

A revision of pipistrelle-like bats (Mammalia: Chiroptera: Vespertilionidae) in East Africa with the description of new genera and species

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Abstract

Vespertilionidae (class Mammalia) constitutes the largest family of bats, with ~500 described species. Nonetheless, the systematic relationships within this family are poorly known, especially among the pipistrelle-like bats of the tribes Vespertilionini and Pipistrellini. Perhaps as a result of their drab pelage and lack of obvious morphological characters, the genus and species limits of pipistrelle-like bats remain poorly resolved, particularly in Africa, where more than one-fifth of all vesper bat species occur. Further exacerbating the problem is the accelerating description of new species within these groups. In this study, we attempt to resolve the systematic relationships among the pipistrelle-like bats of sub-Saharan Africa and Madagascar and provide a more stable framework for future systematic efforts. Our systematic inferences are based on extensive genetic and morphological sampling of > 400 individuals covering all named genera and the majority of described African pipistrelle-like bat species, focusing on previously unstudied samples of East African bats. Our study corroborates previous work by identifying three African genera in Pipistrellini (*Pipistrellus*, *Scotoecus* and *Vansonia*), none of which is endemic to Africa. However, the situation is more complex in Vespertilionini. With broad taxonomic sampling, we confirm that the genus *Neoromicia* is paraphyletic, a situation that we resolve by assigning the species of *Neoromicia* to four genera. *Neoromicia* is here restricted to *Neoromicia zuluensis* and allied taxa. Some erstwhile *Neoromicia* species are transferred into an expanded *Laephotis*, which now includes both long-eared and short-eared forms. We also erect two new genera, one comprising a group of mostly forest-associated species (many of which have white wings) and the other for the genetically and morphologically unique banana bat. All four of these genera, as recognized here, are genetically

distinct, have distinctive bacular morphologies and can be grouped by cranial morphometrics. We also demonstrate that the genus *Nycticeinops*, until now considered monospecific, includes both *Afropipistrellus* and the recently named *Parahypsugo*, thus representing the fifth African genus in Vespertilionini. A sixth genus, *Hypsugo*, is mostly extra-limital to sub-Saharan Africa. Finally, we describe three new species of pipistrelle-like bats from Kenya and Uganda, uncovered during the course of systematic bat surveys in the region. Such surveys are greatly needed across tropical Africa to uncover further bat diversity.

Keywords: Africa, alpha taxonomy, genus revision, Mammalia, mitochondrial DNA, new genera, new species

INTRODUCTION

Vespertilionidae is the largest chiropteran family in the world with roughly 500 described species in 54 genera globally (Moratelli & Burgin, 2019), of which 17 genera and at least 106 species have been reported from Africa (ACR, 2019; Monadjem *et al.*, 2020a). Within this group, the taxonomy of the pipistrelle-like or “pipistrelloid” tribes Pipistrellini and Vespertilionini (*sensu* Amador *et al.*, 2018) of the subfamily Vespertilioninae have been particularly difficult to resolve. The systematic relationships of these bats have been the subject of much debate over the past few decades (Hill & Harrison, 1987; Volleth & Heller, 1994; Hofer & Van Den Bussche, 2003; Roehrs, Lack & Van Den Bussche, 2010; Koubínová *et al.*, 2013; Amador *et al.*, 2018; Moratelli & Burgin, 2019) and a strongly supported phylogeny, particularly of basal nodes, has not yet been published. Furthermore, species limits are poorly known for many taxa (Andriollo, Naciri, & Ruedi, 2015), and new species and genera continue to be described (Benda *et al.*, 2016; Hutterer *et al.*, 2019; Görföl *et al.*, 2020).

The high diversity of pipistrelle-like bats in Africa has been overshadowed by the ambiguity of species relationships and further complicated by the local or regional focus of previous analyses (Monadjem *et al.*, 2013; Goodman *et al.*, 2015, 2017; Hutterer *et al.*, 2019). For example, in the past decade, two new species have been described in the genus *Neoromicia* (Monadjem *et al.*, 2013; Decher *et al.*, 2015), a third in *Pipistrellus* (Monadjem *et al.*, 2020b), and a fourth in *Parahypsugo* (Hutterer *et al.*, 2019), all from the Upper Guinea forest zone of West Africa. Furthermore, the phylogenetic relationships of pipistrelle-like bats in this region have been investigated with mtDNA markers and a new genus (*Parahypsugo*) was recognized based on genetic and morphological characters (Hutterer & Kerbis Peterhans, 2019; Monadjem *et al.*, 2020b). Similarly, the species identities and relationships of pipistrelle-like bats in Madagascar have also been reexamined (Goodman & Ranivo, 2004; Bates *et al.*, 2006; Goodman *et al.*, 2012,

2015), as have the southern African *Neoromicia* (Goodman *et al.*, 2017). In stark contrast, the pipistrelle-like bats of East Africa have received almost no attention and many basic taxonomic and systematic questions remain unanswered (Patterson & Webala, 2012). Yet, East Africa appears to be a hub of cryptic diversity in other bat families and genera examined to date (Demos *et al.*, 2018, 2019a,b, 2020; Patterson *et al.*, 2018, 2019, 2020). Mizerovská *et al.* (2019) argued that this is also true for non-volant faunas, and we expect this to be true for pipistrelle-like bats too.

Numerous systematic problems remain unresolved with pipistrelle-like bats, particularly within the Vespertilionini. The genus *Neoromicia* has been the focus of much attention (Monadjem *et al.*, 2020a). Previous studies have suggested that it may be paraphyletic (Koubínová *et al.*, 2013; Monadjem *et al.*, 2013; Goodman *et al.*, 2015), and a close relationship between the distinctly long-eared *Laephotis* species and some members of the genus *Neoromicia* has been reported (Hooper & Van Den Bussche, 2003; Görföl & Csorba, 2018). Furthermore, the placement of *Neoromicia nana* (sometimes previously called *Pipistrellus nanus* or *Hypsugo nanus*) has been problematic. For example, unlike other species allocated to *Neoromicia*, *Neo. nana* presents a distinctive character set: the 1st upper premolar is present; the braincase is obviously and highly inflated; there is a distinct thumbpad present at the base of the thumb; and the lower 3rd molar is “nyctalodont” (Monadjem *et al.*, 2010; Van Cakenberghe & Happold, 2013). Another taxonomic problem relates to the newly described Afrotropical genus *Parahypsugo* which is rendered paraphyletic by *Pipistrellus (Afropipistrellus) grandidieri* (Monadjem *et al.*, 2020b), and the relationship of these two groups have not yet been investigated with respect to *Nycticeinops*.

On the other hand, the systematic relationships within the Pipistrellini are somewhat clearer (Hooper & Van Den Bussche, 2003; Amador *et al.*, 2018). Sub-Saharan Africa was previously thought to be home to two genera, *Pipistrellus* and *Scotoecus*. However, a recent study demonstrated that *Pipistrellus rueppellii* is sister to *Pipistrellus* + *Nyctalus* + *Glischropus* (Koubínová *et al.*, 2013), rendering that concept of *Pipistrellus* paraphyletic. Based on this evidence, and the distinctive morphology of *Pip. rueppellii*, this species has since been placed in its own genus *Vansonia*, which was formerly a subgenus of *Pipistrellus* (Moratelli & Burgin, 2019). In addition, new species continue to be described in this tribe (Monadjem *et al.*, 2020b).

The main objectives of this study are: 1) to present a phylogeny for pipistrelle-like vespertilionids (tribes Pipistrellini and Vespertilionini) in sub-Saharan Africa based on a unique dataset of over 400 specimens that have

been sequenced and examined morphologically; 2) investigate the putative paraphyly within the genus *Neoromicia* and resolve this taxonomic problem; and 3) to use an integrative taxonomic approach to describe three East African species new to science.

MATERIAL AND METHODS

Study sites

Most of the material newly reported in this study was collected in the course of systematic surveys in Eastern, Central, and Southern Africa over the last three decades by Field Museum scientists and a host of in-country collaborators. This work was centered in East Africa, which is remarkable for a number of reasons: 1) it is bisected by the Equator and consequently is host to remarkable biodiversity in many taxonomic groups, especially bats (Patterson & Webala, 2012). Bats comprise at least a quarter of the megadiverse mammal faunas of Kenya and Uganda (Thorn & Kerbis Peterhans, 2009; Musila *et al.*, 2019); 2) East Africa is a region of long-term tectonic activity creating Africa's tallest mountains and deepest depressions (Spawls & Mathews, 2012), and giving rise to an unparalleled diversity of habitats. In addition to its endemic montane faunas, East Africa is where Africa's great Equatorial rain forest reaches its eastern limits, the Sahel reaches its southeastern limits, the Horn of Africa reaches its southwestern limits, and the Eastern savannas reach their northern limits. The region lies at the nexus of several biodiverse biomes (Linder *et al.*, 2012); and 3) the region's infrastructure and relative political stability have permitted long-term scientific efforts. Several museum scientists documenting the mammal faunas in this region have collected extensive and largely complementary sets of specimens, including associated tissue samples for genomic work, for understanding the regional diversity of Africa's bat faunas. The contributions of the late Bill Stanley throughout Tanzania and Dr. Robert Kityo and his team of students from Makerere University in Uganda deserve special mention here (Kityo & Kerbis, 1996; Stanley *et al.*, 1996, 1998; Kerbis Peterhans *et al.*, 1998; Stanley & Goodman, 2011).

Kenya, which occupies a central position in the region, has been the focus of extensive bat surveys since 2006 organized by Chicago's Field Museum of Natural History (FMNH) in partnership with the National Museums of Kenya (NMK), the Kenya Wildlife Service, Karatina University, and Maasai Mara University. The "Bats of Kenya" project had as its goal the development of a comprehensive understanding of the country's bat diversity, including

the production of a vouchered reference call library. Once fieldwork began, it soon became apparent that existing keys (e.g., Patterson & Webala, 2012) were of limited value in cataloguing the diversity of East African bats—species were too geographically variable, actual species limits were unrecognizable, taxonomic names were being misapplied, including in genomic databases, or all of the above acting in concert. We therefore focused efforts on thorough documentation of each species with which we came into contact. To do this, we traveled to all accessible parts of the country, neglecting only its border regions with South Sudan and Somalia.

Data collection

Our field protocols involved extensive use of hand nets, harp traps, mist nets, and triple-high net suspension systems. Hand nets were used exclusively at day-roost sites. We used both two-bank and four-bank Austbat harp traps (Faunatech.com.au), as well as a discontinued model manufactured by Bat Conservation and Management (batmanagement.com), which also produced our three triple-high systems. On the ground, we deployed 6- and 12-m nylon mist nets in likely flyways and monitored those continuously, typically from dusk to about midnight. The position of all study sites was marked using a Garmin eTrex Vista HCx global positioning system, from which elevation was also read. Bats selected for further investigation were placed into individual cloth bags and transported to a portable flight cage (4 x 4 x 2 m in size) of cloth draped over a jointed PVC frame. Once released, the bats flew around the cage, searching for an exit, and their calls were recorded using a handheld ultrasound detector (Pettersson D1000X; Pettersson Elektronik AB, Uppsala, Sweden; 384 or 500 kHz sampling rate, 16-bit resolution). For sound analysis, a customized 512-point fast Fourier transform (FFT) was used with a Hanning window for both spectrograms and power spectrum. Following Jung, Molinari & Kalko (2014), we characterized echolocation calls by measuring peak frequency or frequency with maximum energy (FME), maximum frequency (StartF), and minimum frequency (EndF) using Kaleidoscope v.3.1.4b (Wildlife Acoustics, USA). The mean of 10 calls with the best signal-to-noise ratios were measured for each bat.

Procedures involving voucher specimens followed guidelines established in mammalogy (Sikes, 2016) and were approved by Field Museum's IACUC (2012-003). After euthanasia with Halothane, individual bats were fumigated in ethyl ether and carefully inspected for ectoparasites, all of which were preserved as a lot in 95% ethanol for parallel studies by parasitologist Carl W. Dick. Total length (head-and-body plus tail), tail length, hindfoot

length (including claw), ear pinna length (from notch), and tragus length (where present) were taken with a ruler in mm. Body mass was weighed using Pesola balances, and recorded to the nearest 0.1 g. In most cases, the pectoral muscle was exposed and two 0.5 cm² samples of muscle were placed within 1–2 hours after the bat's death into a liquid nitrogen dewar. Bat carcasses labeled with individual field numbers were injected with a 10% formalin solution and immersed in that formalin solution for 4–20 days, before being rinsed and transferred to 70% ethanol. In most cases, the skulls of alcohol-preserved bats were removed, skinning the head from the lips back to the neck, severing the spinal column at the occipital condyle and removing the skull; by re-everting the skin of the head around a ball of cotton, the morphology of the ears, lips, and nose is still apparent and can be studied. The skull and mandible were then cleaned by dermestid beetles for study. Although this entire procedure was specific to the “Bats of Kenya” project, most parts of it other than the flight cage and bioacoustic recordings were employed in mammal surveys elsewhere. All specimens and associated tissue samples were deposited in the mammal collections of FMNH, NMK, and other national repositories, as per agreements between collaborating institutions.

DNA extraction, amplification and sequencing

Genomic DNA from frozen tissue samples was extracted using the Wizard SV 96 Genomic DNA Purification System (Promega Corporation, WI, USA) or the DNeasy Blood and Tissue Kit (Qiagen). Specimens were sequenced for mitochondrial cytochrome-*b* (*cyt-b*), using the primer pair LGL 765F and LGL 766R (Bickham, Wood, & Patton, 1995; Bickham *et al.*, 2004). We generated original genetic data from 310 individuals collected at 110 georeferenced localities and complemented them with 108 mitochondrial sequences from 63 unique localities downloaded from GenBank; of these GenBank sequences 28 of the specimens associated with them were examined by the senior author. In total sequence data was obtained for 58 species/putative species in Vespertilionidae. All individuals were sequenced for *cyt-b* in order to maximize assessment of genetic diversity; however, redundant haplotypes were removed for subsequent phylogenetic analyses (see Table S1 for complete list of individuals sequenced). PCR amplification, thermocycler settings, and Sanger sequencing were the same as in Demos *et al.* (2018) and Patterson *et al.* (2018). Chromatograms were edited and assembled in GENEIOUS PRO v.11.1.5 (Biomatters Ltd.). Sequence alignments were made using MUSCLE (Edgar, 2004) with default settings in GENEIOUS Prime v.2020.0.5. Protein-coding sequence data from *cyt-b* were translated to amino acids to establish the absence of premature stop codons, insertions, and deletions.

The sequence alignments used in this study have been deposited on the FIGSHARE data repository (to be added later). Newly generated sequence data have been deposited in GenBank under accession numbers (to be added on acceptance) (see also Table S1).

Phylogenetic analysis

jMODELTEST2 (Darriba *et al.*, 2012) on CIPRES Science Gateway v.3.1 (Miller, Pfeiffer, & Schwartz, 2010) was used to determine the sequence substitution models that best fit the *cyt-b* data using the Bayesian Information Criterion (BIC). Uncorrected *cyt-b* sequence divergences (*p*-distances) among and within species were calculated for *cyt-b* using MEGA X 10.1.7 (Kumar *et al.*, 2018). Maximum-likelihood (ML) analysis was performed with the software IQ-TREE version 1.6.10 (Nguyen *et al.*, 2015; Chernomor, von Haeseler, & Minh, 2016) on the CIPRES portal. Gene tree analyses using a Bayesian Inference (BI) model were generated in MRBAYES v.3.2.7 (Ronquist *et al.*, 2012) on the CIPRES portal for the same alignment as the ML analysis. Two independent runs were conducted in MrBayes using four Markov chains run for 1×10^8 generations under default heating values and sampled every 1000th generation. A conservative 20% burn-in was used and stationarity of the results were assessed using Tracer v1.7 (Rambaut *et al.*, 2018). Majority-rule consensus trees were assembled for each Bayesian analysis.

Craniodental morphology

Eight cranial and four dental measurements were taken with calipers to the closest 0.01 mm following Monadjem *et al.* (2013). The cranial measurements were: greatest skull length (GSKL), from the posterior-most point of the occipital to the anterior-most point of the incisors; condylo-incisive length (CIL), from the occipital condyles to the anterior-most point of the canines; greatest zygomatic breadth (ZYGO), taken as the greatest width across the zygomatic arches; greatest braincase width (GBW), braincase width taken in the frontal plane above the zygomatic arches; greatest skull height (GSH), taken from the lowest point of the basioccipital to the highest point of the cranium; postorbital width (POB), narrowest dorsal width posterior to the postorbital at the constriction of the cranium; greatest mastoid breadth (MAST), greatest breadth of cranium at mastoid processes; and greatest mandible length (MAND), taken from the posterior-most point of the condyles to the anterior-most point of the incisors. The dental measurements included: width across the third molars (M^3 – M^3), taken across the outer-most

point of the alveoli of the third molars; complete upper canine–molar tooth row (C–M³), taken from the anterior-most point of the alveolus of the canine to the posterior-most point of the alveolus of the third molar; width across upper canines (C–C), taken across the outer-most points of the alveoli of the canines; and complete mandibular canine–molar tooth row (c–m₃), taken from the anterior-most point of the alveolus of the canine to the posterior-most point of the third molar. Tooth abbreviations are as follows: C, canine; I, incisor; M, molar; P, premolar; with upper teeth presented in upper case and lower teeth in lower case.

We examined type specimens (listed in Table S1) from: The Natural History Museum (formerly The British Museum of Natural History), London (BMNH); the Muséum national d'Histoire Naturelle, Paris (MNHN); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); the Durban Natural Science Museum, Durban (DM); and The National Museum of Natural History, Washington (USNM).

The type specimens examined were: *Vespertilio capensis* A. Smith, 1829 [BMNH 1849.8.16.21 (lectotype)], *Vespertilio nanus* Peters, 1852 [BMNH 1907.1.1.421 (syntype)], *Neoromicia roseveari* Monadjem *et al.*, 2013 [DM 12617 (holotype)], *Scotophilus rusticus* Tomes, 1861 [BMNH 1907.1.1.419 (lectotype)], *Vesperus tenuipinnis* Peters, 1872 [DM 13235 (neotype)], *Vesperugo grandidieri* Dobson, 1876 [MNHN 1996–2129 (holotype)], *Vesperugo* (*Vesperus*) *brunneus* Thomas, 1880 [BMNH 1880.7.21.7 (holotype)], *Vesperus bicolor* Bocage, 1889 [BMNH 1889.5.1.3 (syntype)], *Vesperugo* (*Vesperus*) *rendalli* Thomas, 1889 [BMNH 1889.3.2.3 (holotype)], *Vesperugo* (*Vesperus*) *flavescens* Seabra, 1900 [MNHN 1900-537 (syntype)], *Vesperugo anchietae* Seabra, 1900 [BMNH 1906.1.3.1 (syntype)]; we follow Kock (2001) in accepting this as a justified emendation, since Seabra, 1900a originally published the name as "*Vesperugo anchieta*" and immediately corrected it to *Vesperugo anchietae* in Seabra 1900b - J. sci. mat. phys. nat., Lisboa, (2) 6 (22): 120], *Pipistrellus minusculus* Miller, 1900 [USNM 84500 (holotype)], *Vespertilio minutus somalicus* Thomas, 1901 [BMNH 1898.6.9.1 (holotype)], *Pipistrellus crassulus* Thomas, 1904 [BMNH 1904.2.8.1 (holotype)], *Pipistrellus nanulus* Thomas, 1904 [BMNH 1904.2.8.8 (holotype)], *Pipistrellus helios* Heller, 1912 [USNM 181813 (holotype)], *Pipistrellus aero* Heller, 1912 [USNM 181812 (holotype)], *Pipistrellus musciculus* Thomas, 1913 [BMNH 1913.2.8.1 (holotype)], *Eptesicus ugandae* Hollister, 1916 [USNM 166520 (holotype)], *Pipistrellus eisentrauti* Hill, 1968 [BMNH 1967.2129 (paratype)], *Laephotis botswanae* Setzer, 1971 [USNM 425349 (holotype)], and *Laephotis namibensis* Setzer, 1971 [USNM 342152 (holotype)], *Neoromicia isabella* Decher, Hutterer & Monadjem, 2015 [ZFMK 2008.0292 (holotype)], *Parahypsugo happoldorum* Hutterer *et al.*, 2019 [ZFMK 2009.0029 (holotype)], and *Pipistrellus simandouensis* Monadjem *et al.*, 2020 [ZFMK 2008-0302

(holotype)]. Of these, the last three mentioned type specimens were sequenced and therefore comparative genetic material was available for them.

We were unable to examine the type specimen of *Vespertilio hesperida* Temminck, 1840 (= *Pipistrellus hesperidus*) [SMF 12381 (lectotype)], but this specimen has received detailed attention in the literature, including its history, type locality, and very detailed description of characters together with craniodental measurements (Kock, 2001). The type locality is not definitely identifiable but is probably coastal Eritrea (Kock, 2001). Other taxa that have been synonymized with *P. hesperidus* include: *Vesperugo subtilis* Sundevall, 1846 (South Africa); *Pipistrellus kuhlii fuscatus* Thomas, 1901 (Kenya); and *Pipistrellus (Romicia) kuhli broomi* Roberts, 1948 (South Africa). Whether any of these may represent subspecies remains uncertain, although there appears to be little difference in the size of this species across its range (Kearney, 2013). Spatial relationships among the aforementioned type specimens and other taxa of African and Malagasy Pipistrellini and Vespertilionini are shown in Fig. 1.

In order to compare the morphology of the various taxa presented in this study, a principal component analysis (PCA) of log-transformed values of craniodental measurements (see Tables S2 and S3 for a list of the most inclusive set of measurements available for each analysis) was conducted on the variance–covariance matrix in the package ‘vegan’ (Oksanen *et al.*, 2019) run in R version 3.6.2 (R Core Team, 2019) and plotted using ggplot2 (Wickham, 2016). We first compared the skulls of the species traditionally placed in the genus *Neoromicia* (e.g. Simmons, 2005) to the four recognized *Laephotis* species. We then compared the skulls of the ‘*Neoromicia capensis*’ group including *Neo. capensis* and *Neo. stanleyi* from the mainland and *Neo. matroka*, *Neo. robertsi*, and *Neo. malagasyensis* from Madagascar. For the analysis involving *Neoromicia* and *Laephotis*, we used a subset of nine craniodental measurements, due to missing measurements from some specimens; these were: GSKL; GSH; GBW; MAST; MAND; C-M³; C-C; M³-M³; and c-m₃ (see above for definitions of these terms).

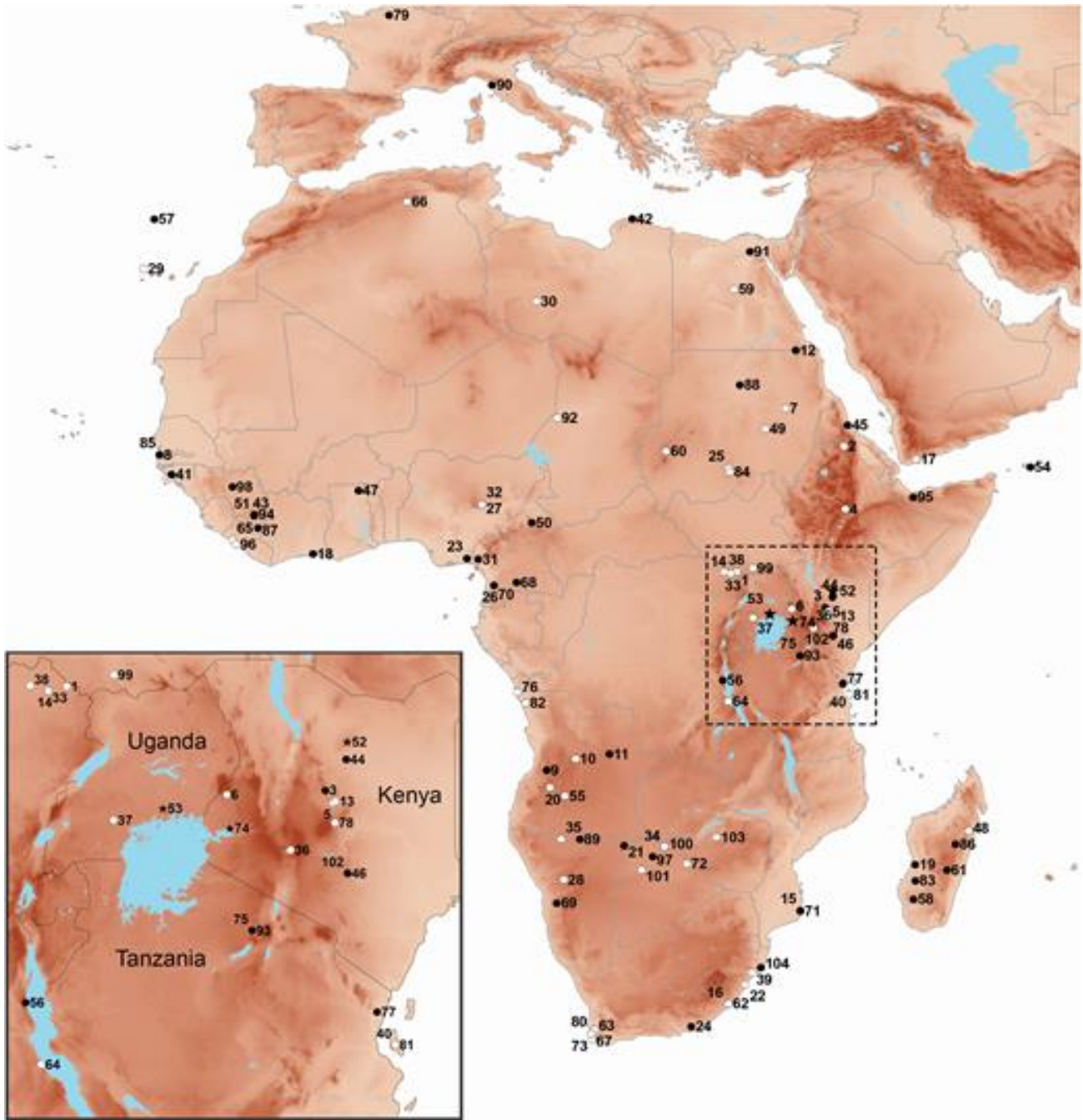


Figure 1. Type localities of taxa of African and Malagasy Vespertilionini and Pipistrellini. Valid species are denoted by filled circles, subspecies and synonyms by open circles and species described herein by stars: 1, *Pipistrellus abaensis* J. A. Allen, 1917; 2, *N[ycticejus]. adovanus* Heuglin, 1877; 3, *Pipistrellus aero* Heller, 1912; 4, *Vespertilio pipistrellus* var. *africanus* Rüppell, 1842; 5, *Nycticeius africanus* G. M. Allen, 1911; 6, *Scotoecus albigula* Thomas, 1909; 7, *Scoteinus schlieffeni albiventer* Thomas & Wroughton, 1908; 8, *Scotophilus albofuscus* Thomas, 1890; 9, *Vesperugo anchietae* Seabra, 1900; 10, *Laephotis angolensis* Monard, 1935; 11, *Eptesicus capensis angolensis* Hill, 1937; 12, *Pipistrellus ariel* Thomas, 1904; 13, *Scotoecus artinii* De Beaux, 1923; 14, *Eptesicus ater* J. A. Allen, 1917; 15, *Pipistrellus nanus australis* Roberts, 1913; 16, *Scoteinus schlieffeni australis* Thomas & Wroughton, 1908; 17, *Scoteinus schlieffeni bedouin* Thomas & Wroughton, 1908; 18, *Pipistrellus eisentrauti bellieri* De Vree, 1972; 19, *Hypsugo bemainty* Goodman et al., 2015; 20, *Vesperus bicolor* Bocage, 1889; 21, *Laephotis botswanae* Setzer, 1971; 22, *Pipistrellus (Romicia) kuhlii broomi* Roberts, 1948; 23, *Vesperugo (Vesperus) brunneus* Thomas, 1880; 24, *Vespertilio capensis*

A. Smith, 1829; 25, *Scotoecus cinnamomeus* Wettstein, 1916; 26, *Pipistrellus crassulus* Thomas, 1904; 27, *Pipistrellus culex* Thomas, 1911; 28, *Vesperus damarensis* Noack, 1889; 29, *Scotophilus darwini* Tomes, 1859; 30, *Pipistrellus deserti* Thomas, 1902; 31, *Pipistrellus eisentrauti* Hill, 1968; 32, *Scotoecus falabae* Thomas, 1915; 33, *Eptesicus faradjus* J. A. Allen, 1917; 34, *Scoteinus schlieffeni fitzsimonsi* Roberts, 1932; 35, *Pipistrellus fouriei* Thomas, 1926; 36, *Pipistrellus kuhlii fuscatus* Thomas, 1901; 37, *Pipistrellus fuscipes* Thomas, 1913; 38, *Eptesicus garambae* J. A. Allen, 1917; 39, *Vespertilio capensis gracilior* Thomas & Schwann, 1905; 40, *Vesperugo (Vesperus) grandidieri* Dobson, 1876; 41, *Vesperus guineensis* Bocage, 1889; 42, *Pipistrellus hanaki* Hulva & Benda, 2004; 43, *Parahypsugo happoldorum* Hutterer, Decher, Monadjem & Astrin, 2019; 44, *Pipistrellus helios* Heller, 1912; 45, *Vespertilio hesperida* Temminck, 1840; 46, *Scotoecus hindei* Thomas, 1901; 47, *Scotophilus hirundo* de Winton, 1899; 48, *Vesperus humbloti* Milne-Edwards, 1881; 49, *Vesperugo hypoleucus* Heuglin [in Fitzinger & Heuglin], 1866; 50, *Pipistrellus inexpectatus* Aellen, 1959; 51, *Neoromicia isabella* Decher, Hutterer & Monadjem, 2016; 52, ***Laephotis kirinyaga*** Monadjem *et al.*, this paper; 53, ***Pseudoromicia kityoi*** Monadjem *et al.*, this paper; 54, *Hypsugo lanzai* Benda, Al-Jumaily, Reiter & Nasher, 2011; 55, *Pipistrellus leucomelas* Monard, 1932; 56, *Parahypsugo macrocephalus* Hutterer & Kerbis Peterhans, 2019; 57, *Vesperugo maderensis* Dobson, 1878; 58, *Eptesicus somalicus malagasyensis* Peterson, Eger & Mitchell, 1995; 59, *Vespertilio marginatus* Cretzschmar, 1830; 60, *Pipistrellus marrensis* Thomas & Hinton, 1923; 61, *Vespertilio matroka* Thomas & Schwann, 1905; 62, *Pipistrellus africanus meesteri* Kock, 2001; 63, *Eptesicus melckorum* Roberts, 1919; 64, *Scotophilus minimus* Noack, 1887; 65, *Pipistrellus minusculus* Miller, 1900; 66, *Vespertilio minuta* Temminck, 1840; 67, *Pipistrella minuta* Loche, 1867; 68, *Pipistrellus musciculus* Thomas, 1913; 69, *Laephotis namibensis* Setzer, 1971; 70, *Pipistrellus nanulus* Thomas, 1904; 71, *Vespertilio nanus* Peters, 1852; 72, *Eptesicus capensis nkatiensis* Roberts, 1932; 73, *Scabrier notius* G. M. Allen, 1908; 74, ***Pseudoromicia nyanza*** Monadjem *et al.*, this paper; 75, †*Scotoecus olduvensis* Gunnell, Butler, Greenwood & Simmons, 2015; 76, *Vesperugo pagenstecheri* Noack, 1889; 77, *Pipistrellus (Pipistrellus) permixtus* Aellen, 1957; 78, *Eptesicus phasma* G. M. Allen, 1911; 79, *Vespertilio pipistrellus* Schreber, 1774; 80, *Vespertilio platycephalus* Temminck, 1832; 81, *Vesperugo pulcher* Dobson, 1875; 82, *Vesperugo pusillus* Peters, 1870; 83, *Pipistrellus raceyi* Bates *et al.*, 2006; 84, *Eptesicus rectitragus* Wettstein, 1916; 85, *Vesperugo (Vesperus) rendalli* Thomas, 1889; 86, *Neoromicia robertsi* Goodman *et al.*, 2012; 87, *Neoromicia roseveari* Monadjem *et al.*, 2013; 88, *V[espertilio]. rueppelii* J. Fischer, 1829; 89, *Scotophilus rusticus* Tomes, 1861; 90, *Vespertilio savii* Bonaparte, 1837; 91, *Nycticejus schlieffenii* Peters, 1859; 92, *Pipistrellus rueppelii senegalensis* Dorst, 1960; 93, †*Nycticeinops serengetiensis* Gunnell *et al.*, 2015; 94, *Pipistrellus simandouensis* Monadjem *et al.*, 2020; 95, *Vespertilio minutus somalicus* Thomas, 1901; 96, *Vesperugo stampflii* Jentink, 1888; 97, *Neoromicia stanleyi* Goodman *et al.*, 2017; 98, *Vesperus tenuipinnis* Peters, 1872; 99, *Eptesicus ugandae* Hollister, 1916; 100, *Neoromicia vansoni* Roberts, 1932; 101, *Pipistrellus vernayi* Roberts, 1932; 102, *Laephotis wintoni* Thomas, 1901; 103, *Scotoecus woodi* Thomas, 1917; 104, *Eptesicus zuluensis* Roberts, 1924. Not mapped: [*Pipistrellus Kuhli*] *latastei* Laurent, 1937; *Vespertilio pusillus* LeConte, 1857; *Vesperugo subtilis* Sundevall, 1846.

Bacular preparation

The baculum (os penis) of selected specimens were prepared by severing the glans penis, rehydration in water, then immersion in dilute sodium hydroxide which was heated to 85 °C for a variable period. To facilitate dissection, the glans was then stained in Alizarin Red, which is calcium-specific and aids in distinguishing the bony baculum from

investing tissues. Bacula were photographed under a stereo microscope, and their morphological descriptions follow the convention of Hill & Harrison (1987).

RESULTS

Phylogenetic analyses

A preliminary alignment of 418 *cyt-b* sequences was assembled that included 310 sequences newly generated for this study and 108 sequences downloaded from GenBank (Table S1). Identical haplotypes were pruned from this alignment resulting in a 334-sequence alignment (85% complete coverage) that was used in ML and BI phylogenetic analyses (complete *cyt-b* ML tree shown in Fig. S1). The best supported substitution model estimated by jMODELTEST2 for the 334 bp *cyt-b* alignment was GTR + I + G. Only the maximum likelihood topology is shown (Figs. 2, 3), but both bootstrap values (BS) and posterior probabilities (PP) are depicted at shared, well supported nodes. Figure 2 depicts phylogenetic relationships among, and branch length ranges within, three genera of Pipistrellini (*Pipistrellus*, *Scotoecus*, *Vansonia*) and six genera of Vespertilionini (*Afronycteris* gen. nov., *Hypsugo*, *Laephotis*, *Neoromicia*, *Nycticeinops*, *Pseudoromicia* gen. nov.).

In the unique haplotype *cyt-b* tree (Fig. 3a-c), several genus-level clusters of taxa are apparent, but these do not coincide with current generic usage. The genus *Neoromicia* as traditionally used is clearly paraphyletic. Some species (*capensis*, *malagasyensis*, *matroka*, *robertsi*, *stanleyi*, and a new species from East Africa) assigned to that genus are more closely related to the four *Laephotis* species than to other *Neoromicia*. This group of 10 species (plus cf. *kirinyaga*) is well supported as sister to another group, which contains the type species of *Neoromicia*, *Neozuluensis*, in close association with *somalica*, cf. *somalica*, cf. *guineensis*, and *bemainty*. As here circumscribed, an expanded *Laephotis* and a restricted *Neoromicia* are sister to another pair of genus-level clusters: one comprises predominantly tropical rainforest species currently assigned to *Neoromicia* (*Neo. brunnea*, *Neo. roseveari*, *Neo. isabella*, and *Neo. rendalli*) and this well supported clade is sister to another distinctive group containing only *Neoromicia nana* (Fig. 3b); these novel groupings are described below as the new genera *Pseudoromicia* gen. nov. and *Afronycteris* gen. nov., respectively. The remaining sub-Saharan Vespertilionini comprise two clusters: the genus *Nycticeinops* (type species *schlieffeni*), hitherto considered monospecific, is flanked by species assigned to *Parahypsugo* (type species *happoldorum*), rendering that taxon paraphyletic. The group also includes *Pipistrellus*

grandidieri, the type species of *Afropipistrellus* (Fig. 3b). This expanded group of *Nycticeinops* lineages is sister to a largely Palearctic and Indo-Malayan cluster of *Hypsugo* species.

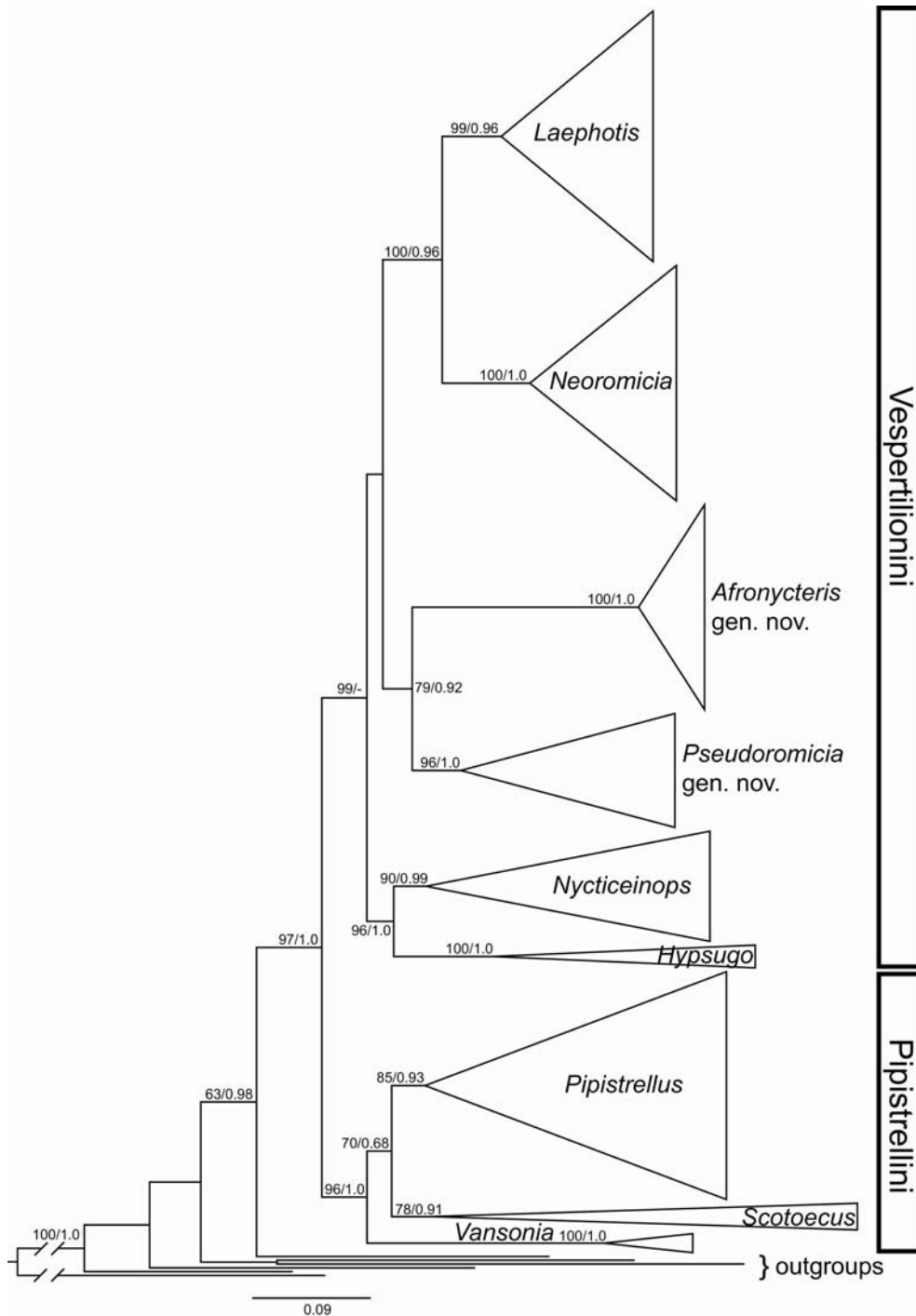
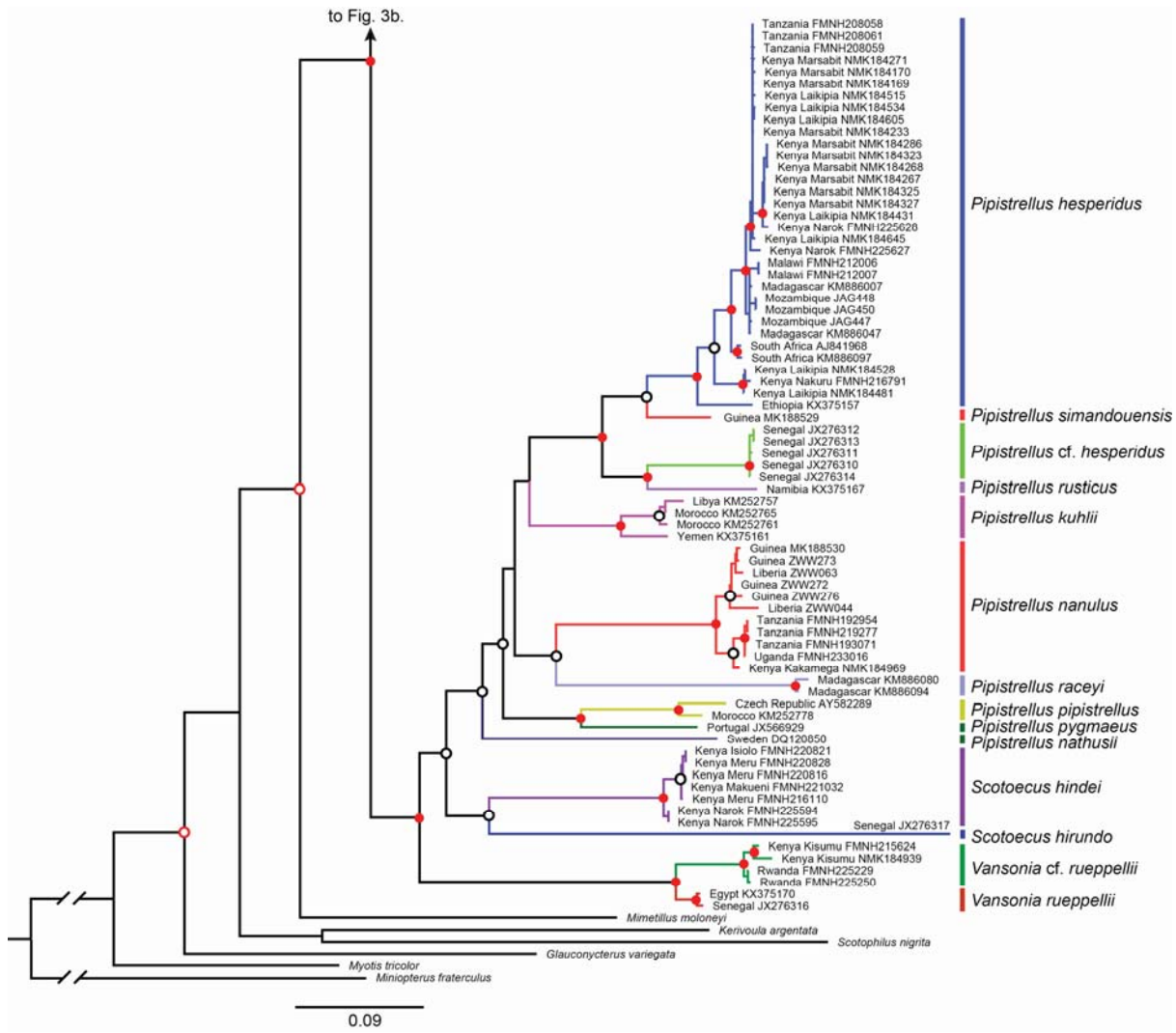
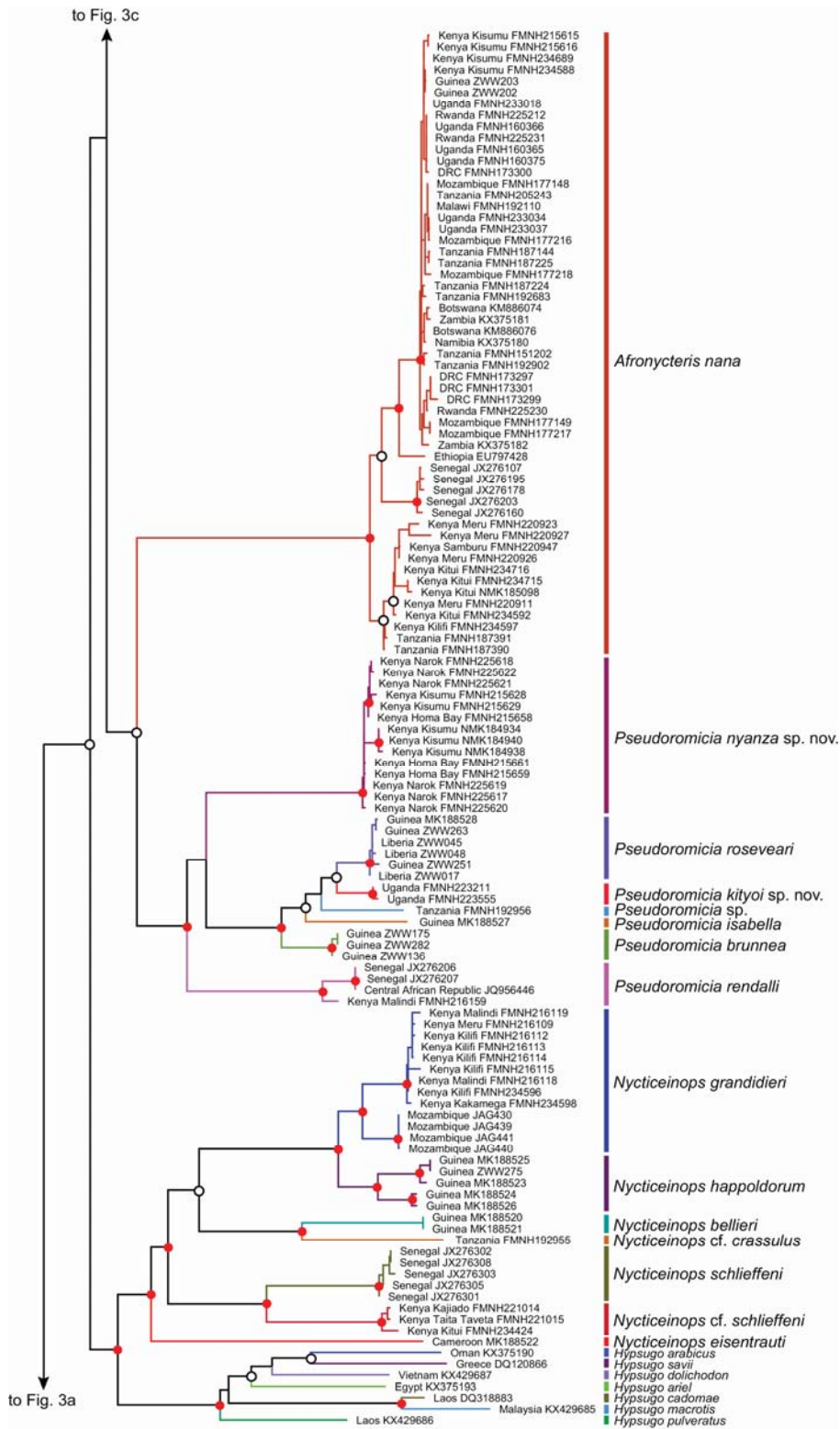


Figure 2. Maximum likelihood phylogeny of intergeneric relationships of mitochondrial cytochrome *b* sequences of Vespertilionidae. The phylogeny was inferred in IQ-TREE, and its topology was similar to the Bayesian phylogeny calculated in MrBayes. Bootstrap (BS) values followed by Bayesian posterior probabilities (PP) are indicated adjacent to nodes (those nodes with both BS < 70% and PP < 0.95 are not labelled).





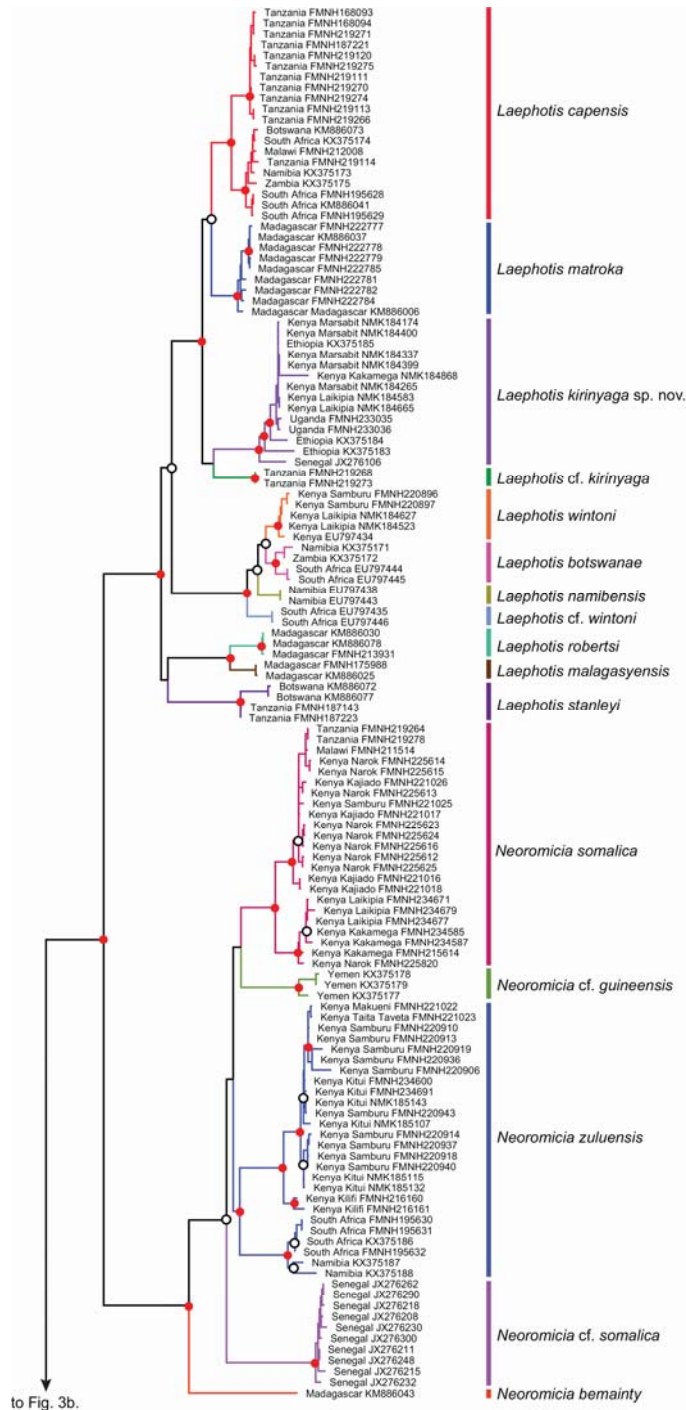


Figure 3. Maximum likelihood phylogeny of mitochondrial cytochrome *b* sequences of Vespertilionidae: (A) *Pipistrellus*, *Scotoecus*, *Vansonia*, and outgroups (B) *Afronycteris*, *Pseudoromicia*, *Nycticeinops*, and *Hypsugo* (C) *Laephotis* and *Neoromicia*. The phylogeny was inferred in IQ-TREE, and its topology was similar to the Bayesian phylogeny calculated in MrBayes. Filled red circles on nodes denote bootstrap (BS) values $\geq 70\%$ and Bayesian posterior probabilities (PP) ≥ 0.95 . Open circles outlined in black indicate BS $\geq 70\%$ and PP < 0.95 , and open circles outlined in red indicate BS $< 70\%$ and PP > 0.95 . Support values for most minor clades are not shown. Specimen localities include counties for Kenya. DRC refers to Democratic Republic of the Congo and CAR to Central African Republic. Museum acronyms are defined in the Material and Methods section. Sequences downloaded from GenBank are indicated by inclusion of GenBank accession numbers (Supporting Information, Table S1). Branch colours indicate individual species/clade membership.

In contrast to the novel groupings found for Vespertilionini, our analyses of Pipistrellini confirmed the existing content and composition of the three genera found in the Afrotropics: our sample included 10 species of *Pipistrellus*, which are sister to the species of *Scotoecus*; this group is then sister to *Vansonia*, comprising only *V. rueppellii*.

The genetic distances for the various genera are shown in Table 1 and distances for 53 Pipistrellini and Vespertilionini species are shown in Table S4. It is noteworthy that genetic distances for the two newly identified lineages (named below), *Pseudoromicia* and *Afronycteris*, are comparable to other long-recognized genera. The genetic distances among the seven currently recognized genera in this study (*Hypsugo*, *Laephotis*, *Neoromicia*, *Nycticeinops*, *Pipistrellus*, *Scotoecus*, and *Vansonia*) range from 0.148 to 0.203 (0.042 to 0.142 intrageneric distances). In comparison, *Pseudoromicia* and *Afronycteris* have genetic distances ranging from 0.157 to 0.196 (with intrageneric distances of 0.097 and 0.032, respectively). *Afronycteris nana* is well supported as monophyletic as are five of seven species within *Pseudoromicia*; the exceptions being *Pse. isabella* and *Pse. sp.* from Tanzania represented by single sequences on relatively long branches (Fig. 3b).

Table 1. Uncorrected *cyt-b* *p*-distances among (below diagonal) and within (numbers on diagonal) nine genera of Vespertilionidae calculated in MEGA X 10.0.5.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
[1] <i>Afronycteris</i>	0.032								
[2] <i>Hypsugo</i>	0.189	0.142							
[3] <i>Laephotis</i>	0.169	0.174	0.076						
[4] <i>Neoromicia</i>	0.183	0.181	0.148	0.069					
[5] <i>Nycticeinops</i>	0.187	0.183	0.172	0.178	0.121				
[6] <i>Pipistrellus</i>	0.196	0.198	0.185	0.182	0.188	0.107			
[7] <i>Pseudoromicia</i>	0.168	0.181	0.157	0.165	0.178	0.182	0.097		
[8] <i>Scotoecus</i>	0.190	0.198	0.176	0.197	0.178	0.175	0.181	0.058	
[9] <i>Vansonia</i>	0.196	0.200	0.190	0.203	0.199	0.192	0.189	0.188	0.042

Morphometric analyses

The PCA ordination on craniodental measurements shows that the species traditionally placed within *Neoromicia* and *Laephotis* fall into four distinct regions of morphospace (Fig. 4). The first two principal axes accounted for over

92% of the variation, with the first axis representing a size gradient with negative loadings on all measurements (Table S2). Hence, the largest species (e.g. *Neo. robertsi*) appear on the left of the ordination and the smallest species (e.g. *Neo. nana*) on the right. The second principal component has both high and low loadings and reflects differences in shape. The largest positive loading is with GSKL (0.488) and the largest negative loading with GSH (-0.656), suggesting that species with higher projections on PCA2 have larger, flatter crania than those with lower ones. These four groups neatly correspond to four distinct bacular types (Fig. 5) and we suggest that they represent different genera (see below). The bacula of these four groups differ in size, shape of the shaft, and the shape of the proximal and distal ends (see Fig. 5); the baculum shape of each group is described in detail in the description of the genera (see below).

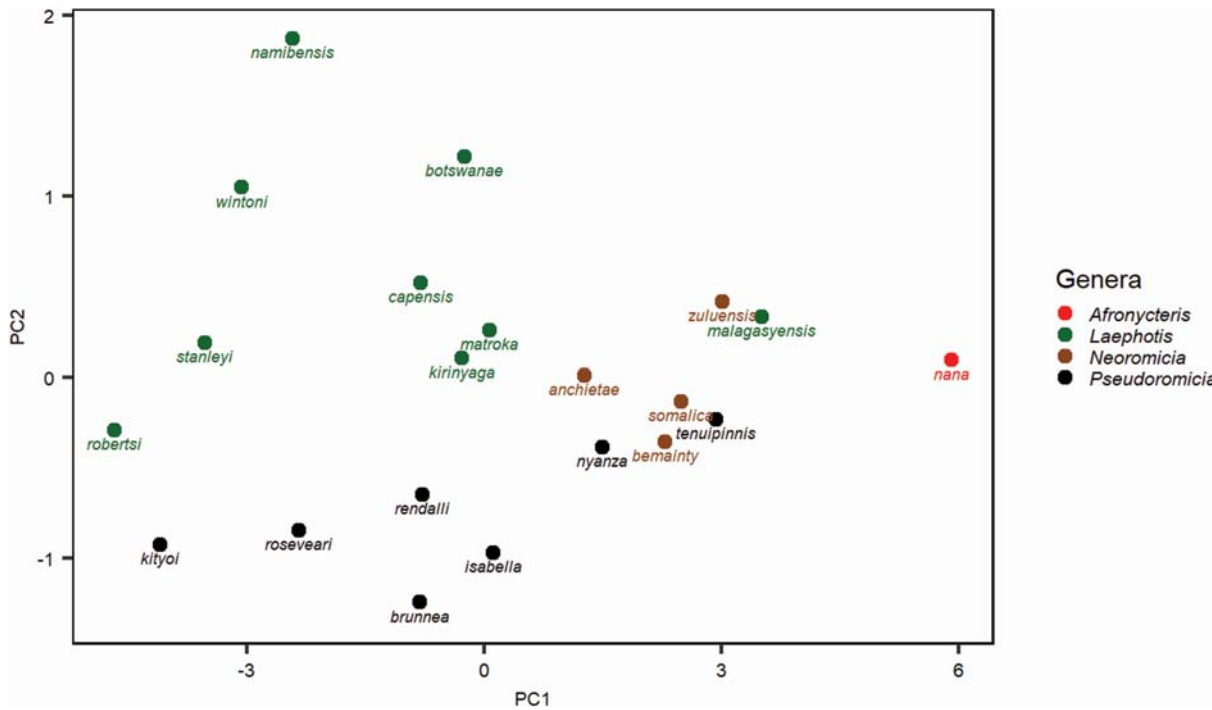


Figure 4. Principal components analysis of craniodental measurements of the species traditionally allocated to the genus *Neoromicia s.l.*; the colours correspond to the four distinct types of bacula exhibited by these species (shown in Fig. 5). Each dot refers to the mean value of the craniodental measurements of examined specimens; see main text for further details.



Figure 5. Bacula of the four clades within formerly or traditionally recognized as *Neoromicia*: A, *Laephotis kirinyaga* (FMNH 234639); B, *Neoromicia somalica* (FMNH 215614); C, *Pseudoromicia kityoi* (FMNH 223211); and D, *Afronycteris nana* (DM 13013). Note the three-pronged tip in *Neoromicia*, the straight shaft with spatulate tip at an angle of 45° in *Laephotis*, the long, curved shaft with bilobed tip in *Pseudoromicia* and the deeply bilobed base and gently curved shaft in *Afronycteris*. Scale bars: 1 mm.

Within the '*Neoromicia capensis*' group, the PCA ordination on craniodental measurements shows that most species occupy separate regions of morphospace (Fig. 6). The first two principal axes accounted for over 81% of the variation, with the former axis representing a size gradient with negative loadings on all measurements (Table S3). Hence, the largest species (e.g. *Neo. stanleyi* and *Neo. robertsi*) are on the left of the ordination and the smallest species (e.g. *Neo. matroka*) on the right. However, there is significant overlap between *Neo. matroka* and *Neo. cf. capensis*. The second principal component has both high and low loadings and represents differences in shape; with all long axis length measurements having positive values, and all width measurements (except MAST and C-C) having negative values (Table S3). The largest positive loading is with $c-m_3$ (0.157) and the largest negative loading with POB (-0.727), suggesting that species with high positive values on PCA2 have longer mandibles and narrower post-orbital constrictions compared to those with lower values. Furthermore, *Neo. capensis* from southern Africa occupies mostly different morphospace compared with *Neo. cf. capensis* from East and West Africa, which we describe as a new species.

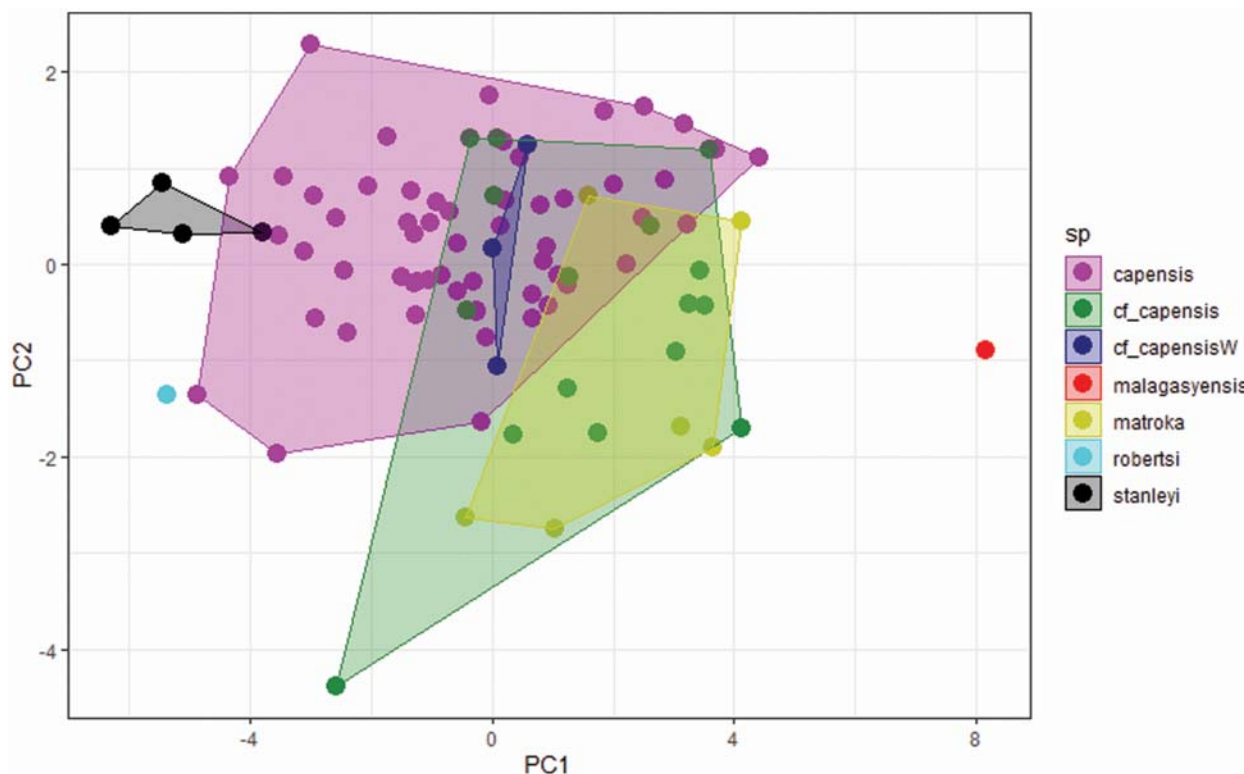


Figure 6. Principal components analysis of craniodental characters of the short-eared species of *Laephotis* as recognized in this study.

Taxonomic conclusions

Our phylogenetic analyses show support for the genera *Pipistrellus* and *Vansonia*, but clearly indicate the paraphyly of the genera *Neoromicia* and *Parahypsugo* as currently recognized (Moratelli & Burgin, 2019; Monadjem *et al.*, 2020b).

Our phylogeny supports synonymizing *Parahypsugo* with *Afropipistrellus* because the addition of *N. grandidieri* to the group of species recognized by Hutterer *et al.* (2019) as *Parahypsugo* (type species *P. happoldorum* plus *P. bellieri*, *P. crassulus*, and *P. eisentrauti*, with *P. macrocephalus* added subsequently by Hutterer & Kerbis Peterhans (2019)) renders *Parahypsugo* a junior synonym of *Afropipistrellus*. The strong divergence of “*Parahypsugo eisentrauti*” places it immediately outside the group *Afropipistrellus* + *Nycticeinops*, but this appraisal is based on only 764 base pairs of *cyt-b*. Therefore, we propose that *Afropipistrellus* (with *Parahypsugo* as a synonym) be synonymized with *Nycticeinops*.

We suggest restricting *Neoromicia* to the type species *N. zuluensis*, the sister species *N. somalica*, and the sister taxa *N. bemaityi* and *N. anchietae*. Further, we suggest that the “*Laephotis*” clade (Fig. 2) that includes the genus *Laephotis* and several species currently placed in the genus *Neoromicia* (including *N. capensis*, *N. stanleyi*, and the Malagasy species *N. matroka*, *N. robertsi*, and *N. malagasyiensis*) be recognized under the genus *Laephotis*. The third clade, which includes mostly tropical rainforest species of *Neoromicia* s.l. (including *N. brunnea*, *N. roseveari*, *N. isabella*, and *N. tenuipinnis*), as well as the widely distributed *N. rendalli*, currently has no preexisting name, for which we describe a new genus (see below). A new genus is also needed for the ubiquitous banana bat, formerly known as *Neoromicia nana*.

Our phylogeny supports the recognition of *Vansonia* as a distinct genus (rather than a subgenus of *Pipistrellus*), since it is sister to *Pipistrellus* + *Scotoecus*.

This generic rearrangement of the African members of the Vespertilionini and Pipistrellini is also reflected in certain morphological traits, particularly bacular shape, and where information is available, penial characteristics (Fasel, Mamba, & Monadjem, 2020).

Based on the molecular and morphological evidence presented above, we further describe three new species within the *Laephotis* and gen. nov. clades from East Africa.

TAXONOMY

FAMILY VESPERTILIONIDAE GRAY, 1821

TRIBE VESPERTILIONINI GRAY, 1821

NEOROMICIA ROBERTS, 1926

Synonymy

Vesperugo Bocage, 1889 (part, not Keyserling and Blasius, 1839)

Vespertilio Thomas, 1901 (part, not Linnaeus, 1758)

Eptesicus G.M. Allen, 1911 (part, not Rafinesque, 1820)

Pipistrellus Zammarano, 1930 (part, not Kaup, 1829)

Complete synonymic histories for the species of *Neoromicia* are given in ACR (2019)

Description of genus: This genus was originally created for the species *Neoromicia zuluensis*, based on it having “the cranium slightly raised above the level of the muzzle” (Roberts, 1926). The close relationship between this taxon and *Neoromicia somalica* (Thomas, 1901) has long been recognized and the two are sister taxa in our phylogeny.

Based on our genetic and morphometric analyses presented above, we have further expanded this genus to include the following species: *Neoromicia guineensis* (Bocage, 1889); *Neoromicia anchietae* (Seabra, 1900); and *Neoromicia bemainty* (Goodman et al., 2015). These are all small-sized pipistrelle-like bats with a distinct bacular morphology (Fig. 5b). The baculum (ca. 1.5-2.0 mm in length) is shorter than in *Pseudoromicia* and similar in length to *Laephotis* and *Afronycteris*. It has a characteristic shape with a thick base that is weakly bilobed, a shaft with a straight outer margin and slightly curved inner margin, and a unique three-pronged (cross-shaped) tip that is set at a slight angle to the shaft (Fig. 5b). They also have a more inflated braincase than *Laephotis* species, but not as inflated as

Afronycteris, from which they differ in many other respects (for more details see the description in the *Afronycteris* account). They lack the white wings of *Pseudoromicia* and have bicoloured fur on both the upper and under parts. All five species are essentially savanna or woodland species with four of them occurring in southern and eastern Africa and Madagascar.

LAEPHOTIS THOMAS, 1901

Synonymy

Vespertilio A. Smith, 1829 (part, not Linnaeus, 1758)

Hypsugo Kolenati, 1860 (part, not Kolenati, 1856)

Scotophilus Tomes, 1861 (part, not Leach, 1821)

Vesperugo Dobson, 1878 (part, not Keyserling and Blasius, 1839)

Vesperus Jentink, 1887 (part, not Keyserling and Blasius, 1839)

Eptesicus Matschie, 1897 (part, not Rafinesque, 1820)

Scabrifer G.M. Allen, 1908

Rhinopterus G.M. Allen, 1939 (part, not Miller, 1906)

Pipistrellus Heller & Volleth, 1984 (part, not Kaup, 1829)

Nycterikaupius (part, not Menu, 1987)

Neoromicia Volleth et al., 2001 (part, not Roberts, 1926)

Complete synonymic histories for the species of *Laephotis* are given in ACR (2019)

Description of genus: This genus was originally created for the species *Laephotis wintoni*, with the name referring to the large “sail-like” ears of that species. A second, closely related species with large ears was described a quarter of a

century later *Lae. angolensis* Monard 1935, and two more species in 1971 *Lae. botswanae* Setzer, 1971, and *Lae. namibensis* Setzer, 1971. The baculum (1.5-2.0 mm in length) of *Laephotis* as defined herein is shorter than in *Pseudoromicia* and similar in length to *Neoromicia* and *Afronycteris*. It has a characteristic shape with a bilobed base, straight shaft with a spatulate tip and is at an angle of about 45° to the shaft (Fig. 5a).

Based on our genetic and morphometric analyses presented above, we have further expanded this genus to include the following species: *Laephotis capensis* (A. Smith, 1829), *Laephotis matroka* (Thomas & Schwann, 1905), *Laephotis robertsi* (Goodman et al. 2012), *Laephotis malagasyensis* (Peterson, Eger & Mitchell, 1995), and *Laephotis stanleyi* (Goodman et al. 2017). *Laephotis* is readily distinguished by its bacular morphology (Hill & Harrison, 1987). It is easily separated from *Afronycteris* based on external features (see the latter account for details). This genus may also be distinguished from *Neoromicia* by its larger size. Furthermore, the cranium is more robust in *Laephotis* and obviously flattened compared with *Neoromicia* and *Pseudoromicia*. *Laephotis* also lacks the white wings of *Pseudoromicia* and is mostly associated with arid savannas and grasslands. Of the nine species that we recognize in this genus, all except the one we describe here are restricted to eastern and southern Africa and Madagascar; and none are associated with rainforests of tropical Africa.

LAEPHOTIS KIRINYAGA MONADJEM, PATTERSON, WEBALA & DEMOS, **SP. NOV.**

EAST AFRICAN SEROTINE

LSID: <http://zoobank.org/urn:lsid:zoobank.org:pub:71737F08-2938-4403-8385-5438B2E5EABE>

Synonymy

Eptesicus capensis: Kingdon (1974)

Pipistrellus capensis garambe: Thorn & Kerbis Peterhans (2009) (in part)

Neoromicia capensis: Patterson & Webala (2012)

Neoromicia somalica: Benda et al. (2016) (in part)

Holotype: FMNH 234558, field number BDP 7516. This specimen was collected by Bruce D. Patterson, Paul W. Webala, Carl W. Dick, and Beryl Makori. It is an adult male with muscle tissue in liquid nitrogen, the body fixed in formalin and preserved in ethanol, now with skull extracted and cleaned.

Type locality: Marsabit National Park, 1.3 km SE of campground near Headquarters, Marsabit County, Kenya (2.3090°N, 38.0001°E) (Fig. 1). The type specimen was netted on 27 July 2015 at an elevation of 1280 m above sea level.

Paratypes: One other male (FMNH 234559) was captured at the same location and on the same night as the type specimen and is considered a paratype. Seven other individuals (FMNH 234546, FMNH 234549-234553, FMNH 234556-234557, four males and three females), were collected close to the type locality at elevations ranging from 1157-1356 m from 16-26 July 2015 (Table S1) ; they closely resemble the holotype genetically (Fig. 3c) and morphologically (Tables 2-4) and are also considered paratypes.

Table 2. External measurements (mm) and mass (g) of *Laephotis kirinyaga* **sp. nov.** from Marsabit National Park, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements of the holotype, other individuals of the new species, and other “short-eared” species of *Laephotis*. Measurements for the three Malagasy endemics *Lae. robertsi*, *Lae. matroka* and *Lae. malagasyensis* taken from Goodman *et al.* (2017).

Specimen or taxon	Total length	Tail length	Hindfoot length	Ear length	Forearm length	Body mass
<i>Laephotis kirinyaga</i> sp. nov.	80	32	6	12	31.5	4.7
Holotype FMNH 234558						
<i>Laephotis kirinyaga</i> sp. nov. (other specimens)	82.8 \pm 5.67, 74–95, n = 16	32.6 \pm 2.22, 28–37, n = 16	6.5 \pm 0.97, 5–8, n = 16	11.5 \pm 1.10, 9–13, n = 16	31.5 \pm 1.35, 30.5–34.1, n = 16	5.3 \pm 0.87, 4–7, n = 16
<i>Laephotis capensis</i>	88.7 \pm 7.09, 76–102, n = 24	34.9 \pm 3.83, 26–40, n = 24	7.4 \pm 0.84, 6–8, n = 24	12.8 \pm 1.46, 11–17, n = 24	33.4 \pm 2.22, 29.1–37.1, n = 38	5.7 \pm 1.23, 3–8, n = 18
<i>Laephotis stanleyi</i>	93.3 \pm 6.42, 83–101, n = 8	39.7 \pm 4.46, 34–48, n = 5	7.3 \pm 0.76, 6–9, n = 8	12.3 \pm 1.91, 10–15, n = 8	37.0 \pm 1.58, 34–39, n = 8	6.5 \pm 0.30, 6.1–6.8, n = 7
<i>Laephotis robertsi</i>	91.0 \pm 4.06, 84–94, n = 5	34.6 \pm 2.07, 31–36, n = 5	5.4 \pm 0.55, 5–6, n = 5	13.0 \pm 0, 13–13, n = 5	35.5 \pm 1.41, 34.5–38.0, n = 5	8.5 \pm 1.72, 7.4–11.5, n = 5
<i>Laephotis matroka</i>	82.1 \pm 3.18, 77–86, n = 12	32.2 \pm 2.76, 27–36, n = 12	4.6 \pm 0.51, 4–5, n = 12	11.8 \pm 0.76, 11–13, n = 12	32.1 \pm 1.51, 30–34, n = 12	5.3 \pm 0.88, 4.0–7.5, n = 12
<i>Laephotis malagasyensis</i>	81.3 \pm 1.15, 80–82, n = 3	36.0 \pm 1.00, 35–37, n = 3	4.8 \pm 0.50, 4–5, n = 4	12.0 \pm 0.82, 11–13, n = 4	31.3 \pm 0.96, 31–32, n = 4	4.5 \pm 0.53, 3.7–6.0, n = 4

Table 3. Cranial measurements (mm) of specimens of *Laephotis kirinyaga* **sp. nov.** from Marsabit National Park, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements of the holotype, other individuals of the new species, and other “short-eared” species of *Laephotis*. Measurements for the three Malagasy endemics *Lae. robertsi*, *Lae. matroka* and *Lae. malagasyensis* taken from Goodman *et al.* (2017).

Specimen or taxon	GSKL	ZYGO	POB	MAST	GBW	GSH	MAND
<i>Laephotis kirinyaga</i> sp. nov.	13.21	8.41	3.62	7.00	6.74	4.60	9.49
Holotype FMNH 234558							
<i>Laephotis kirinyaga</i> sp. nov. (other specimens)	13.55 \pm 0.43, 12.89–14.25, n = 16	8.71 \pm 0.37, 7.95–9.73, n = 16	3.71 \pm 0.21, 3.34–4.16, n = 16	7.49 \pm 0.32, 6.96–8.09, n = 16	7.07 \pm 0.22, 6.72–7.49, n = 16	4.68 \pm 0.30, 4.22–5.49, n = 16	9.85 \pm 0.33, 9.36–10.52, n = 16
<i>Laephotis capensis</i>	14.05 \pm 0.48, 13.09–15.35, n = 58	8.95 \pm 0.37, 8.24–9.62, n = 57	3.68 \pm 0.13, 3.42–4.00, n = 57	7.87 \pm 0.34, 7.07–8.74, n = 57	7.28 \pm 0.24, 6.81–7.72, n = 57	4.57 \pm 0.19, 4.17–5.11, n = 57	10.35 \pm 0.43, 9.41–11.17, n = 57
<i>Laephotis stanleyi</i>	15.2 \pm 0.21, 14.8–15.4, n = 7	9.6 \pm 0.29, 9.3–10.0, n = 6	3.7 \pm 0.21, 3.5–4.1, n = 7	8.4 \pm 0.10, 8.2–8.5, n = 7	-	-	10.6 \pm 0.32, 10.2–11.0, n = 6
<i>Laephotis robertsi</i>	14.7 \pm 0.19, 14.4–14.8, n = 4	9.9 \pm 0.37, 9.5–10.4, n = 4	4.0 \pm 0.24, 3.6–4.1, n = 4	8.4 \pm 0.22, 8.2–8.7, n = 4	-	-	10.6 \pm 0.15, 10.4–10.7, n = 4
<i>Laephotis matroka</i>	13.1 \pm 0.33, 12.4–13.4, n = 12	8.8 \pm 0.28, 8.4–9.2, n = 9	3.5 \pm 0.14, 3.3–3.8, n = 12	7.5 \pm 0.25, 7.2–7.9, n = 12	-	-	9.0 \pm 0.21, 8.7–9.3, n = 10
<i>Laephotis malagasyensis</i>	12.6 \pm 0.38, 12.4–13.3, n = 5	8.5 \pm 0.26, 8.3–8.8, n = 5	3.4 \pm 0.18, 3.2–3.7, n = 5	7.2 \pm 0.32, 6.9–7.7, n = 5	-	-	8.3 \pm 0.13, 8.2–8.5, n = 5

Table 4. Dental measurements (mm) of specimens *Laephotis kirinyaga* **sp. nov.** from Marsabit National Park, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements of the holotype, other individuals of the new species, and other “short-eared” species of *Laephotis*. Measurements for the three Malagasy endemics *Lae. robertsi*, *Lae. matroka* and *Lae. malagasyensis* taken from Goodman *et al.* (2017).

Specimen or taxon	C-M ³	C-C	M ³ -M ³	c-m ₃
<i>Laephotis kirinyaga</i> sp. nov.	4.75	4.13	5.65	5.01
Holotype FMNH 234558				
<i>Laephotis kirinyaga</i> sp. nov. (other specimens)	4.79 \pm 0.17, 4.50–5.09, n = 16	4.28 \pm 0.18, 4.03–4.55, n = 16	5.72 \pm 0.20, 5.43–6.09, n = 16	5.09 \pm 0.19, 4.85–5.61, n = 16
<i>Laephotis capensis</i>	4.96 \pm 0.21, 4.49–5.53, n = 10	4.45 \pm 0.17, 4.02–4.81, n = 57	5.81 \pm 0.23, 5.34–6.30, n = 57	5.29 \pm 0.26, 4.75–5.81, n = 57
<i>Laephotis stanleyi</i>	5.1 \pm 0.13 4.9–5.3, n = 7	4.6 \pm 0.20 4.3–4.8, n = 7	6.1 \pm 0.17 5.8–6.3, n = 7	-
<i>Laephotis robertsi</i>	5.4 \pm 0.13 5.2–5.5, n = 4	4.9 \pm 0.17 4.6–5.0, n = 4	6.5 \pm 0.10 6.4–6.6, n = 4	-
<i>Laephotis matroka</i>	4.5 \pm 0.17 4.2–4.8, n = 12	4.1 \pm 0.17 3.9–4.4, n = 12	5.6 \pm 0.20 5.3–5.9, n = 12	-
<i>Laephotis malagasyensis</i>	4.2 \pm 0.13 4.1–4.4, n = 5	3.8 \pm 0.16 3.6–4.0, n = 5	5.2 \pm 0.30 5.0–5.7, n = 5	-

Etymology: The specific epithet is a Kikuyu word for Mount Kenya and reflects the species' distribution in the northern highlands of Kenya. It is used as a noun in apposition.

Diagnosis: This species is similar in size and appearance to its sister species *Laephotis capensis*. It is easily distinguished from the long-eared *Laephotis* species by its shorter ears. Of the short-eared *Laephotis* species, *Lae. stanleyi* and *Lae. robertsi* are significantly larger in forearm length and most craniodental measurements (Tables 2-4). In contrast, *Lae. malagasyensis* is smaller, especially in cranial measurements (Table 3). *Lae. matroka* is similar in external and craniodental measurements but is typically darker brown above and medium brown below (Goodman, 2011). In any case, *Lae. robertsi*, *Lae. malagasyensis* and *Lae. matroka* are all endemic to Madagascar (Goodman *et al.*, 2012, 2017) and genetically distinct from *Lae. kirinyaga* (Fig. 3c). *Lae. kirinyaga* resembles closely *Lae. capensis*, from which it differs by 8.3% on the *cyt-b* gene (Table S4). Externally, the two species are alike and broadly overlap in size, but *Lae. kirinyaga* averages smaller in most measurements, particularly total and forearm lengths (Table 2). Similarly, *Lae. capensis* is on average larger for all craniodental measurements (but with significant overlap), except greatest skull height, which is greater in *Lae. kirinyaga*. This is borne out in the lateral profile of the skull which is visibly flatter in *Lae. capensis* (Fig. 7). These two species occupy mostly separate regions in multivariate space (Fig. 6), but again with some overlap. In contrast, the three specimens assigned to *Lae. kirinyaga* from Ethiopia and Guinea, for which genetic data are lacking, fall completely within the multivariate space of the *Lae. kirinyaga* specimens that have been sequenced.

Description: External characters: *Laephotis kirinyaga* sp. nov. is a medium-sized pipistrelle-like bat with strongly contrasting fur dorsally and ventrally. The dorsal pelage is medium brown with most individual hairs being tipped light yellowish-brown, giving the bat a brightly coloured appearance. The ventral pelage is cream-white to light cream-brown with a dark base. The ears are short and rounded, and the tragus is curved distally on both anterior and posterior margins, ending in a rounded tip as in *Lae. capensis* (Monadjem *et al.*, 2020a). The ears and muzzle are dark brown in colour while the skin around the eyes is dark brown in the type specimen (Fig. 8a) but mostly pinkish in the paratypes.

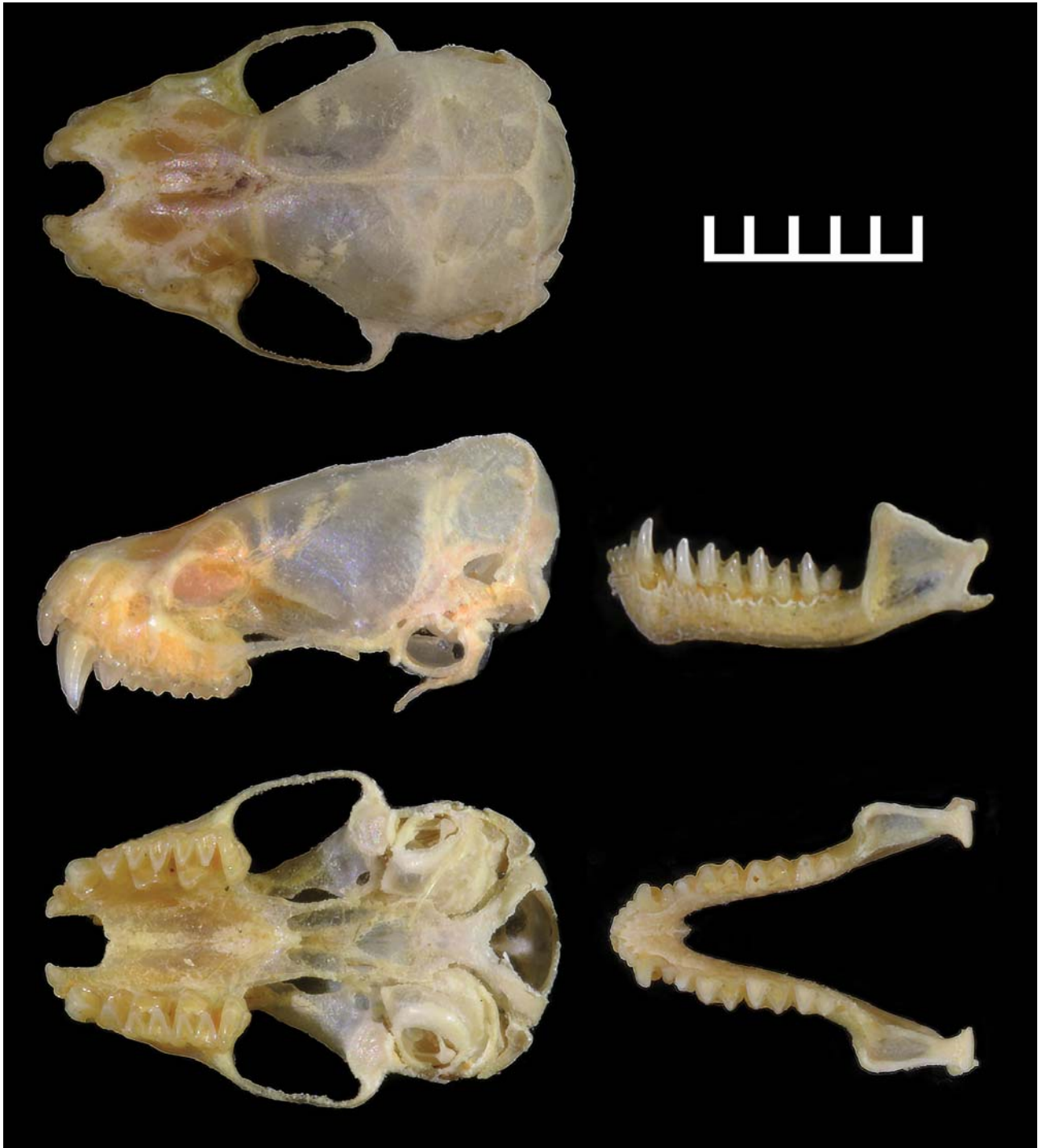


Figure 7. Plate showing the cranium and mandible of *Laephotis kirinyaga* (FMNH 234558). Scale bar = 5 mm.



Figure 8. A, portrait of *Laephotis kirinyaga* (FMNH 234558), showing bright brown upper parts and off-white under parts, with bicoloured hairs. The skin around the eye is blackish in the holotype, but distinctly pinkish in most of the paratypes. B, portrait of *Pseudoromicia nyanza* (FMNH 215626), showing the distinctive white wings and under parts of this species.

Craniodental characters: The skull is relatively robust as in *Lae. capensis* but less so than in *Lae. stanleyi*. In lateral profile, the cranium is distinctly straight, rising only very gently up from the rostrum to the top of the braincase. An occipital “helmet” is present but poorly developed, while the sagittal and lambdoidal crests are visible. The zygomatic arches are relatively robust as in *Lae. capensis* (Fig. 7). The dentition in *Lae. kirinyaga* is typical of the genus with I 2/3, C 1/1, P 1/3, M2/3. In the upper tooth row, I¹ is unicuspid and I² is small, not reaching halfway up the length of I¹. The P¹ is absent, putting C in contact with P². The m₃ is myotodont sensu Van Cakenberghe & Happold (2013).

Biology: This species has been infrequently captured across the highlands of Kenya on both sides of the Rift Valley. It is present in wet tropical forest (e.g. Kakamega forest with ca. 1,900 mm of rainfall per annum), less mesic montane forest (Marsabit National Park) and relatively dry savanna woodlands (e.g. Loll Daiga Hills conservancy ca. 600 mm), hence aridity per se does not seem to be an important variable in its distribution. However, it has only been recorded at elevations above 1,000 m (current records are all between 1,160 m and 1,700 m), and this may be an important limit on its geographical distribution. We also include two specimens (FMNH 233035, 233036) from Murchison Falls National Park, Uganda (1,180 m above sea level) in this new species. Two specimens from Ethiopia (identified as “*Neoromicia somalica*” by Benda *et al.* (2016)) also group with *Lae. kirinyaga* in the phylogeny, as does a specimen from Senegal (Koubínová *et al.*, 2013), suggesting that this newly described species has a wide distribution north of the equator. We recommend, based on its relatively large distribution range and habitat preference that it be listed as ‘Least Concern’ on the IUCN red list. However, we did not examine the specimens from Ethiopia and Senegal and so recommend a detailed morphological investigation before our hypothesis concerning the geographical range of this species is accepted. The type specimen echolocated at a peak frequency (start and end frequencies) of 44.9 kHz (74.3 – 41.6 kHz). The mean (\pm SD) peak frequency for 14 other individuals at the type locality was 43.9 ± 0.91 kHz (73.9 ± 9.43 – 41.8 ± 1.64 kHz).

PSEUDOROMICIA MONADJEM, PATTERSON, WEBALA & DEMOS, GEN. NOV.

Synonymy

Vesperus Peters 1872 (part, not Keyserling and Blasius, 1839)

Vesperugo Dobson 1878 (part, not Keyserling and Blasius, 1839)

Eptesicus Matschie, 1897 (part, not Rafinesque, 1820)

Vespertilio Miller, 1900 (part, not Linnaeus, 1758)

Pipistrellus Monard, 1935 (part, not Kaup, 1829)

Nycterikaupius (part, not Menu, 1987)

Neoromicia Kearney et al., 2002 (part, not Roberts, 1926)

Complete synonymic histories for the species placed herein in *Pseudoromicia* are given in ACR (2019)

Type species: *Pseudoromicia tenuipinnis* (Peters, 1872)

Included species: *Pseudoromicia brunnea* (Thomas, 1880); *Pseudoromicia isabella* (Decher, Hutterer & Monadjem, 2015); *Pseudoromicia rendalli* (Thomas, 1889); *Pseudoromicia roseveari* (Monadjem et al., 2013); *Pseudoromicia tenuipinnis* (Peters, 1872); as well as two newly described species (see below).

Etymology: The genus *Neoromicia*, to which members of *Pseudoromicia* gen. nov. were previously allocated, was named to mean “new *Romicia*”; *Romicia* is now an invalid name, but was originally given to *Romicia calcarata* Gray, 1838 (now considered a synonym of *Pipistrellus kuhlii*). *Pseudoromicia* derives from the fact that members of this newly described genus resemble and have been confused with *Neoromicia* species.

Diagnosis: These are small to medium-sized vespertilionids with a simple muzzle. The tragus is typically curved anteriorly with a notch at the base of the posterior margin. The pelage of the upper and under parts is variably coloured but in most species tends to be unicoloured dorsally and bicoloured ventrally; in contrast, dorsal pelage is bicoloured in *Afronycteris*, *Laephotis* and *Neoromicia*. Four of the seven species in this genus have translucent white wing membranes, while membranes are dark brown or blackish in colour in the remaining three species. The cranium is slightly inflated to relatively flattish in lateral profile, in contrast it is highly inflated in *Afronycteris* and moderately inflated in *Neoromicia* sensu stricto, whereas it is flattened in *Laephotis*. The outer incisors are usually half the length or less of the inner incisors, the latter being weakly bicuspid or unicuspid. The P¹ is absent, contrasting with *Afronycteris* in which it is present and relatively large. The baculum (ca. 3.0 mm in length) is distinctly longer than any of the other three genera previously included in *Neoromicia*, with a robust trilobed base, and strongly arched shaft leading to a bilobed tip (Fig. 5c).

Distribution: This genus is widely distributed across sub-Saharan Africa. However, all but one of the species is associated with equatorial tropical forest and woodland belt. One species, *Pse. rendalli*, extends far into savanna habitats, ranging from 13°N to 28°S.

Systematic relationships: The genera *Pseudoromicia* gen. nov. and *Afronycteris* gen. nov. are sister to the genera *Laephotis* and *Neoromicia* as now understood (see below).

PSEUDOROMICIA KITYOI MONADJEM, KERBIS PETERHANS, NALIKKA, BABYESIZA, DEMOS & PATTERSON, **SP. NOV.**

KITYO'S SEROTINE

Holotype: FMNH 223211, field number JCK 7436. This specimen was collected by Betty Nalikka and Sadic Waswa Babyesiza during a field training exercise with Julian Kerbis Peterhans. It is an adult male preserved in ethanol, with skull extracted and cleaned, and tissue taken from breast muscle and preserved in DMSO.

Type locality: Mabira Forest Reserve, 0.79 km north-east of Nagojje Station, Mukono District of the Central Region, Uganda; geographical coordinates: 0.4451°N, 32.88876°E (Fig. 1). The type specimen was netted on 19 October 2012

in cultivated gardens directly adjacent (see Fig. S2 for a photograph of the type locality) to Mabira forest at an elevation of 1130 m above sea level.

Paratype: One other male (FMNH 223555) was netted at the same location and on the same night as the holotype, and closely resembles it genetically (Fig. 3b) and morphologically (Tables 5-7) and can therefore be considered a paratype.

Etymology: This species is named in honour of Prof. Robert M. Kityo, mammalogist, mentor, and long-serving curator at the Museum of Zoology, Makerere University, in recognition of his valuable contributions to bats and small mammal research in the region. His welcoming nature, curiosity, hospitality, and support have facilitated numerous and diverse research agendas over the decades for both national and international researchers.

Diagnosis: This is the largest member of the genus *Pseudoromicia*, with forearm length of 37 and 38 mm (Table 5) and greatest skull length of 14.70 and 14.99 mm for the two known specimens (Table 6). By comparison, the maximum greatest skull length in *Pse. roseveari* (which is the second largest member of the genus) is 14.5 mm (Table 6). *Pse. brunnea* is far smaller in forearm length and most craniodental measurements. Therefore, this species is readily diagnosable by size alone. It can easily be distinguished from the white-winged members of this genus (*Pse. rendalli*, *Pse. isabella*, and *Pse. tenuipinnis*) by its dark wings.

Description: External characters: *Pse. kityoi* sp. nov. is a large-sized pipistrelle-like bat, similar in size to the largest members of the *Nycticeinops* group, specifically *Nyc. macrocephalus* and *Nyc. happoldorum*, which were both described in the genus *Paraphypsugo* (Hutterer & Kerbis Peterhans, 2019; Hutterer *et al.*, 2019). Despite its large size, this species is similar in external features to other black-winged members of *Pseudoromicia*. The pelage is medium brown above and slightly paler below. The individual hairs are unicoloured on the upper parts and bicoloured under parts, with the proximal half darker than the distal half. Like *Pse. brunnea* and *Pse. roseveari*, the patagium and uropatagium are both dark in colour. The ears are short and rounded, and the tragus has a curved outer margin as is typical of the genus (Monadjem *et al.*, 2013).

Craniodental characters: The skull is robust for a *Pseudoromicia*, even more so than in *Pse. roseveari*. The rostrum has a shallow depression, and the brain case is moderately inflated as in other members of the genus. There is no occipital “helmet” as seen in the cranium of *Laephotis capensis* (Monadjem *et al.*, 2020a). The sagittal and lambdoidal crests are visible, and the zygomatic arches are robust for a pipistrelle-like bat (Fig. 9). The dentition in

Table 5. External measurements (mm) and mass (g) of *Pseudoromicia kityoi* **sp. nov.** from Mabira Forest Reserve, Uganda and *Pseudoromicia nyanza* **sp. nov.** from Kisumu, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements are of the holotypes, other individuals of the two new species, and other species of *Pseudoromicia*. The three species listed above the horizontal black line are dark-winged, the four below are white-winged (see text for more details).

Specimen or taxon	Total length	Tail length	Hindfoot length	Ear length	Forearm length	Body mass
<i>Pseudoromicia kityoi</i> sp. nov. Holotype FMNH 223211	88	34	10	10	38.0	7.9
<i>Pseudoromicia kityoi</i> sp. nov. Paratype FMNH 223555	89	36	9	10	37.0	8.0
<i>Pseudoromicia roseveari</i>	87.3 \pm 2.95, 83–93, n = 10	39.7 \pm 2.65, 34–44, n = 9	9.9 \pm 1.10, 8–11, n = 10	12.9 \pm 0.64, 12–14, n = 8	36.5 \pm 1.54, 32.6–38.0, n = 10	6.5 \pm 0.50, 6.0–7.0, n = 10
<i>Pseudoromicia brunnea</i>	84.8 \pm 3.14, 80–89, n = 15	35.9 \pm 1.55, 33–38, n = 15	7.79 \pm 0.97, 7–10, n = 14	12.4 \pm 0.83, 11–14, n = 15	34.6 \pm 1.06, 32.8–36.7, n = 15	6.0 \pm 1.04, 4.8–9.4, n = 15
<i>Pseudoromicia nyanza</i> sp. nov. Holotype: FMNH 215626	83	30	7	11	31.0	8.3
<i>Pseudoromicia nyanza</i> sp. nov. (other specimens)	83.5 \pm 2.73, 79–89, n = 13	33.3 \pm 2.29, 30–38, n = 13	7.5 \pm 0.66, 7–9, n = 13	13.0 \pm 0.64, 11–13, n = 13	31.2 \pm 1.24, 29.0– 33.0, n = 13	6.1 \pm 0.99, 4.8–8.3, n = 13
<i>Pseudoromicia rendalli</i>	88.5 \pm 3.92, 82–95, n = 15	37.0 \pm 3.15, 32–42, n = 9	7.5 \pm 0.90, 6–9, n = 8	11.3 \pm 1.57, 9–13, n = 9	34.8 \pm 1.30, 33.4–37.0, n = 9	5.8 \pm 0.94, 4.0–6.8, n = 6
<i>Pseudoromicia isabella</i>	78.8 \pm 2.73, 74–82, n = 15	29.3 \pm 4.23, 24–36, n = 6	6.9 \pm 1.18, 5–8, n = 6	12.3 \pm 1.37, 10–14, n = 6	30.6 \pm 1.47, 28.0– 31.9, n = 6	4.7 \pm 0.87, 4.0–6.0, n = 6
<i>Pseudoromicia tenuipinnis</i> sensu stricto (West Africa)	74.2 \pm 2.17, 72–77, n = 5	29.2 \pm 0.84, 28–30, n = 5	6.5 \pm 0.80, 5–7, n = 7	12.7 \pm 0.91, 12–14, n = 7	29.4 \pm 1.18, 28.1– 32.0, n = 6	4.0 \pm 0.29, 3.5–4.4, n = 6

Table 6. Cranial measurements (mm) of specimens of *Pseudoromicia kityoi* **sp. nov.** from Mabira Forest Reserve, Uganda and *Pseudoromicia nyanza* **sp. nov.** from Kisumu, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements are of the holotypes, other individuals of the two new species, and other species of *Pseudoromicia*. The three species listed above the horizontal black line are dark-winged, the four below are white-winged (see text for more details).

Specimen or taxon	GSKL	ZYGO	POB	MAST	GBW	GSH	MAND
<i>Pseudoromicia kityoi</i> sp. nov. Holotype FMNH 223211	14.99	9.63	3.99	8.25	7.67	5.46	11.25
<i>Pseudoromicia kityoi</i> sp. nov. Paratype FMNH 223555	14.70	9.54	3.91	8.19	7.51	5.38	10.76
<i>Pseudoromicia roseveari</i>	14.13 \pm 0.45, 13.40–14.50, n = 10	8.85 \pm 0.50, 8.00–9.50, n = 9	3.80 \pm 0.19, 3.50–4.09, n = 10	7.84 \pm 0.26, 7.50–8.40, n = 10	7.31 \pm 0.35, 6.87–7.40, n = 10	5.21 \pm 0.12, 5.10–5.40, n = 7	10.40 \pm 0.30, 9.80–10.70, n = 9
<i>Pseudoromicia brunnea</i>	13.73 \pm 0.35, 13.10–14.24, n = 15	8.68 \pm 0.49, 7.70–9.61, n = 14	3.92 \pm 0.23, 3.60–4.45, n = 15	7.50 \pm 0.24, 7.10–7.93, n = 15	7.08 \pm 0.26, 6.65–7.69, n = 15	5.14 \pm 0.25, 4.80–5.50, n = 8	10.06 \pm 0.32, 9.40–10.66, n = 14
<i>Pseudoromicia nyanza</i> sp. nov. Holotype: FMNH 215626	13.20	8.12	3.69	7.31	6.90	5.05	8.97
<i>Pseudoromicia nyanza</i> sp. nov. (other specimens)	12.96 \pm 0.25, 12.48–13.43, n = 17	8.06 \pm 0.30, 7.54–8.69, n = 17	4.00 \pm 0.23, 3.69–4.70, n = 17	7.32 \pm 0.21, 6.99–7.76, n = 17	6.95 \pm 0.20, 6.73–7.45, n = 17	4.81 \pm 0.17, 4.54–5.14, n = 17	9.06 \pm 0.19, 8.80–9.53, n = 18

<i>Pseudoromicia rendalli</i>	13.57 ± 0.48, 12.98–14.70, n = 11	9.05 ± 0.42, 8.40–9.90, n = 10	3.98 ± 0.13, 3.80–4.17, n = 12	7.76 ± 0.32, 7.18–8.33, n = 12	7.25 ± 0.31, 6.80–7.80, n = 12	5.05 ± 0.27, 4.70–5.57, n = 8	9.95 ± 0.33, 9.40–10.50, n = 12
<i>Pseudoromicia isabella</i>	13.12 ± 0.15, 12.99–13.34, n = 5	8.28 ± 0.43, 7.58–8.65, n = 5	3.68 ± 0.15, 3.50–3.89, n = 5	7.27 ± 0.19, 6.96–7.48, n = 5	6.77 ± 0.16, 6.53–6.92, n = 5	4.97 ± 0.09, 4.88–5.06, n = 3	9.64 ± 0.20, 9.32–9.87, n = 5
<i>Pseudoromicia tenuipinnis</i> sensu stricto (West Africa)	12.43 ± 0.28, 12.00–12.78, n = 10	7.48 ± 0.50, 6.80–8.19, n = 9	3.79 ± 0.20, 3.47–4.25, n = 10	6.88 ± 0.14, 6.75–7.22, n = 10	6.51 ± 0.13, 6.40–6.81, n = 10	4.68 ± 0.34, 4.40–5.41, n = 7	8.77 ± 0.38, 8.20–9.33, n = 10

Table 7. Dental measurements (mm) of specimens of *Pseudoromicia kityoi* **sp. nov.** from Mabira Forest Reserve, Uganda and *Pseudoromicia nyanza* **sp. nov.** from Kisumu, Kenya. Measurements presented as mean \pm standard deviation, range and sample size (n). Measurements are of the holotypes, other individuals of the two new species, and other species of *Pseudoromicia*. The three species listed above the horizontal black line are dark-winged, the four below are white-winged (see text for more details).

Specimen or taxon	C-M ³	C-C	M ³ -M ³	c-m ₃
<i>Pseudoromicia kityoi</i> sp. nov. Holotype FMNH 223211	5.20	4.74	6.10	5.63
<i>Pseudoromicia kityoi</i> sp. nov. Paratype FMNH 223555	5.12	4.61	6.09	5.59
<i>Pseudoromicia roseveari</i>	5.03 \pm 0.20, 4.80–5.30, n = 10	4.34 \pm 0.25, 3.80–4.70, n = 10	6.00 \pm 0.25, 5.50–6.30, n = 10	5.25 \pm 0.32, 5.00–5.97, n = 9
<i>Pseudoromicia brunnea</i>	4.86 \pm 0.13, 4.60–5.07, n = 15	4.22 \pm 0.24, 3.63–4.63, n = 15	5.86 \pm 0.26, 5.50–6.55, n = 15	5.30 \pm 0.33, 4.80–5.86, n = 15
<i>Pseudoromicia nyanza</i> sp. nov. Holotype: FMNH 215626	4.31	4.19	5.26	4.62
<i>Pseudoromicia nyanza</i> sp. nov. (other specimens)	4.27 \pm 0.10, 4.04–4.46, n = 18	4.07 \pm 0.11, 3.89–4.29, n = 18	5.24 \pm 0.17, 4.93–5.49, n = 18	4.62 \pm 0.11, 4.42–4.80, n = 18
<i>Pseudoromicia rendalli</i>	4.68 \pm 0.18, 4.44–5.10, n = 12	4.38 \pm 0.25, 4.00–4.80, n = 12	5.65 \pm 0.32, 5.10–6.22, n = 10	5.07 \pm 0.22, 4.60–5.49, n = 12
<i>Pseudoromicia isabella</i>	4.49 \pm 0.05, 4.43–4.56, n = 5	4.40 \pm 0.18, 4.15–4.59, n = 5	5.51 \pm 0.11, 5.33–5.61, n = 5	5.04 \pm 0.19, 4.86–5.35, n = 5
<i>Pseudoromicia tenuipinnis</i> sensu stricto (West Africa)	4.23 \pm 0.14, 3.90–4.35, n = 10	3.81 \pm 0.29, 3.30–4.14, n = 9	5.03 \pm 0.18, 4.70–5.29, n = 9	4.63 \pm 0.23, 4.40–5.24, n = 10

Pse. kityoi is typical of the genus with I 2/3, C 1/1, P 1/3, M2/3. In the upper tooth row, I¹ is unicuspid and I² is tiny, extending just beyond the cingulum of I¹. The P¹ is absent, putting C in contact with P². The m₃ is myotodont sensu Van Cakenberghe & Happold (2013).



Figure 9. Plate showing the cranium and mandible of *Pseudoromicia kityoi* (FMNH 223211). Scale bar = 5 mm.

Biology: Due to the paucity of specimens, almost nothing can be said about the biology of this species. The only two known specimens were captured within 200 meters from the edge of Mabira Forest in a domestic garden (Fig. S2). However, considering that most members of this genus are restricted to tropical rainforest habitats, and that the

two known specimens of this species were captured in a remnant patch of rainforest, its global distribution may be both fragmented and limited in extent. Urgent surveys are required to assess the status of this species at Mabira Forest Reserve, which has been steadily losing habitat to agriculture over the past few decades (Boffa *et al.*, 2008). We suggest that this species may be present in other Congo basin forest patches in Uganda (e.g. Semliki, Kibale, Kashyoha-Kitomi) and Kenya (Kakamega) although extensive surveys at Kakamega forest have failed to locate this species there (Webala *et al.*, 2019). Due to the limited information available on this species, we recommend that it be given the IUCN conservation status of 'Data Deficient', but we note that because of its presumed close association with rapidly disappearing forest habitat, this species is probably of conservation concern.

Its closest known relative is *Pseudoromicia roseveari*, recently described from Mt Nimba and with a limited distribution in the borderland zone between Liberia and Guinea (Monadjem *et al.*, 2013; Decher *et al.*, 2015; Mamba *et al.*, In press), some 4,700 km to the west. Whether either species occurs in the vast tropical rainforests between these two sites is unknown and deserves investigation.

***PSEUDOROMICIA NYANZA* MONADJEM, PATTERSON, WEBALA & DEMOS, SP. NOV.**

NYANZA SEROTINE

Neoromicia tenuipinnis: Patterson & Webala (2012)

Neoromicia tenuipinnis: Musila *et al.* (2019)

Neoromicia tenuipinnis Rydell *et al.* (2020)

Holotype: FMNH 215626, field number BDP 5719. This specimen was collected on 8 Jan 2012 by Bruce D. Patterson, Paul W. Webala, and Carl W. Dick. It is an adult male, formalin-fixed and preserved in ethanol; its skull has been extracted and cleaned, its glans penis removed, and the baculum stained and extracted. Muscle tissue was also preserved at the time of capture in liquid nitrogen.

Type locality: Kisumu Impala Sanctuary, State Lodge Campsite, Kisumu County [formerly Nyanza province], Kenya, at an elevation of 1130 m above sea level; geographical coordinates: 0.10961°S, 34.74593°E (Fig. 1). The sanctuary borders both Lake Victoria and Kenya's fifth largest city, Kisumu, and is only 0.34 km² in area. Vegetation consisted of open parkland, short-statured trees, and shrubs.

Paratype: Four other individuals (FMNH 215625, FMNH 215627, FMNH 215628, FMNH 215629), all females, were collected at the same location and on the same night as the holotype, and closely resemble it genetically (Fig. 3b) and morphologically (Tables 5-7), qualifying them as paratypes.

Etymology: This species is named after the region where it was found, Nyanza, which derives from the Bantu word for "large body of water." Covering nearly 60,000 km², Lake Victoria surely qualifies. The name is used as a noun in apposition.

Diagnosis: This is a medium-sized member of the genus *Pseudoromicia*, with a mean forearm length of 31.2 (Table 5) and greatest skull length of 12.96 mm (Table 6). It is genetically distinct from all other *Pseudoromicia* species (Fig. 3b). Furthermore, it is readily distinguished from the dark-winged members of this genus (*Pse. roseveari*, *Pse. brunnea* and *Pse. kityoi*) by its white wings. It can be distinguished from *Pse. rendalli* by its smaller size (mostly non-overlapping forearm length and craniodental measurements (Tables 5-7) and weakly bicuspid I¹ (unicuspid in *Pse. rendalli*). It is significantly larger than *Pse. tenuipinnis* with hardly any overlapping external and craniodental measurements (Tables 5-7); furthermore, its dorsal fur is medium-brown and bicoloured (dark-brown and unicoloured in *Pse. tenuipinnis*). It is most like *Pse. isabella* in size and external appearance but that species has rusty tips to the fur on its upper parts, whereas *Pse. nyanza* has white-tipped hairs. The taxon *Eptesicus ater* J. A. Allen, 1917, which was described from north-eastern DRC, is currently considered a synonym of *Pse. tenuipinnis* (Simmons, 2005) and is far smaller than *Pse. nyanza*, with a reported total length of 68 mm. Furthermore, *Pse. tenuipinnis* has "brownish black" fur on its back (Allen, Lang, & Chapin, 1917) contrasting with the light-tipped fur of *Pse. nyanza*.

Description: External characters: *Pse. nyanza* sp. nov. is a medium-sized pipistrelle-like bat with white patagial and uropatagial membranes (Fig. 8b). The dorsal pelage is medium brown with white-tipped hairs over most of the back. The ventral hairs are pure-white with a dark base. The ears are short and rounded, and the tragus is broad and truncated as in *Pse. tenuipinnis* (Monadjem *et al.*, 2013).

Craniodental characters: The skull is relatively gracile as in *Pse. tenuipinnis* and *Pse. isabella*. In lateral profile, the cranium slopes gently up from the rostrum to the top of the braincase. There is no occipital “helmet” and the sagittal and lambdoidal crests are absent. The zygomatic arches are fragile as in *Pse. tenuipinnis* and *Pse. isabella* (Fig. 10). The dentition in *Pse. nyanza* is typical of the genus with I 2/3, C 1/1, P 1/3, M2/3. In the upper tooth row, I¹ is weakly but distinctly bicuspid and I² is moderate in size, slightly more than half the length of I¹. The P¹ is absent, putting C in contact with P². The m₃ is myotodont sensu Van Cakenberghe & Happold (2013).

Biology: Judged by how frequently this species is captured, it is common west of the Rift Valley in Kenya (B.D. Patterson & Paul W. Webala, personal observation). It seems to prefer forest edge habitats and avoids the forest interior (Rydell *et al.*, 2020, as *Neoromicia tenuipinnis*). However, its distribution beyond western Kenya is not known. It seems to be associated with the high plateau of western Kenya, which extends into eastern Uganda, so it presumably also occurs there. Thorn & Kerbis Peterhans (2009) recorded “*Pipistrellus tenuipinnis*” as occurring widely in Uganda. The cranial measurements of specimens from Budongo, Entebbe, and Sango Bay (at elevations similar to those we report from Kenya), all fall neatly within the range of *Pse. nyanza* and are generally larger than those for *Pse. tenuipinnis*. It would be instructive to re-examine these specimens (in the collections of the BMNH and LACM) to confirm their identities and hence help determine the western limits of the distribution of *Pse. nyanza*. However, records from the eastern DRC apparently refer to true *Pse. tenuipinnis*, due to their small size, with total length “about 72 mm” (Allen *et al.*, 1917). We speculate that, despite the rather limited geographical range of *Pse. nyanza* (even if Uganda is included), this species is currently not threatened as it survives in human-altered habitats, and therefore we recommend the IUCN conservation status of ‘Least Concern’. The type specimen echolocated at a peak frequency (start and end frequencies) of 40.4 kHz (56.4 – 39.3 kHz). The mean (\pm SD) peak frequency for 16 individuals at the type locality was 40.4 \pm 0.84 kHz (55.1 \pm 7.91 – 39.5 \pm 0.68 kHz).

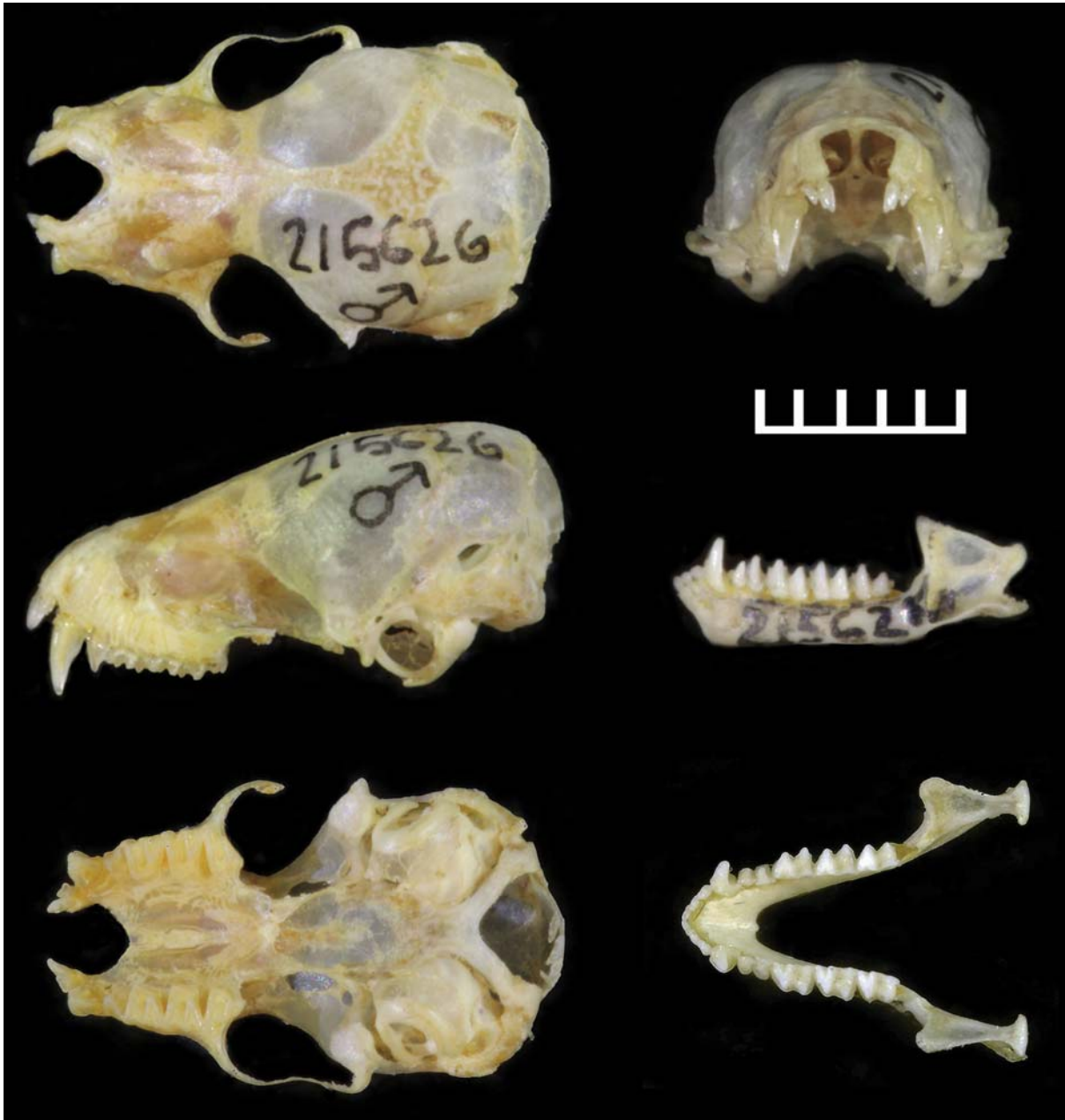


Figure 10. Plate showing the cranium and mandible of *Pseudoromicia nyanza* (FMNH 215626). Scale bar = 5 mm.

***AFRONYCTERIS* MONADJEM, PATTERSON & DEMOS, GEN. NOV.**

Synonymy

Vespertilio Peters, 1852 (part, not Linnaeus, 1758)

Hypsugo Kolenati, 1860 (part, not Kolenati, 1856)

Vesperugo Dobson, 1875 (part, not Keyserling and Blasius, 1839)

Pipistrellus Miller, 1900 (part, not Kaup, 1829)

Myotis Matschie, 1907 (part, not Kaup, 1829)

Neoromicia Shortridge, 1934 (part, not Roberts, 1926)

Eptesicops Roberts, 1951 (part, not Roberts, 1926)

Complete synonymic histories for the species placed herein in *Afronycteris* are given in ACR (2019)

Type species: *Afronycteris nana* (Peters, 1852)

Included species: *Afronycteris helios* (Heller, 1912)

Etymology: The generic name refers to the wide distribution of the type species *Afronycteris nana* on the African continent, south of the Sahara. This species ranges, without obvious breaks in distribution, from Senegal in the west to Ethiopia and south to South Africa, being absent only from the more arid desert and semi-desert environments associated with the Sahel and Chalbi Desert in the north and the Namib and Kalahari deserts in the southwest (Happold, 2013a).

Diagnosis: Small-sized vespertilionids with the simple muzzle characteristic of this family. The cranium in lateral view is distinctly inflated, more so than any other member of the tribe Vespertilionini. The tragus is characteristically hatchet-shaped with the posterior margin having an abrupt angle and lacking a notch at its base as illustrated in Van Cakenberghe & Happold (2013). The tragi of *Pseudoromicia* gen. nov., *Neoromicia*, and *Laephotis* all have a notch at the base of the posterior margin. The pelage of the upper and under parts is bicoloured with the basal portion of each hair darker than the terminal portion. There is a distinct thumbpad at the base of the thumb, thought to be useful in climbing on smooth leaves. The outer incisor I² is well developed, reaching almost the same length as the I¹, the latter being slightly bicuspid or unicuspid; in *Laephotis*, *Neoromicia*, and *Pseudoromicia* gen. nov., I² is typically half the length of I¹ or shorter. The P¹ is present and relatively large, whereas this tooth is absent in *Pseudoromicia* gen. nov., *Neoromicia* (except *N. bemaity* and *N. anchietae*), and *Laephotis*. The baculum (ca. 2.0 mm in length) is

shorter than in *Pseudoromicia* and similar in length to that of *Laephotis* and *Neoromicia*. It has a distinctly and deeply bilobed base, and gently curved shaft leading to a spatulate tip (Fig. 5d).

Distribution: This genus is endemic to sub-Saharan Africa, probably occurring in suitable habitats across its wide range. It occurs throughout the Upper Guinea rainforest zone, extending northward into Sudanian savanna, possibly extending into the Sahel along major rivers and wetlands (Happold, 2013a). It occurs throughout mesic portions of Central and East Africa, but records are sparser in the Horn of Africa (Lanza, Funaioli, & Riccucci, 2015). It is widespread in the wetter parts of southern Africa, avoiding the dry south-western region of South Africa, much of Botswana and Namibia (Monadjem *et al.*, 2010).

Systematic relationships: *Afronycteris* gen. nov. is sister to another newly described genus (see below) but the two genera can easily be distinguished by external characteristics, cranial features, and shape of the baculum (see 'Diagnosis' above for details).

DISCUSSION

In this paper, we review nearly all the sub-Saharan pipistrelle-like bats in the tribes Vespertilionini and Pipistrellini. Within this region, the tribe Pipistrellini is represented by the sister genera *Pipistrellus* and *Scotoecus*, with *Vansonia rueppellii* (formerly considered as a member of *Pipistrellus*) sister to these two. *Vansonia* must be considered a valid genus (Koubínová *et al.*, 2013; Moratelli & Burgin, 2019), because *Scotoecus*, *Nyctalus* and *Glischropus* otherwise would render *Pipistrellus* paraphyletic. None of these three genera are endemic to sub-Saharan Africa (or even to Africa) (Moratelli & Burgin, 2019). Furthermore, based on the cytochrome *b* gene, *Mimetillus* does not fall into either of these two tribes; instead, it is sister to them. It was placed in the Vespertilionini by Simmons (2005), but this is the first time that it has been included in a comprehensive molecular phylogeny of these two tribes. Additional genetic data are needed to securely place and classify *Mimetillus*.

Generic delimitation within the tribe Vespertilionini is both subtle and complicated, as amply illustrated by the group's tortured synonymic history (Table 8). In resolving the nomenclature of *Neoromicia* as traditionally conceived, we were faced with three options: either (1) to combine all members of this group plus the four known species of *Laephotis* in a single undifferentiated genus; (2) to treat *Laephotis*, *Neoromicia*, and the newly named groups *Afronycteris* and *Pseudoromicia* as subgenera or (3) to treat all four clades as distinct genera. Assigning ranks

Table 8. Recent changes to the taxonomy of African and Malagasy Vespertilionini and Pipistrellini. Taxa listed in parentheses need genetic confirmation of their generic allocation; those listed in square brackets require careful delimitation and taxonomic description.

Simmons (2005) ^a	Simmons & Cirranello (2020)	This study
<i>Neoromicia nanus</i>	<i>Laephotis nanus</i>	<i>Afronycteris nana</i>
<i>Pipistrellus helios</i>	<i>Laephotis helios</i>	(<i>Afronycteris helios</i>) ^b
<i>Hypsugo ariel</i>	<i>Hypsugo ariel</i>	<i>Hypsugo ariel</i>
<i>Hypsugo musciculus</i>	<i>Hypsugo musciculus</i>	(<i>Hypsugo musciculus</i>)
<i>Laephotis angolensis</i>	<i>Laephotis angolensis</i>	(<i>Laephotis angolensis</i>)
<i>Laephotis botswanae</i>	<i>Laephotis botswanae</i>	<i>Laephotis botswanae</i>
<i>Neoromicia capensis</i>	<i>Laephotis capensis</i>	<i>Laephotis capensis</i>
-	-	<i>Laephotis kirinyaga</i> sp. nov.
<i>Neoromicia somalicus malagasyiensis</i>	<i>Laephotis malagasyiensis</i>	<i>Laephotis malagasyiensis</i>
<i>Neoromicia capensis</i>	<i>Laephotis matroka</i>	<i>Laephotis matroka</i>
<i>Laephotis namibensis</i>	<i>Laephotis namibensis</i>	<i>Laephotis namibensis</i>
-	<i>Laephotis robertsi</i>	<i>Laephotis robertsi</i>
-	<i>Laephotis stanleyi</i>	<i>Laephotis stanleyi</i>
<i>Laephotis wintoni</i>	<i>Laephotis wintoni</i>	<i>Laephotis wintoni</i>
-	-	[<i>Laephotis</i> cf. <i>wintoni</i>]
<i>Hypsugo anchietae</i>	<i>Laephotis anchietae</i>	(<i>Neoromicia anchietae</i>) ^c
-	<i>Hypsugo bemaity</i>	<i>Neoromicia bemaity</i>
<i>Neoromicia guineensis</i>	<i>Laephotis guineensis</i>	(<i>Neoromicia guineensis</i>) ^d
<i>Neoromicia somalica</i>	<i>Laephotis somalicus</i>	<i>Neoromicia somalica</i>
-	-	[<i>Neoromicia</i> cf. <i>somalica</i>]
<i>Neoromicia zuluensis</i>	<i>Laephotis zuluensis</i>	<i>Neoromicia zuluensis</i>
<i>Hypsugo crassulus bellieri</i>	<i>Parahypsugo bellieri</i>	<i>Nycticeinops bellieri</i>
<i>Hypsugo crassulus crassulus</i>	<i>Parahypsugo crassulus</i>	<i>Nycticeinops crassulus</i>
<i>Hypsugo eisentrauti</i>	<i>Parahypsugo eisentrauti</i>	<i>Nycticeinops eisentrauti</i>
<i>Neoromicia capensis grandidieri</i>	<i>Pipistrellus grandidieri</i>	<i>Nycticeinops grandidieri</i>
-	<i>Parahypsugo happoldorum</i>	<i>Nycticeinops happoldorum</i>
-	<i>Parahypsugo macrocephalus</i>	(<i>Nycticeinops macrocephalus</i>) ^e
<i>Nycticeinops schlieffeni</i>	<i>Nycticeinops schlieffeni</i>	<i>Nycticeinops schlieffeni</i>
-	-	[<i>Nycticeinops</i> cf. <i>schlieffeni</i>]
<i>Neoromicia brunnea</i>	<i>Laephotis brunneus</i>	<i>Pseudoromicia brunnea</i>
-	<i>Laephotis isabella</i>	<i>Pseudoromicia isabella</i>
-	-	<i>Pseudoromicia kityoi</i> sp. nov.
-	-	<i>Pseudoromicia nyanza</i> sp. nov.
<i>Neoromicia rendalli</i>	<i>Laephotis rendalli</i>	<i>Pseudoromicia rendalli</i>
-	<i>Laephotis roseveari</i>	<i>Pseudoromicia roseveari</i>
<i>Neoromicia tenuipinnis</i>	<i>Laephotis tenuipinnis</i>	<i>Pseudoromicia tenuipinnis</i>
<i>Pipistrellus areo</i>	<i>Pipistrellus areo</i>	(<i>Pipistrellus areo</i>)
<i>Pipistrellus hesperidus</i>	<i>Pipistrellus hesperidus</i>	<i>Pipistrellus hesperidus</i>
-	-	[<i>Pipistrellus</i> cf. <i>hesperidus</i>]
<i>Pipistrellus inexpectatus</i>	<i>Pipistrellus inexpectatus</i>	(<i>Pipistrellus inexpectatus</i>)
<i>Pipistrellus nanulus</i>	<i>Pipistrellus nanulus</i>	<i>Pipistrellus nanulus</i>
<i>Pipistrellus permixtus</i>	<i>Pipistrellus permixtus</i>	(<i>Pipistrellus permixtus</i>)
<i>Pipistrellus raceyi</i>	<i>Pipistrellus raceyi</i>	<i>Pipistrellus raceyi</i>

<i>Pipistrellus rusticus</i>	<i>Pipistrellus rusticus</i>	(<i>Pipistrellus rusticus</i>)
-	-	<i>Pipistrellus simandouensis</i>
<i>Scotoecus albigula</i>	<i>Scotoecus albigula</i>	(<i>Scotoecus albigula</i>)
<i>Scotoecus albofuscus</i>	<i>Scotoecus albofuscus</i>	(<i>Scotoecus albofuscus</i>)
<i>Scotoecus hindei</i>	<i>Scotoecus hindei</i>	<i>Scotoecus hindei</i>
<i>Scotoecus hirundo</i>	<i>Scotoecus hirundo</i>	<i>Scotoecus hirundo</i>
<i>Pipistrellus rueppellii</i>	<i>Pipistrellus rueppellii</i>	<i>Vansonia rueppellii</i>
-	-	[<i>Vansonia cf. rueppellii</i>]
<i>Mimetillus moloneyi</i>	<i>Mimetillus moloneyi</i> ^f	

^a Two additional species listed were *Neoromicia melckorum*, now regarded as a synonym of *Laephotis capensis* (Goodman *et al.*, 2017), and *Neoromicia flavescens*, now considered a nomen dubium (see Thorn *et al.*, 2007)

^b See Happold & Van Cakenberghe (2013) for problems with this name

^c Allocation based on its close genetic relationship with *bemainty*

^d Allocation based on its bacular morphology

^e Allocation based on its morphological similarity to *happoldorum*

^f Shown by our genetic analysis to fall outside Vespertilionini and Pipistrellini

to clades is always a subjective task. Because zoological nomenclature serves both information storage and retrieval functions (Mayr, 1969), it is important that rank assignments be more or less equivalent among comparable groups and that systematists strive to conserve the stability of binomial nomenclature insofar as possible. Morphological discontinuities, genetic distances, and chronological ages have all been used in determination of group ranks. Here we note that each of the genera we recognize is distinguished by trenchant genetic distances (Table 1) and morphological discontinuities (e.g. Fig. 5) that are comparable to those among other recognized genera of Vespertilionini. Furthermore, the group's nomenclatural history and phylogenetic relationships make it impossible to conserve traditional binomial usage.

There is renewed attention being paid to the utility of the subgenus category as a means to incorporate phylogenetic information without disrupting binomial usage (Voss *et al.*, 2014; Teta, 2018). Yet in our case, both options 1 (one undifferentiated genus) and 2 (the use of subgenera) would only complicate matters for other biologists using scientific nomenclature. In fact, *Laephotis* Thomas, 1901 has priority over *Neoromicia* Roberts, 1926 or other later proposed names. Therefore, option 1 entails recognizing all these species in the genus *Laephotis* and would thus change the generic assignment of all 17 species currently recognized in *Neoromicia*. In turn, option 2 would cause the same disruption plus levy the additional nomenclatural burden of subgenera to the disruption produced by option 1. Our proposal (option 3) conserves the usage of both *Laephotis* and *Neoromicia* insofar as possible, expanding previous concepts of the former to include short-eared forms and restricting application of the latter to forms more closely related to *N. zuluensis*. It underscores the discovery of a distinctive, largely white-winged clade that is mainly restricted to tropical forests with the new name *Pseudoromicia* and highlights the phyletic remoteness of the ubiquitous banana bat by placing it (or them) in the genus *Afronycteris*.

In our new conception, the genus *Laephotis* includes the long-eared species traditionally recognized by that name (*Lae. wintoni*, *Lae. angolensis*, *Lae. botswanae* and *Lae. namibensis*) as well as what was previously called *Neo. capensis* and allied species (all short-eared by comparison). Based on our phylogeny, the long-eared species of *Laephotis* are sister to a group comprising (*Lae. capensis* + *Lae. matroka*) + *Lae. kirinyaga* sp. nov. The clade of *Lae. robertsi* + *Lae. malagasyensis* is sister to all these above-mentioned species, and the recently described *Lae. stanleyi* is sister to this broader group. The close relationship between the long-eared *Laephotis* and some species formerly recognized as *Neoromicia* has long been noted (Hooper & Van Den Bussche, 2003) and discussed (e.g. Roehrs *et al.* 2010; Koubínová *et al.* 2013). Furthermore, this is not a unique instance where a distinctive long-eared vesper taxon

has been shown to be deeply embedded in an otherwise short-eared group. The Neotropical genus-group *Histiotus* renders even New World members of the genus *Eptesicus* paraphyletic (Amador *et al.*, 2018). Interestingly, bacular morphology (see Fig. 5) supports our revised definition of this genus, as both long-eared and short-eared members exhibit comparable bacular morphologies (Hill & Harrison, 1987). Skull morphometrics also distinguish them as a group (Fig. 4). This suggests that the lengthening of ear pinnae in vespertilionid bats may occur rapidly, possibly as an adaptive response (e.g. for gleaning prey off the ground), and may not be a good character in defining generic limits. All members of the more expansive genus *Laephotis* dictated by our analyses are endemic to sub-Saharan Africa (including Madagascar).

Neoromicia as we refine its application here comprises the type species of the genus *Neo. zuluensis* and its sister *Neo. somalica*. In addition, we include *Neo. bemaity* and *Neo. anchietae* in this genus, a relationship also noted previously (Goodman *et al.*, 2015, 2017). All of these species are relatively small-bodied forms with similar unique three-pronged (cross-shaped) tip to the baculum (Hill & Harrison, 1987).

The newly described genus *Pseudoromicia* comprises a group mostly associated with African tropical forests. Many species possess highly distinctive white wings, which judged from our phylogeny appears ancestral for this genus. This genus has the highest diversity in the Upper Guinea zone of West Africa, where up to four species may co-occur in the same patch of forest (Monadjem, Richards, & Denys, 2016). One species (*Pse. rendalli*), though, is associated with wetlands outside of forested habitats and ranges widely across the continent with little geographical structuring. Interestingly, the white-winged form present in western Kenya and previously identified as *Neoromicia tenuipinnis* (Musila *et al.*, 2019) is not closely related to *Pse. tenuipinnis* sensu stricto (as defined by us). Additionally, a specimen collected from Minziro Forest, NW Tanzania and previously identified as *Neoromicia tenuipinnis* (Stanley & Foley, 2008) does not group with our newly described species of western Kenya *Pse. nyanza*. In fact, it is highly genetically distinct and may belong to an undescribed species. Two of the three known dark-winged species occur in West Africa, with *Pse. brunnea* ranging into the Lower Guinea forests of Cameroon (Fahr, 2013). The third species is described here as *Pse. kityoi*, which is currently only known from a small forest in central Uganda; additional surveys may show it to range more widely in the region.

The widespread and relatively abundant species previously identified as *Neoromicia nana* (as well as the poorly understood *Neoromicia helios*) is not similar to any of these other groups. We demonstrate that it is highly

genetically distinct and is sister to *Pseudoromicia*. Furthermore, it has a suite of unique characters not shared with members of the genus *Pseudoromicia*, such as an inflated cranium, disk pads at the base of its thumb, the presence of a small upper premolar, a large and long outer upper incisor, and a uniquely structured baculum. It belongs in its own genus, which we have named *Afronycteris* gen. nov.

In addition to *Laephotis*, *Pseudoromicia*, *Afronycteris* and *Neoromicia*, the following taxa are also documented in the sub-Saharan region: *Afropipistrellus*, *Nycticeinops*, and *Hypsugo*. *Hypsugo* is only represented in the sub-Saharan region by *H. ariel* based on a single record in Sudan (Koopman, 1975), and is unlikely to be widespread beyond the arid Sahel. In contrast, *Afropipistrellus* comprises a purely African lineage mostly associated with rainforest; one species (*Afr. grandidieri*) is associated with moist woodlands (Monadjem *et al.*, 2020b). The rainforest members of this group were recently described in the new genus *Parahypsugo* (Hutterer *et al.*, 2019), but genetic material now available for *Afr. grandidieri*, type species of *Afropipistrellus* (Thorn, Kock, & Cuisin, 2007), show that it clearly falls into this same group and *Afropipistrellus* has priority over *Parahypsugo*. Our alignment also included a 762-bp *cyt-b* sequence from an individual identified as *Parahypsugo eisentrauti*. This individual was not recovered with *Afropipistrellus*, which grouped instead with *Nycticeinops*. As an expression of our taxonomic conservatism, we regard *Parahypsugo* as a junior synonym of *Afropipistrellus*, and synonymize the latter with *Nycticeinops*, provisionally including the anomalous sequence reported for *Parahypsugo eisentrauti*. This transforms *Nycticeinops*, which is traditionally regarded as monospecific, into a genus containing at least seven species. We note that the intra-generic distance within *Nycticeinops* is relatively large compared with other genera within the Pipistrellini and Vespertilionini but is still lower than the inter-generic distances (see Table 1). In this genus, the substantial, geographically structured differentiation of *Nycticeinops schlieffeni* into eastern and western clades (also noted by Koubínová *et al.* (2013)) and of *Nyc. grandidieri* into East and Southern African clades deserve further study.

Including the three new species described in this paper, there are now 46 valid named species of Vespertilionini and Pipistrellini recorded from sub-Saharan Africa (Table 8), five of which are endemic to Madagascar (Goodman, 2011; Goodman *et al.*, 2012, 2015). Of the remaining 41 species, 15 (or more than a third) of them have been recorded from Kenya, and 20 (49%) species from East Africa, demonstrating the importance of this region for pipistrelle-like bats diversity. This corroborates previous studies showing Kenya to be a hub of genetic diversity for other bat groups such as the speciose genera *Miniopterus*, *Hipposideros*, *Rhinolophus*, and *Scotophilus* (Demos *et al.*,

2018, 2019a,b, 2020; Patterson *et al.*, 2020), and further emphasizes the need for continued taxonomic surveys in the region.

We were not able to gather genetic material for all sub-Saharan species of the tribes Pipistrellini and Vespertilionini, and therefore leave a number of taxonomic issues outstanding (Table 8). We did not include *Vesperugo anchietae* Seabra in our phylogeny, but we did include *Pse. bemaity* (Goodman *et al.*, 2015), which is a closely related species (Monadjem *et al.*, 2010, 2020a), suggesting that the former also belongs in *Pseudoromicia*. We are not sure whether *Pipistrellus aero* Heller is represented in our phylogeny, as we did not sample at the type locality, and no DNA sequences of this species are available on Genbank. We could not include topotypical *Pipistrellus crassulus* Thomas, but we suspect from its close morphological similarity to *Nyc. bellieri* (De Vree, 1972), that it will eventually be shown to belong to *Nycticeinops*. Furthermore, we included a specimen from Tanzania in our phylogeny that we tentatively identified on craniodental grounds as *Parahypsugo crassulus* (Fig. 3b). This specimen clearly groups with other members of *Afropipistrellus* and further supports the contention that *crassulus* belongs in the genus *Nycticeinops*.

Specimens from Yemen identified as *Neoromicia guineensis* (Benda *et al.*, 2011; Juste *et al.*, 2013) are clearly sister to *Neo. somalica*, but *N. guineensis* has yet to be sequenced at its type locality (Guinea-Bissau) and the Yemeni specimens may represent a different species. We are not sure whether our samples include *Pipistrellus helios* Heller. Judging by the apparent deep divisions within the clade (with an intra-specific cytochrome *b* divergence of 3.2% - see Table S4) that we have named *Afr. nana*, more than one species may be involved. The relationship between *helios* and *Afr. nana* requires further study. We were unable to include *Pipistrellus inexpectatus* Aellen in our tree. However, a recent study based on COI gene suggested that this species may not belong in *Pipistrellus* at all, but it was unclear whether true *inexpectatus* had been sampled (Monadjem *et al.*, 2020b). Finally, we were also lacking genetic material from either *Hypsugo musciculus* Thomas, 1913 or *Pipistrellus permixtus* Aellen, 1957 (the latter only known from the holotype from Dar-es-Salam, Tanzania) so we cannot say anything about their generic relationships. It is worth noting that the origins of *P. permixtus* have been disputed since it is morphologically more closely allied to that of Palaearctic and Oriental members of the genus such as *P. pipistrellus* and *P. nathusii* than to any African species (Aellen, 1957; Happold, 2013b).

In conclusion, based on extensive genetic sampling and morphological investigation, we have taken important steps towards resolving the systematic relationships of a poorly understood group of pipistrelle-like bats in the tribes Vespertilionini and Pipistrellini in sub-Saharan Africa. Furthermore, we have addressed pending taxonomic issues by describing two new genera and three new species within the Vespertilionini.

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