [Goto Description]. Holotype: ZMB 4096: ad ♀. Presented/Donated by: Schlegel. See Turni and Kock (2008), who report it as missing. Neotype: DNSM 13235: ad ♂, skull and alcoholic. Collected by: Dr. Ara Monadjem; collection date: 7 January 2012. Neotype designated by Decher *et al.* (2016: 270). Locality: Liberia: base of Mount Nimba: near Yekepa. - Comments: The publication covers a meeting held on 18 April 1872. Kock (1969a: 162) indicated that the type locality quoted by Ellerman *et al.* (1953: 77, Kuilu River, Congo [B]) is an unjustified assumption. - Etymology: From the feminine scientific Latin adjective *tenuipìnnis*, meaning "slender-winged", made up of the Latin adjective *tènuis*, meaning "slender" and the Latin substantive *pìnna*, meaning "wing": the adjective refers to the slender shape of the wings (see Lanza *et al.*, 2015: 455).

1878. *Vesperugo (Vesperus) tenuipinnis:* Dobson, Catalogue of the Chiroptera of the collection of the British Museum, 200. Publication date: 15 June 1878. (Name Combination).

1889. *Vesperus bicolor* Bocage, J. Sci. mat. phys. nat., ser 2, 1 (1): 5. Publication date: March 1889. Type locality: Angola: Caconda [13 42 S 15 05 E, 1 900 m]. [Goto Description]. Syntype: NHMUK 1889.5.1.3: ad ♂, skull and alcoholic. Collected by: José Alberto de Oliveira Anchieta. Syntype: NHMUK 1889.5.1.5: ad ♂. - Comments: Bocage (1889a: 6) mentions 2 ♀♀ specimens.

1889. *Vesperus tenuipennis:* Noack, Zool. Jb. Syst., 4: 215, 239, 261. (Lapsus).

1897. *Eptesicus tenuipinnis:* Matschie, Arch. Naturgesch. Berlin, 63 (1): 84. (Name Combination).

1897. *Vesperugo (Vesperus) bicolor:* Trouessart, Catalogus Mammalium tam viventium quam fossilium, fasc I: 110.

1900. *Vespertilio tenuipennis:* Miller, Proc. Wash. Acad. Sci., 2: 649. Publication date: 28 December 1900. (Lapsus).

1916. *E[ptesicus] bicolor:* Wettstein, Anz. kais. Akad. Wiss., Wien, 53: 201.

1917. *Eptesicus ater* J.A. Allen, Bull. Am. Mus. Nat. Hist., 37 (18): 443. Publication date: 29 September 1917. Type locality: Congo (Democratic Republic of the): Oriental province: Uele district: Faradje [03 44 N 29 43 E]. [Goto Description]. Holotype: AMNH 48988: ad ♂, skin and skull. Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition; collection date: 1 March 1911; original number: 1466. Topotype: AMNH 49423: alcoholic (skull not removed). Collected by: Herbert Lang, James Paul Chapin and The American Museum Congo Expedition.

1923. *Eptesicus tenuipennis:* Kershaw, Rev. Zool. afr., 11 (4): 358. (Lapsus).

1935. *Pipistrellus bicolor:* Monard, Arq. Mus. Bocage, 6: 31.

1936. *Eptesicus bicolor:* St. Leger, Novit. Zool., 40: 79.

1950. *Eptesicus tenuipinnis ater:* Sanborn, Publ. Cult. Comp. Diamantes Angola, Lisboa, 10: ???. (Name Combination).

1952. *Eptesicus tennuipinnis:* Cozens and Marchant, Niger. Fld. , 17 (3): 127. (Lapsus).

1953. *Eptesicus (Eptesicus) bicolor:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77.

1953. *Eptesicus (Eptesicus) tenuipinnis ater:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1953. *Eptesicus (Eptesicus) tenuipinnis tenuipinnis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1953. *Eptesicus (Eptesicus) tenuipinnis:* Ellerman, Morrison-Scott and Hayman, Southern African mammals 1758 to 1951, 77. (Name Combination).

1956. *Ephesicus tenuipinnis:* Theodor, Parasitology, 46: ???. (Lapsus).

1956. *Eptesicus tenuipinnis tenuipinnis:* Eisentraut, Zool. Jb. Syst., 84 (3): 531. (Name Combination).

1987. *Nycterikaupius tenuipinnis:* Menu, Palaeovert., 17 (3): 109. Publication date: 15 November 1987. (Name Combination).

1987. *Pipistrellus (Neoromicia) tenuipinnis:* Hill and Harrison, Bull. Br. Mus. (nat. Hist.) Zool., 52 (7): 282. (Name Combination).

1992. *Pipistrellus tenuipinnis:* Duckworth and Timmins, The bats of Nechisar National Park, 36. (Name Combination).

1993. *Eptesicus (Neoromicia) tenuipinnis:* Koopman, in: Wilson and Reeder, Mammal species of the World (2nd Edition): Chiroptera, 218. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] t[enuipinnis] ater:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1994. *P[ipistrellus (Neoromicia)] t[enuipinnis] tenuipinnis:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 117. (Name Combination).

1994. *P[ipistrellus (Pipistrellus)] bicolor:* Koopman, in: Niethammer, Schliemann and Starck, Handbook of Zoology, volume II (Mammalia) Chiroptera, (60) 114.

2002. *Eptesicus tennnuipinnis:* Fenton and Bogdanowicz, Can. J. Zool., 80: 1008. (Lapsus).

2002. *Eptesicus tenuippinis:* Fenton and Bogdanowicz, Can. J. Zool., 80: 1013. (Lapsus).

2006. *Neoromicia tenuipinnis:* Van Cakenberghe, Kearney and Seamark, African Chiroptera Project, Pretoria, 140 - 142. (Name Combination).

2019. *L[aephotis] tenuipinnis:* M. Taylor, Bats: An illustrated guide to all species, 283. Publication date: 11 April 2019. (Name Combination).

2019. *Laephotis tenuipinnis:* M. Taylor, Bats: An illustrated guide to all species, 284. Publication date: 11 April 2019. (Name Combination).

2020. *Pseudoromicia tenuipinnis:* Monadjem, Demos, Dalton, Webala, Musila, Kerbis Peterhans and Patterson, Zool. J. Linn. Soc., 191 (4): 1132. Publication date: 10 September 2020. (Current Combination).

2023. *Pseudoroemecia tenuipinnis:* Dick, Verreth, Webala and Patterson, ZooKeys, 1169: 74. Publication date: 13 July 2023. (Lapsus).

2025. *Pseudoromicia cf. tenuipinnis:* Torrent, Juste, Garin, Aihartza, Dalton, Mamba, Tanshi, Powell, Padidar, Garcia Mudarra, Richards and Monadjem, Zool. J. Linn. Soc., 204 (2):5, 7. Publication date: 13 June 2025. (Name Combination).

? *Neoromicia tenuipinnis ater:* (Name Combination).
? *Neoromicia tenuipinnis tenuipinnis:* (Name Combination).

GENERAL COMMENTS:
Bocage (1889a: 6) mentions two female specimens only.

TAXONOMY:
Eptesicus bicolor was tentatively included here by Hayman and Hill (1971: 43), but this may be an older name for *Pipistrellus anchietai*; see Koopman (1975: 404). Koopman (1994: 117) mentions this species in the genus *Pipistrellus*.

Helbig *et al.* (2010: 168) suggest that *tenuipinnis* needs to be transferred to a genus that needs to be newly created or resurrected from the current synonymy.

The species was transferred to the genus *Laephotis* by Welch *et al.* (2018: 283), but based on cyt-*b* sequence analyses was transferred once again by Monadjem *et al.* (2020a: 1132) to the genus *Pseudoromicia*.

COMMON NAMES:
Castilian (Spain): Murciélago. Chinese: 白翼伏翼. Czech: netopýr běloblanný. English: Slender-winged Pipistrelle Bat, White-winged Pipistrelle Bat, White-winged Serotine, White-winged Bat. French: Sérotine à ailes blanches, Pipistrelle à ailes blanches. German: Weißflügel-Zwergfledermaus, Weißflügel Pipistrelle, Weissfluegel-Hausfledermaus. Italian: Pipistrèllo di Peters. Tshokwe (Angola): Kafukufuku, Kateta.

CONSERVATION STATUS:
Global Justification
Listed as Least Concern (LC ver 3.1 (2001)) in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (Fahr, 2008a; IUCN, 2009; Monadjem and Fahr, 2017f).

Assessment History
Global
2016: LC ver 3.1 (2001) [assessed as *Neoromicia tenuipinnis*] (Monadjem and Fahr, 2017f). 2008: LC ver 3.1 (2001) [assessed as "*Pipistrellus tenuipinnis*"] (Fahr, 2008a; IUCN, 2009). 2004: LC ver 3.1 (2001) (Fahr, 2004j; IUCN, 2004). 1996: LR/lc [assessed as "*Eptesicus tenuipinnis*"] (Baillie and Groombridge, 1996).

Regional
None known.

MAJOR THREATS:
There appear to be no major threats to this species as a whole (Fahr, 2008a; IUCN, 2009; Monadjem and Fahr, 2017f).

CONSERVATION ACTIONS:
Fahr (2008a) [in IUCN (2009)] and Monadjem and Fahr (2017f) reports that there appear to be no direct conservation measures in place. It is not known if the species is present in any protected areas.

GENERAL DISTRIBUTION:
Pseudoromicia tenuipinnis is a sub-Saharan species which is widely distributed through West, Central and parts of East Africa. It ranges from Senegal in the west, through West Africa, to Cameroon and Central Africa including much of the Congo basin, into Uganda and East Africa including Ethiopia, Kenya and Tanzania. It has been recorded as far south as southern Democratic Republic of the Congo and northern Angola. It occurs at elevations of up to 3,200 m asl.

Benda *et al.* (2025: 99) mention that Monadjem *et al*. (2024) assigned 55 eastern African *Pseudoromicia tenuipinnis* specimens to *P. nyanza* *P. tenuipinnis* should then be restricted to West and Central Africa.

Native: Angola (Crawford-Cabral, 1989; Monadjem *et al.*, 2010d: 569); Burundi; Cameroon; Central African Republic; Congo (Bates *et al.*, 2013: 337); Congo (The Democratic Republic of the) (Schouteden, 1944; Hayman *et al.*, 1966; Van Cakenberghe *et al.*, 1999; Dowsett *et al.*, 1991: 259; Monadjem *et al.*, 2010d: 569); Côte d'Ivoire; Equatorial Guinea; Ethiopia (Lavrenchenko *et al.*, 2004b: 147); Gabon; Gambia; Ghana; Guinea (Konstantinov *et al.*, 2000: 145); Guinea-Bissau (Rainho and Ranco, 2001: 66); Kenya; Liberia (Monadjem and Fahr, 2007: 50); Nigeria; Rwanda; Senegal; Sierra Leone; Tanzania; Togo; Uganda (Kityo and Kerbis, 1996: 62).

GENERAL DESCRIPTION OF EXTERNAL MORPHOLOGY:
Tragus: Monadjem *et al.* (2013c: 204) gives a line drawing of the tragus of specimen DNSM 13235 from Mount Nimba, Liberia.

DETAILED MORPHOLOGY:
Baculum
The basal lobes of *Pseudoromicia tenuipinnis* were long and elongate, terminating in a rounded lobular structure, the total length (1.97 mm), the

angle of shaft curvature, measured from mid-shaft to the shaft base, was more acute in *tenuipinnis* (43°) than in *L.* cf. *rendalli* (58°) (Monadjem *et al.*, 2013c: 197). Line drawings of dorsal and ventral views of specimen DNSM 13235 from Mount Nimba, Liberia are shown in Monadjem *et al.* (2013c: 204). See Hill and Harrison (1987).

ECHOLOCATION:
Musila *et al.* (2018c: 43) [referring to Monadjem *et al.* (2010d: 478)] mention a shallow, frequency modulate call, which sweeps down from 62 to 37 kHz.

MOLECULAR BIOLOGY:
Karyotype
McBee *et al.* (1987) reported 2*n* = 36, FN = 52, BA = 18, a submetacentric X chromosome and an acrocentric Y chromosome.

HABITAT:
In their study at the Mount Nimba area, Monadjem *et al.* (2016y: 370) recorded this species in two small settlements.

DIET:
Feacal pellets of 2 bats from Cameroon examined by Waghiiwimbom *et al.* (2019a: 156), contained the following volume (± SD) and frequency percentages: Lepidoptera (57.9 ± 3.9; 100), Diptera (29.6 ± 5.9; 100), Coleoptera (7.4 ± 0.8; 100), Hemiptera (2.7 ± 0.5; 70), Hymenoptera (2.4 ± 0.3; 60).

For these bats, Cabrera-Campos *et al.* (2021: Suppl.) estimated the food transit time to be about 64 minutes, and the digestibility rate about 82.0 %.

PREDATORS:
Mikula *et al.* (2016: Supplemental data) mention the Bat hawk (*Macheiramphus alcinus* Bonaparte, 1850) as diurnal avian predator of "*E. tenuipinnis*".

POPULATION:
Structure and Density
This species is rather common in suitable habitat. It is most often found in small groups of fewer than 20 animals (Fahr, 2008a; IUCN, 2009; Monadjem and Fahr, 2017f).

Trend
2016: Unknown (Monadjem and Fahr, 2017f).
2008: Unknown (Fahr, 2008a; IUCN, 2009).

PARASITES:
ACARI
Macronyssidae
Orlova *et al.* (2020c: 952) mention the presence of *Steatonyssus after* Radovsky and Yunker, 1963 on bats in Angola.

Sarcoptidae
Fain (1959e: 145) described *Notoedres (Notoedres) schoutedeni* from "*Eptesicus tenuipinnis*" and "*E. ater*" from Buta, Stanleyville (= Kisangani), Mauda, and Tshuapa, DRC.

HEMIPTERA
Cimicidae
Aphrania recta Ferris and Usinger, 1957, recorded from Sierra Leone (Haeselbarth *et al.*, 1966: 12), and DRC (Kock and Aellen, 1987: 876).

DIPTERA
Streblidae
Raymondia intermedia Jobling, 1936 in Sierra Leone (Haeselbarth *et al.*, 1966: 102).

Nycteribiidae
Basilia ansifera Theodor, 1956 mainly a West African species, reaching Lake Victoria in the east and Lake Nyasa in the south, nearly all localities lie between 15° latitude north and south (Haeselbarth *et al.*, 1966: 110). *Basilia robusta* Theodor, 1956 (Haeselbarth *et al.*, 1966: 111; Dick *et al.*, 2023).

VIRUSES:
In their overview table, Maganga *et al.* (2014a: 8) reported that no viruses were ever found in this bat species.

Coronaviridae
None of the 33 Kenyan bats tested by Tao *et al.* (2017: Suppl.) was positive for CoV.

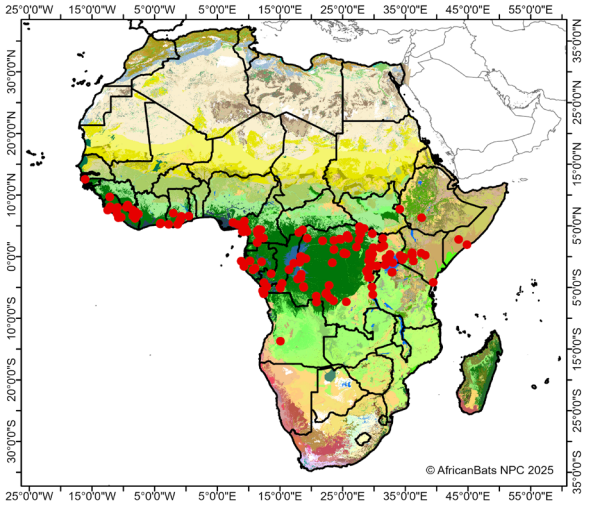

Figure 406. Distribution of *Pseudoromicia tenuipinnis*.

DISTRIBUTION BASED ON VOUCHER SPECIMENS: "Africa", Angola, Burundi, Cameroon, Central African Republic, Congo, Congo (Democratic Republic of the), Côte d'Ivoire, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Sudan, Tanzania, Togo, Uganda.

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Centro de Zoologia, Lisbon - J. Crawford Cabral;
David C.D. Happold Collection, Canberra - Dr. David Happold, Dr. Meri Happold;
Ditsong National Museum of Natural History, Pretoria – Dr. Teresa Kearney curator 2002 - present, Onica Mukuwana collection manager 2014 – 2017;
Durban Natural Science Museum - Dr. Peter Taylor was curator 1989-2010, followed by Dr. Leigh Richards;
Field Museum of Natural History, Chicago - Dr. Steve M. Goodman, Dr. Bruce D. Patterson, Dr. Bill Stanley;
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Museum of Comparative Zoology, Harvard - Mrs. Maria E. Rutzmoser;
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Museum National D'Histoire Naturelle, Paris - Dr. Michel Tranier, Dr. J. Cuisin;
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Museo Civico di Storia Naturale, Milan - Dr. Luigi Cagnolaro;
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Midwastern State University, Wichita Falls - Frederick B. Stangl;
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Glossary

Abdomen The belly; that part of the pelage covering the belly region.

Abdominal Of the abdomen.

Abundance The representation of a species in a sampling unit based on the number of individuals, biomass, cover, or similar measures.

Adult Sexually mature

Allopatric Populations or taxa with geographically separated ranges.

Allotype *n.* See under type.

Alpha taxonomy The description and naming of organisms.

Alveolus Socket in jaw where tooth is implanted.

Angular process Projection at the lower posterior part of each mandible.

Anterior Towards the front; fore.

Antitragus Lobe at the basal part of the outer margin of the ear.

Arboreal Living in trees.

Arthropods Invertebrate animals with a hard, joined exoskeleton, e.g. insects, crabs, spiders, …

Articles *n.* The mandatory provisions of the ICZN

Aspect ratio Forearm length (elbow to wrist) + wing tip (wrist to tip of digit III)/length of fifth finger.

Assemblage A group of related organisms living in the same place.

Auditoriry bullae See bulla.

Available name A scientific name applied to an animal taxon that is not excluded under Article 1.3 and that conforms to the provisions of Articles 10 to 20.

Axillary Pertaining to the armpit.

Bachelor colony A group of pre- and post-pubertal males that roosts separately from females, usually during the reproductive period (includes non-harem males).

Baculum (os penis) Bone supporting the penis (and as such only found in males).

Basal metabolic rate Rate of energy expenditure while at rest, post-absorptive, and at thermoneutrality; expressed as kJ. g 1 h 1 (see also roosting metabolic rate).

Bat detector Electronic device sensitive to ultrasonic and audible sounds produced by bats (e.g. QMC mini bat detector, Holgate bat detector, leak detector, ...).

Bat pass One pass by one individual through air space as sampled with a bat detector. (see also feeding buzz).

Bicuspidate With two cusps.

Bifid With two distal processes.

Biodiversity The variety of living species of organisms on Earth. Also: The spatial, temporal, and/or compositional makeup of the individuals, populations, species, and/or communities in a defined set.

Breeding season The period beginning with courtship and ending with weaning. (see also mating, parturition).

Buccal pad Oval epithelial structure of the lipoid substances, situated in the angles of the mouth between the cheeks and posterior teeth.

Bulla (*sing.*) / bullae (*pl.*) Dome-shaped protuberance from the underside of the skull enclosing the inner ear.

Calcar A cartilaginous spur supporting the free margin of the tail membrane [=uropatagium] from the ankle.

Call structure Pattern of frequency change over time in vocalizations; sonograph or period meter display.

Canine teeth Eye teeth, usually long, and sharp pointed.

Carnivorous Flesh eating (e.g. insects, fish, amphibians, reptiles, birds, mammals).

Carpal Wrist bone

Cavernicolous Living in caves.

CF Constant frequency (pure tone) component of ultrasonic pulses produced by some echolocating bats (used for ranging and judging velocity and direction of movement).

Cheek teeth The chewing teeth; those posterior to the canine in each toothrow.

Chiropterophily Mutualistic associations between flowers and flower-visiting bats.

Circadian Relating to a period of approximately 24 hours.

Clade A group of organisms that consists of a common ancestor and all of its descendants.

Cluster A group of (closely together) roosting bats.

Code *n.* (1) An abbreviation of the title International Code of Zoological Nomenclature

Cohort life table A life table constructed from a mortality schedule of individuals that started life together.

Colony Usually a specified aggregation of bats (e.g. maternity colony, hibernating colony, bachelor colony, ...).

Communal roost A roost used simultaneously by more than one individual.

Community A group of populations that coexist in space and time and interact with each other directly or indirectly.

Condylobasal length A technical measurement taken on a prepared skull, being the length of the ventral aspect in the midline from the posterior surfaces of the occipital condyles to the anterior margin of the premaxilla.

Condylocanine length A measurement similar to the condylobasal length, taken parallel to the axis of the skull from the posterior surfaces of the occipital condyles to the anterior surfaces of the canines.

Conserved name A name otherwise unavailable or invalid that the Commission, by the use of its plenary power, has enabled to be used as a valid name by removal of the known obstacles to such use (see conserve).

Contig A set of DNA sequences that overlap to provide a continuous representation of a genomic region.

Contour hairs The close-fitting hairs that form the principal covering of a mammal's body.

Cotype *n.* See under type.

Crepuscular Pertaining to the twilight periods of dawn and dusk.

Critically Endangered (CR) A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered (see Section V), and it is therefore considered to be facing an extremely high risk in the wild.

Crown age The crown age of a phylogeny is the time between the present and the moment of at which the first diversification (resulting in two lineages) happened.

See: https://search.r-project.org/CRAN/refmans/beautier/html/get_crown_age.html

Cryptic species Two or more distinct species that are erroneously classified (and hidden) under one species name.

Cusp A raised point on the crown of a tooth.

Dactylopatagium The part of the wing membrane between the 2nd and 3rd digits.

Daily Energy Budget (DEB) Amount of energy assimilated or expended daily to sustain free-living existence.

Data Deficient (DD) A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. A taxon in this category may be well studied, and its biology well known, but appropriate data on abundance and/or distribution are lacking. Data Deficient is therefore not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that threatened classification is appropriate. It is important to make positive use of whatever data are available. In many cases great care should be exercised in choosing between DD and a threatened status. If the range of a taxon is suspected to be relatively circumscribed, and a considerable period of time has elapsed since the last record of the taxon, threatened status may well be justified.

Date of publication *n.* Of a work (and of a contained name and nomenclatural act): the date on which copies of the work become available by purchase or free distribution. If the actual date is not known, the date to be adopted is regulated by the provisions of Article 21.2-7.

Day roost A site or structure used by bats during the day.

DEB See Daily Energy Budget

Deciduous teeth Milk teeth.

Delayed development A condition where the blastocyst implants without delay after entering the uterus but subsequent embryonic development ceases temporarily or proceeds slowly. (see also delayed implantation).

Delayed fertilization See Delayed ovulation.

Delayed implantation A condition where the blastocyst remains in the uterine lumen for a variable period before it implants.

Delayed ovulation A condition in which ovulation is postponed for a period of time following copulation and where spermatozoa are stored in the female reproductive tract. In temperate regions this period is prolonged by hibernation (also called delayed fertilization).

Description *n.* A statement in words of taxonomic characters of a specimen or a taxon [Arts. 12,13].

Original The description of a nominal taxon when it is established.

Diastema Gap between the constituent teeth of a tooth row.

Digit Finger or toe.

Dispersal Usually refers to the movement of an individual away from its place of birth or origin, but also can refer to movements of individuals away from a roost for foraging purposes.

Distal Further away from the centre of the body, or from the point of origin, e.g. of a limb.

Diurnal Active during daylight.

Divergence The amount of evolutionary differentiation of a particular species from other species in a set.

Diversity

Alpha Mean biodiversity (variability) measured at a specified grain within a focus.

Beta The effective number of units within a focus; differences in unit composition along an environmental gradient or among units in a landscape.

Gamma Total biodiversity (variability) measured at a particular extent.

Dorsal Of or towards the back or upper surface.

East Africa Traditionally used for the area currently covering Uganda, Kenya, Rwanda, Burundi and Tanzania.

Eastern Africa Eastern part of the African continent, which is wider than East Africa.

Echolocation Orientation by reference to echoes of emitted sound reflected off solid surfaces.

Ecomorphology Inferential relationships between morphology and ecology.

Endangered (EN) A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered (see Section V), and it is therefore considered to be facing a very high risk of extinction in the wild.

Endemic A taxon primarily (if not only) occurring in a specific country or area.

Endoskeleton The internal, bony skeleton.

Estrus See Oestrus.

Evolutionary host Host species in which a pathogen, such as a virus, has evolved or is naturally found. In evolutionary or natural hosts, infections induce few or no symptoms.

Extant *a.* (1) Of a taxon: having living representatives. (2) Of specimen: still in existence.

Extinct (EX) *a.* Of a taxon: having no living representatives. IUCN - A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual) throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life cycle and life form (IUCN 2001).

Extinct in the Wild (EW) *a.* A taxon is extinct in the Wild when it is known only to survive in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to a taxon's life cycle and life form.

False nipples Supernumerary (pubic) nipples that function as "holdfasts" for suckling young, and which are present in several species of some Old World families.

Fat index The ratio of grams of fat/grams of lean dry mass.

Feeding buzz A rapid series of pulses made by an echolocating bat in its final approach to a prey item. (also see bat pass).

Feeding roost A site used by bats to consume prey too large to consume during flight and as a night-time refuge from predators. (see also night roost).

Fledging period Time when young bats begin to make foraging flights.

Flock An assemblage of bats in flight.

FM Frequency modulated pulses produced by some echolocating bats (mostly used for the discrimination of size and shape).

Forearm That part of the arm between the elbow and the wrist.

Frugivory The habit of eating fruit.

Functional group A set of organisms that uses biotic or abiotic resources in a similar way.

Genus Baird *et al.* (2025: 14) operationally define a genus using the 2 "Sigma Genus Concept" as follows: "*A genus is a formally recognized taxon containing one species or a monophyletic lineage of species. Genera are morphologically and/or genetically distinct from other genera, and genetic as well as morphological and other heritable biological features can be used for diagnoses. Genetic divergence estimates between sister genera should comprise a range between those of subgenera or congeneric species and higher taxa such as tribe, subfamily, or family. Operationally using genetic distance values, this range is set at two standard*

deviations below the mean as the minimum value for a valid genus, and two standard deviations above the mean as the minimum value for a new higher taxon such as tribe or subfamily."

Gestation period Time period during which a pregnant female carries the developing embryo before birth.

Gleaning A foraging tactic used by some bats whereby prey items are taken from a surface (e.g. ground, leaves, tree trunk, ...)

Gregarious Habitually living with numbers of its own species.

Guano Fecal and urinary waste that accumulates within or below a roost.

Guard hairs Long hairs, less numerous than and projecting beyond the contour hairs.

Guild A group of organisms that use biotic or abiotic resources in a similar way, including the environmental conditions within which they can function.

Harem A group of females associated with a single adult male. (See Lewis (1992) for a discussion on the use of the word "Harem".)

Heterothermy The ability to regulate body temperature physiologically, but temperature is not regulated precisely or at the same level at all times.

Hibernaculum Type of roost used by temperate zone bats in winter (e.g. caves, mines, buildings).

Hibernation The assumption of a state of greatly reduced core temperature for prolonged periods of time during cold seasons by an animal which has an active body temperature near 37°C, yet it retains the ability to spontaneously arouse without absorbing heat from the environment.

Homeothermy Regulated maintenance of the body temperature near 37°C.

Homing Refers to the return of individuals to their place of birth or origin or roost.

Homologs Genes or proteins that show a similarity of structure or function based on descendance from a common evolutionary ancestor.

Homonym *n.* (1) In the family group: each of two or more available names having the same spelling, or differing only in suffix, and denoting different nominal taxa. (2) In the genus group: each of two or more names having the same spelling and denoting different nominal taxa. (3) In the species group: each of two or more available specific or subspecific names having the same spelling, or spellings, or spellings deemed under Article 58 to be the same, and established for different nominal taxa, and either originally (primary homonymy) or subsequently (secondary homonymy) combined with the same generic name [Art. 53.3].

Homonymy *n.* (1) The relationship between homonyms. (2) The state of being homonymous.

Immature An animal which has attained adult dimensions but not sexual maturity.

Incisor teeth The front teeth, borne on the premaxilla.

Insectivorous Eating insects, or more generally, arthropods.

Intercanine breath *(C-C)* Distance between the outer surfaces of the two upper canines of either jaw.

Interfemoral membrane Membrane extending immediately after the body and from the inner margins of legs, enclosing whole or a part of the tail.

Internarial Between the nostrils.

Junior homonym Of two homonyms: the latter established, or in the case of simultaneous establishment to one not given precedence under Article 24.

Juvenile An animal which has not reached adult physical dimensions; characterized by unfused epiphyses. (see also immature).

Kilohertz (kHz) 1,000 cycles per second.

Kilojoule (kJ) 4.19 x kcal.

Lactation Active milk production by mammary gland.

Lappet Small protuberent flap, e.g. of skin.

lapsus calami (*sing.* and *pl.*), *n.* A Latin term meaning "slip (or slips) of the pen", i.e. an error (or errors) made by an author in writing a text, such as a misspelling of a name; contrasted with copyist's or printer's errors [Art. 32.5.1].

Lateral Towards the side of the body; away from the midline.

Least Concern (LC) A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened. Widespread and abundant taxa are included in this category.

Lek An assembly area used by adult males for courtship display and copulation with females.

Light-sampling Behaviour associated with the onset of nightly emergence where one or more individuals fly in the vicinity of the exit before emergence.

Lingual Towards the tongue or the inside of the mouth.

Longitudinal Extending lengthwise.

Lunar phobia Avoidance response to bright moonlight, where flight activity either becomes reduced or ceases.

Maternity colony An aggregation of female bats during pregnancy and lactation.

Maternity roost A site used by females during pregnancy and lactation.

Mating The pairing of a male and female during courtship and copulation.

Mating Systems See Dorrestein *et al.* (2024: 6)

Monogamy A single male and single female either mate exclusively with each other or form a pair bond for one or multiple seasons. This system can be further subdivided into:

Mating monogamy - A single male and a single female form a pair bond and mate exclusively with each other during a mating season. They do not necessarily maintain this pair bond during multiple mating seasons. As no extra-pair copulation occurs by definition, this can be regarded 'true' monogamy

Social monogamy - A single male and single female form a pair bond but may participate in extra-pair copulations. A pair may stay together for one or multiple mating seasons.

Polygamy Mating system where one or both sexes mate with multiple partners. Also in this system, a number of subcategories can be distinguished:

Female defence polygyny - Males defend multiple females within the females' home ranges to the exclusion of other males. When the females move away, the male moves with the group. Females may secure extra-group/harem copulations. Sometimes multiple males defend the females.

Resource defence polygyny - Males set up a mating territory in or around a resource (roost or foraging site) that is essential to females. They mate with and may defend the females that are using this site. Females may participate in extra-group/harem copulations, or reside in multiple harems over the course of a mating season. In
some instances, multiple males defend a mating territory.

Lek-like mating system - Males establish mating territories that include resources that are not essential to females but that act as a proxy of male quality. Mating territories are clustered as in a lek. Females can move freely among males.

Exploded classical lek - A male defends a mating territory that does not contain resources that are essential to females. Females base their mate choice solely on male quality. Mating territories are spaced out at the scale of the lek but clustered at the landscape scale (e.g. *Epomops franqueti* (?)).

Clustered classical lek - A male defends a mating territory that does not contain resources that are essential to females. Females base their mate choice solely on male quality or phenotypic proxies thereof. Mating territories are highly clustered in space (e.g. *Hypsignathus monstrosus*).

Promiscuity Mating occurs randomly among males and females, but reproductive success may vary between males, due to sperm competition.

Maxillary toothrow The row of teeth on one side of the upper jaw borne on the maxillary bone, i.e. canine, premolars and molars.

Median Of the midline, with reference to an organ or to the body as a whole.

Megabats A traditional name for the suborder of bats that included the Old World fruit bats. The name was initially given as this family (Pteropodidae) contains the largest bat species.

Melanistic Abnormally dark or black in colour.

Mesial Towards the midline of the body.

Metacarpal The long bone joining the base of each finger to the wrist skeleton.

Microbiome A community of microorganisms, such as bacteria, fungi, and algae, that can be found living together in a specific habitat. The mammalian gut microbiome is recognized as a key regulator of host health and disease.

Migration Regular seasonal movements.

Molar Member of the posterior cheek teeth, never more than three in number in any toothrow, which do not have deciduous precursors.

Monestrous See Monoestrus

Monoestrus Pertains to species that have a single oestrous cycle per year.

Monophyly The grouping of an organism and all of its descendants in a clade.

Monotocous Production of one young per pregnancy.

Monotypy *n.* The situation arising (1) when an author establishes a nominal genus or subgenus for what he or she considers to be a single taxonomic species and denotes that species by an available name (the nominal species so named is the type-species by monotypy) [Art. 68.3]; or (2) when an author bases a nominal species-group taxon on a single specimen but does not explicitly designates it as holotype (holotype by monotypy; see Article 73.1.2).

Multiple original spelling See under spelling.

Name combination The unique combination of a genus and specific epithet (or subspecific epithet) to form the scientific name of a then-valid species or subspecies (and forms or varieties in older literature); name combinations are not type-bearing synonyms, rather representing the history of taxonomic change associated with a name moving between genera, species, and subspecies.

Near Threatened (NT) A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future.

Nectarivorous Feeding on nectar.

Neonate A newborn young.

Net nights The product of the number of mist nets and the number of nights that nets are employed for the purpose of capturing bats (the size of nets should be designated).

New replacement name (*nomen novum*) A name established expressly to replace an already established name. A nominal taxon denoted by a new replacement name (*nomen novum*) has the same name-bearing type as the nominal taxon denoted by the replaced name [Arts. 67.8, 72.7]. See emendation, substitute name.

Niche The range of ecological conditions in which a species will persist.

Night roost Roost site used at night for resting, consuming and digesting prey, and predator avoidance.

***nomen dubium* (*pl. nomina dubia*)** *n.* A Latin term meaning "a name of unknown or doubtful application."

***nomen novum* (*pl. nomina nova*)** *n.* A Latin term equivalent to new replacement name.

***nomen nudum* (*pl. nomina nuda*)** *n.* A Latin term referring to a name that, if published before 1931, fails to conform to Article 12; or, if published after 1930, fails to conform to Article 13. A *nomen nudum* is not an available name, and therefore the same name may be made available later for the same or a different concept; in such a case it would take authorship and date [Arts. 50, 21] from that act of establishment, not from any earlier publication as a *nomen nudum*.

***nomen oblitum* (*pl. nomina oblita*)** *n.* A Latin term (meaning forgotten name) applied after 1 January 2000 to a name, unused since 1899, which as a result of an action taken under Article 23.9.2 does not take precedence over a younger synonym or homonym in prevailing usage; the younger name which takes precedence over the *nomen oblitum* may be called a *nomen protectum (q.v.)*. The term *nomen oblitum* was also applied to a disused senior synonym rejected between 6 November 1961 and 1 January 1973 under Article 23b of the Code editions then in force (see Article 23.12.2). *Nomina oblita* remain available names; see Articles 23.9 and 23.12 for conditions controlling their use as valid names.

nomen protectum *n.* A Latin term (meaning protected name) applied to a name which has been given precedence over its unused senior synonym or senior homonym relegated to the status of *nomen oblitum* (*q.v.*, and see Article 23.9.2).

Nomenclature The process of assigning scientific names to taxa based on a set of standardized rules in which each species has a 2-part name, starting with a genus and ending in a specific epithet (Binomial Nomenclature); nomenclatural changes result in changes to the name used for a taxon that do not change its taxonomic concept; zoological nomenclature for species-, genus-, and family-rank names are governed by the rules published in the ICZN Code (ICZN 1999), written by the International Commission on Zoological Nomenclature (ICZN).

Not Evaluated (NE) A taxon is Not Evaluated when it is has not yet been evaluated against the criteria.

Nulliparous Pertains to a female which has not given birth (includes individuals which are: immature, mature but not inseminated, mature and primigravid).

Oestrus A period when females allow males to mate with them (specifically near the time of ovulation, except in temperate zone hibernators).

Omnivory The habit of feeding on a mixed diet (feeding across two or more trophic levels).

Opportunistic feeding Pertains to a feeding habit where individuals consume the most abundant prey items.

Parous Pertains to a female which has given birth (may include females which have been inseminated, not inseminated, pregnant, or lactating).

Parturition Delivery of infants or pups.

Parturition period The time of year when females give birth to young.

Patagium A sheet-like membrane formed by a double layer of stretched skin.

Pectoral Pertaining to the chest.

Pelage The coat of hair or fur covering a mammal.

Phalanx (*sing.*) / phalanges (*pl.*) Element of the skeleton of a digit.

Philopatry The seasonal return of a bat to its place of birth or to the same hibernaculum.

Phylogenetic diversity The extent to which species within a set are closely or distantly related.

Phylogeny The pattern of relationships among taxa based on evolutionary ancestry.

Pinna External ear.

Piscivory The habit of eating fish.

Plagiopatagium Membrane which forms the part of the wing that extends laterally from the fifth digit of the wing to the ankle.

Polyandry Polyandry is a form of polygamy; in sexually reproducing animals, where females have multiple male mates.

Polyestrous See Polyoestrus

Polygynandry Polygynandry is a form of polygamy; in sexually reproducing animals, it is a multi-male and multi-female mating system. Polygynandry encapsulates both polygyny (males having multiple female mates) and polyandry (females having multiple male mates) within the same species.

Polygyny Polygyny is a form of polygamy; in sexually reproducing animals, where males have multiple female mates

Polyoestrous Subject to recurrent oestrus.

Polyoestrus Pertains to species that have two or more oestrous cycles per year.

Polytocous Producing more than one young per pregnancy.

Posterior Behind; hind.

Post-lactating Reproductive state of a female when lactation has ceased and milk can no longer be expressed from the nipples.

Post-partum oestrus An oestrus immediately following birth (see polyoestrous).

Premolar Member of the anterior cheek teeth, never more than four in number in any toothrow, which succeed a deciduous set.

Preoccupied name An otherwise available scientific name that matches the spelling of an older name within the same taxonomic rank, making it unavailable for nomenclatural use; in species-rank names, the preoccupying name can either be originally described in the same genus (Primary Homonym), or subsequently moved into that genus (Secondary Homonym); when the name for a currently recognized species is preoccupied, a Nomen Novum/Nomina Nova (new name) should be described to replace the preoccupied name.

Primary homonym Each of two or more identical specific or subspecific names established for different nominal taxa and originally combined with the same generic name [Art. 57.2]. For variant spellings deemed to be identical see Article 58.

Propatagium The membrane between the wrist and the body that forms the leading edge of the wing.

Proximal Nearer to the centre of the body, or to the origin, e.g. of a limb.

Pteropodid A member of the Megabats or Old World fruit bats (family Pteropodidae).

Pubertal Pertains to a male undergoing spermatogenesis for the first time, or a female undergoing first oestrus.

Refuging species Pertains to species, in which members form roosting aggregations.

Regionally Extinct (RE) Category for a taxon when there is no reasonable doubt that the last individual potentially capable of reproduction within the region has died or has disappeared from the wild in the region, or when, if it is a former visiting taxon, the last individual has died or disappeared in the wild from the region. The setting of any time limit for listing under RE is left to the discretion of the regional Red List authority, but should not normally pre-date 1500 AD.

Rejected name (1) A name which, under the provisions of the Code, cannot be used as a valid name and which is set aside in favour of another name. (2) A name which, as a matter of taxonomic judgment, is either treated as a junior subjective synonym (*q.v.*) of a name used as valid or is believed not to be applicable to the taxon under consideration.

Reservoir An organism in which an infectious pathogen naturally lives and reproduces.

Resistance Mechanisms evolved by a host to directly limit pathogen burden, leading pathogens to evolve methods to subvert this resistance.

Rhinarium The pad of flesh, usually hairless and often moist, surrounding the nostrils of many mammals.

Roost Site used by bats when not in flight.

Roost fidelity The tendency of a bat to return repeatedly to a certain roost (e.g. cave, tree hollow, barn) or general area (foliage).

Roosting metabolic rate Rate of energy expenditure under natural or semi-natural conditions (includes costs associated with specific dynamic action, movements, clustering, grooming, social interactions, ...).

Rostrum Anterior part of the skull in front of the orbits.

Sanguivory The habit of feeding on blood.

Sella Part of the noseleaf of horseshoe bats.

Senior homonym Of two homonyms: the first established, or in the case of simultaneous establishment the one given precedence under Article 24.

***Sensu lato* (*s. lat.* or *s.l.*)** A Latin term meaning "in the wide sense". Contrast with *sensu stricto (s. str.)*.

***Sensu stricto* (*s. str.* or *s.s.*)** A Latin term meaning "in the strict sense". Often used in conjunction with a name when referring to the nominal taxon in the narrow sense of its subordinate nominotypical taxon (contrast with *sensu lato (s. lat.)*.

sensu A Latin term meaning "in the sense of". Often used to refer to the usage of a name by a (cited) author in a sense different from that of the original author or some other previous author. See also auctorum.

Septum A narrow sheet of skin or flesh forming a partition.

Sibling species Cryptic sister species; two species that are the closest relative of each other and have not been distinguished from one another taxonomically.

Silent heat The occurrence of ovulation without fertilization, prior to behavioural oestrus and insemination.

Sister taxa Two taxa that are derived from the same immediate common ancestor.

Species (*sing.* and *pl.*) *n.* (1) The rank next below the genus group; the basic rank of zoological classification. (2) A taxon at the rank of species. (3) A group of living organisms consisting of similar individuals capable of interbreeding

Species group *n.* In the zoological classification, the lowest-ranking group of taxa the names of which are regulated by the Code. The species group includes all taxa at the ranks of species and subspecies [Art. 45.1].

***species inquirenda* (*pl. species inquirendae*)** *n.* A Latin term meaning a species of doubtful identity needing further investigation.

Specimen *n.* An example of an animal, or a fossil or work of an animal, or of a part of these. See Article 72.5 for the kinds of specimen eligible to be name-bearing types of nominal species-group nominal taxa.

Spelling

Spelling variants A difference in spelling from the original spelling of a scientific name, which can be incorrect in the original publication (Incorrect Original Spelling) or later publications (Incorrect Subsequent Spelling), or a purposeful change considered to be unjustified (Unjustified Emendation) or justified (Justified Emendation) according to the ICZN Code; justified spelling changes are usually those of specific epithets with adjective etymological roots, which change to match the etymological gender of the genus, or to Latinized names with non-standard characters (e.g., ñ, ö), although there are other rare exceptions allowing for justified emendations to the original spelling of a name.

Stem age A clade's stem age represents the time that this clade descended from a common ancestor with its sister clade. The stem age of a clade is always at least as old, and usually older, than the crown age.

See:
https://bio.libretexts.org/Bookshelves/Evolutionary_Developmental_Biology/Phylogenetic_Comparative_Methods_(Harmon)/11%3A_Fitting_Birth-Death_Models/11.02%3A_Clade_Age_and_Diversity

Subadult Approaching maturity but not fully adult.

Subsequent monotypy The situation arising when a nominal genus or subgenus was established before 1931 without any included nominal species, and when only a single taxonomic species denoted by an available name was first subsequently referred to it [Art. 69.3].

Subtriangular Approximately triangular.

Suppression, *n.* (suppress, *v.*) A ruling by the Commission, using its plenary power, (1) that a work is to be deemed, for nomenclature purposes, as unpublished, or that names and acts in it are not available; or (2) that an available name is never to be used as valid because (a) it is available only for the purpose of homonymy ("partial suppression") or (b) it is not available for the purposes of priority and homonymy ("total suppression"; but a totally suppressed species-group name may still denote the type species of a nominal genus or subgenus [Art. 81.2.1]); or (3) that an available name is only to be used as valid under stated conditions (e.g. when not considered a synonym of a particular later name) ("conditional suppression").

Swarming The activity of bats (males and females) from mid-summer through early autumn at sites that ultimately are used as hibernacula (the latter part of this interval is coincident with mating in temperate regions).

Sympatric Species or populations that occur together without inbreeding.

Synanthropy The association of bats with man.

Synonym *n.* Each of two or more names of the same rank used to denote the same taxonomic taxon.

Junior synonym Of two synonyms: the later established, or in the case of simultaneous establishment that not given precedence under Article 24. See also Article 23.9.

Objective synonym Each of two or more synonyms that denote nominal taxa with the same name-bearing type, or (in the cases of family-group and genus-group taxa) that denote nominal taxa with name-bearing types whose own names are themselves objectively synonymous.

Senior synonym Of two synonyms: the earlier established, or in the case of simultaneous establishment that given precedence under Article 24. See also Article 23.9.

Subjective synonym Each of two or more names whose synonymy is only a matter of individual opinion. i.e. it is not objective. See also Article 61.3.1.

Synonymy *n.* (1) The relationship between synonyms. (2) A list of synonyms.

Syntype *n.* See under type.

Taxon, (*pl.* taxa) *n.* A taxonomic unit, whether named or not: i.e. a population, or group of populations of organisms which are usually inferred to be phylogenetically related and which have characters in common which differentiate (*q.v.*) the unit (*e.g.* a geographic population, a genus, a family, an order) from other such units. A taxon encompasses all included taxa of lower rank (*q.v.*) and individual organisms. The Code fully regulates the names of taxa only between and including the ranks of superfamily and subspecies. (2) A species or infraspecific entity whose extinction risk is being assessed.

Taxonomic guild A group of organisms that both share a common ancestor and use biotic or abiotic resources in a similar way.

Taxonomic information

Taxonomy, *n.* (taxonomic, *a.*) The theory and practice of classifying organisms. See taxonomic information, taxonomic taxon.

Alpha taxonomy Deals with species and subspecies.

Beta taxonomy Deals with higher taxonomic groups (genus, family, order, …).

Tent-making The modification of leaves for use as roosts.

Terminal Last or end member of a row or series.

Terrestrial Living on the ground.

Thermal conductance A measure of the insulative properties of the skin and/or pelage.

Thermoneutrality The ambient temperature at which the basal metabolic rate of a homeotherm is minimal.

Tibia The principal bone of the lower leg, from knee to heel.

Time-activity budget The amount of time allocated to various activities (e.g. day roosting, night roosting, flight, rest, grooming), expressed in absolute time units or by percent of total activity.

Tolerance Host mechanisms that evolved to alleviate disease severity, thus having a mostly neutral effect on the pathogen.

Topotype See under type.

Torpor A state in which an animal's body temperature is depressed below homeothermic levels and that results in a lowered metabolic rate and an inability to perform normal locomotor function (e.g. flight).

Tragus A cutaneous and cartilaginous projection arising from the emergence of pinna.

Transient roost Temporary roost used by bats enroute during migration.

Trap-lining A foraging behaviour characteristic of some nectarivorous bats wherein regular and repeated visits are made to flowers along a fixed route.

Type *n.* A term used alone, or forming part of a compound term, to denote a particular kind of specimen or taxon.

Allotype A term, not regulated by the Code, for a designated specimen of opposite sex to the holotype [Recommendation 72A].

Cotype A term not recognized by the Code, formerly used for either syntype or paratype, but that should not now be used in zoological nomenclature [Recommendation 73E].

Genotype A term not recognized by the Code, formerly used for type species, but that should not now be used in zoological nomenclature [Recommendation 67A].

Holotype The single specimen designated or otherwise fixed as the name-bearing type of a nominal species or subspecies when the nominal taxon is established.

Lectotype A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies [Art. 74].

Name-bearing type The type genus, type species, holotype, lectotype, series of syntypes (which together constitute the name-bearing type) or neotype that provides the objective standard of reference whereby the application of the name of a nominal taxon can be determined.

Neotype The single specimen designated as the name-bearing of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no name-bearing type is believed to be extant. If stability and universality are threatened, because an existing name-bearing type is either taxonomically inadequate or not in accord with the prevailing usage of a name, the Commission may use its plenary power to set aside that type and designate a neotype.

Paralectotype Each specimen of a former syntype series remaining after the designation of a lectotype [Art. 721.3, Recommendation 74F].

Paratype Each specimen of a type series other than the holotype [Recommendation 73D].

Syntype Each specimen of a type series (*q.v.*) from which neither a holotype nor lectotype has been designated [Arts. 72.1.2, 73.2, 74]. The syntypes collectively constitute the name-bearing type.

Topotype, *n.* (topotypic, *a.*) A term, not regulated by the Code, for a specimen originating from the type locality of the species or subspecies to which it is thought to belong, whether or not the specimen is part of the type series.

Type genus *n.* The nominal genus that is the name-bearing type of a nominal family-group taxon.

Type host *n.* The host species with which the name-bearing type of a nominal species or subspecies was associated [Recommendation 76A.1].

Type locality *n.* The geographical place of capture, collection, or observation of the name-bearing type of a nominal species or subspecies [Art. 76.1, Recommendation 76A].

Type series *n.* The series of specimens, defined in Articles 72.4 and 73.2, on which the original author bases a new nominal species-group taxon. In the absence of a holotype designation, any such specimen is eligible for subsequent designation as the name-bearing type (lectotype); pending lectotype designation, all the specimens of the type series are syntypes and collectively they constitute the name-bearing type. Excluded from the type series are any specimens that the original author expressly excludes or refers to as distinct variants, or doubtfully includes in the taxon.

Type species *n.* The nominal species that is the name-bearing type of a nominal genus or subgenus.

Type specimen A term used in previous editions of the Code for a holotype, lectotype or neotype, or for any syntype; also used generally for any specimen of the type series (*q.v.*).

Ultrasonic Pertains to sound frequencies above the audible range (usually frequencies greater than 20 kHz).

Unavailable name A scientific name that does not meet the standards for nomenclatural availability according to the ICZN Code, often resulting from the name being improperly published (Unpublished Name) or published without a taxonomic description (Nomen Nudum/Nomina Nuda), among other reasons.

Uropatagium Membrane extending between the tail and hind legs (also called interfemoral membrane).

Vagrant A taxon that is currently found only occasionally within the boundaries of a region.

Valid name A scientific name that represents the correct name for a biological taxon as defined by the rules in the ICZN Code and recognized by a particular authority; usually but not always the oldest available name.

Ventral Of or towards the undersurface.

Virome A compilation of viruses described by sequencing of viral nucleic acids and found within a specific organism or ecosystem.

Visitor (also, visiting taxon) A taxon that does not reproduce within a region but regularly occurs within its boundaries either now or during some period of the last century. Regions have several options on how to decide the boundaries between visitors and vagrants, e.g., using a pre-set percentage of the global population found in the region or predictability of occurrence.

Vulnerable (VU) A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable (see Section V), and it is therefore considered to be facing a high risk of extinction in the wild.

Water index The ratio of grams of water/grams of lean dry mass.

Weaning Time when a juvenile begins to take food other than its mother's milk.

Whispering bat A species which emits low intensity echolocation pulses (e.g. *Plecotus, Megaderma. Nycteris*).

Wing-loading The ratio of body mass (g)/wing area (cm^2).

Yearling An animal at the beginning of its second year of life.

Zeitgeber An environmental clue (e.g. light) that synchronizes, entrains, or modifies a circadian rhythm.

Zoonotic disease An infectious disease caused by a pathogen, such as a virus, that can spillover from a non-human to a human and vice versa.

Zygoma (*sing.*) / zygomata (*pl.*) Cheek bone.

Zygomatic width (Zyg): The breadth of a skull between the outer surfaces of the zygomata.

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