RESEARCH ARTICLE

# Taxonomic re-evaluation of New World *Eptesicus* and *Histiotus* (Chiroptera: Vespertilionidae), with the description of a new genus

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https://zoobank.org/DD7FB01D-3EA4-46C1-9623-1BB0F4A80750

ABSTRACT. *Eptesicus* Rafinesque, 1820 is widely distributed in the Old and New World (26 species), and *Histiotus* Gervais, 1856 is a South American endemic (11 species). Molecular phylogenies have recovered *Eptesicus* (sensu lato) as polyphyletic, with New World *Eptesicus* and the sister genus *Histiotus* in a paraphyletic American clade sister to Old World *Eptesicus*. Based on these phylogenetic reconstructions, authors have treated *Histiotus* as either a subgenus of *Eptesicus* or restricted *Eptesicus* to the New World species, treating *Histiotus* as a full genus, and using the name *Cnephaeus* Kaup, 1829 at the generic rank to comprise Old World *Eptesicus*. Based on recently published molecular studies, and on novel qualitative and quantitative morphological comparisons of representatives of *Histiotus* and New and Old World *Eptesicus*, we provide evidence for restricting the name *Eptesicus* to the species *E. fuscus* (Palisot de Beauvois, 1796) and *E. guadeloupensis* Genoways & Baker, 1975, allocating the remaining New World species under a new genus, keeping *Histiotus* as a full genus, and raising *Cnephaeus* to generic rank to comprise all Old World taxa currently under *Eptesicus*. This arrangement resolves the paraphyly of New World *Eptesicus*, and promotes taxonomic stability for *Histiotus*, which is a well-established genus of easily recognizable Neotropical bats and treated separate from *Eptesicus* by most authorities.

KEY WORDS. *Cnephaeus*, morphometrics, *Neoeptesicus*, nomenclature, systematics, taxonomy.

## INTRODUCTION

Vespertilionidae is the third largest family of mammals in species richness, and the largest bat family (Moratelli et al. 2019). The family currently comprises 526 species, arranged into 59 genera, and four subfamilies (Mammal Diversity Database 2022): Vespertilioninae, Kerivoulinae, Murininae, and Myotinae. Among them, Vespertilioninae is the largest

subfamily with 291 species distributed in 46 genera and nine tribes: Pipistrellini, Vespertilionini, Eptesicini, Perimyotini, Antrozoini, Plecotini, Lasiurini, Scotophilini, and Nycticeiini (Moratelli et al. 2019). Eptesicini is found nearly worldwide, and includes 63 species in 11 genera: *Thainycteris*, *Arielulus*, *Glauconycteris*, *Hesperoptenus*, *Ia*, *Scotomanes*, *Scoteanax*, *Scotorepens*, *Lasionycteris*, *Histiotus*, and *Eptesicus*. Eptesicini is surpassed in species richness only by Vespertilionini

(Moratelli et al. 2019). The type genus, *Eptesicus* Rafinesque, 1820, comprises 26 species distributed across Eurasia, Africa, and the Americas (Simmons 2005, Moratelli et al. 2019, Acosta et al. 2021, Ramírez-Chaves et al. 2021). The type species is *Eptesicus fuscus* (Palisot de Beauvois, 1796), which is widespread in North, Central, and northern South America (Moratelli et al. 2019). Eleven other species are known from the genus in the New World, and restricted to the Neotropics (Simmons 2005, Davis and Gardner 2008, Moratelli et al. 2019): *E. brasiliensis* (Desmarest, 1819); *E. innoxius* (Gervais, 1841); *E. furinalis* (d'Orbigny & Gervais, 1847); *E. andinus* Allen, 1914; *E. diminutus* Osgood, 1915; *E. chiriquinus* Thomas, 1920; *E. guadeloupensis* Genoways & Baker, 1975; *E. taddeii* Miranda, Bernardi & Passos, 2006; *E. ulapesensis* Sánchez et al., 2019; *E. langeri* Acosta et al., 2021; and *E. orinocensis* Ramírez-Chaves et al., 2021.

Fourteen species occur in the Old World, widely distributed across Africa, Europe, and Asia (Moratelli et al. 2019): *E. serotinus* (Schreber, 1774); *E. hottentotus* (Smith, 1833); *E. nilssonii* (Keyserling & Blasius, 1839); *E. isabellinus* (Temminck, 1840); *E. pachyomus* (Tomes, 1857); *E. bottae* (Peters, 1869); *E. pachyotis* (Dobson, 1871); *E. floweri* (de Winton, 1901); *E. platyops* (Thomas, 1901); *E. ognevi* Bobrinski, 1918; *E. gobiensis* Bobrinski, 1926; *E. tatei* Ellerman & Morrison-Scott, 1951; *E. japonensis* Imaizumi, 1953; and *E. anatolicus* Felten, 1971. The oldest generic name for this Old World lineage is *Cnephaeus* Kaup, 1829, with *Vespertilio serotinus* Schreber, 1774, as the type species.

Initial taxonomic arrangements for the family were based mostly on cranial and dental morphology, later refined by bacular morphology and karyotypic and molecular data (Tate 1942, Hill and Harrison 1987, Volleth et al. 2006). Recently, molecular analyses have revealed that similar phenotypes evolved independently (Volleth et al. 2006, Roehrs et al. 2011, Amador et al. 2018, Ruedi et al. 2017). Phylogenetic reconstructions based mainly on molecular evidence have resulted in several taxa formerly treated as part of *Eptesicus* being rearranged in different genera, including the following: *Vespadelus* Troughton, 1943, a former synonym of *Eptesicus* recognized as a valid genus based on karyotypic and molecular evidence that place it within Vespertilionini, closely related to Pipistrellini (Volleth and Tidemann 1991, Volleth and Heller 1994, Amador et al. 2018); *Neoromicia* Roberts, 1926, formerly a subgenus of *Eptesicus*, and now elevated to generic level and placed within Vespertilionini based on karyotypic evidence (Volleth et al. 2001, Simmons 2005, Amador et al. 2018); *Arielulus* Hill and Harrison, 1987, a former synonym of *Eptesicus* later recognized as a valid genus and placed within Eptesicini based on karyotypic, molecular, and morphological evidence (Volleth and Heller 1994, Csorba and Lee 1999, Simmons 2005, Amador et al. 2018); *Rhyneptesicus* Bianchi, 1917, formerly a subgenus of *Eptesicus*, now elevated to generic level and placed as sister to Pipistrellini based on morphological and molecular evidence (Horáček et al. 2000, Juste et al. 2013, Amador et al. 2018); and *Cassistrellus* Ruedi et al., 2017, a genus recently described based on molecular evidence, which was previously related to *Eptesicus* based on morphology (Ruedi et al. 2017).

In addition to the former subgenera of *Eptesicus* mentioned above, additional subgenera, such as *Rhinopterus* Miller, 1916, and *Amblyotus* Kolenati, 1858, are still recognized by some authors despite the lack of molecular support (Tate 1942, Hill and Harrison 1987, Simmons 2005, Artyushin et al. 2018). *Rhinopterus* includes only *Eptesicus floweri* (de Winton, 1901) from northern Africa, and has not been assessed phylogenetically (Hill and Harrison 1987, Simmons 2005, Artyushin et al. 2018). *Amblyotus* includes the *E. nilssonii* species group and has been treated as either a subgenus or as a full genus. However, recent molecular studies by Artyushin et al. (2009, 2018) have brought into question the species composition of *Amblyotus* because their phylogenetic reconstruction does not recover all the species currently assigned to this genus as monophyletic. Also, *E. nilssonii* and *E. serotinus* mtDNA haplotypes are remarkably similar, which can be explained by some extent of introgression (Artyushin et al. 2009).

Recently, molecular phylogenies based on mitochondrial (e.g., Cyt-b, ND1, 12S, 16S) and nuclear (e.g., DMP1, RAG1, RAG2, BRCA1, vWF) genes, and ultra-conserved elements (UCEs) have recovered *Eptesicus* (sensu lato) as polyphyletic and consisting of a paraphyletic clade of Old World *Eptesicus* sister to a paraphyletic New World clade composed of American *Eptesicus* and, surprisingly, *Histiotus* Gervais, 1856 (Hoofer and Van Den Bussche 2003, Hoofer et al. 2006, Roehrs et al. 2010, 2011, Juste et al. 2013, Amador et al. 2018, Yi and Latch 2022). *Histiotus* is, nevertheless, easily distinguished from *Eptesicus* on several external and cranial traits (Hoofer and Van Den Bussche 2003, Handley and Gardner 2008), and is endemic to South America where 11 species are recognized (Moratelli et al. 2019, Rodríguez-Posada et al. 2021, Velazco et al. 2021): *H. velatus* (I. Geoffroy St.-Hilaire, 1824); *H. macrotus* (Poeppig, 1835); *H. montanus* (Philippi & Landbeck, 1861); *H. magellanicus* (Philippi, 1866); *H. colombiae* Thomas, 1916; *H. laephotis* Thomas, 1916; *H. alienus* Thomas, 1916; *H. humboldti* Handley, 1996; *H. diaphanopterus* Feijó et al., 2015; *H. cadenai* Rodríguez-Posada et al., 2021; and *H. mochica* Velazco et al., 2021.

Those recent molecular findings led to differing opinions about genus-level resolution, and two alternative treatments have been proposed: (1) to treat *Histiotus* as a subgenus of *Eptesicus* and restore the name *Cnephaeus* as a subgenus to contain the Old World species (Hoofer and Van Den Bussche 2003, Hoofer et al. 2006, Juste et al. 2013, Amador et al. 2018); or (2) to restrict *Eptesicus* to the New World taxa and treat *Histiotus* and *Cnephaeus* as genera (Hoofer and Van Den Bussche 2003, Solari and Martínez-Arias 2014). This question remains unresolved, and species-group names have been used in different combinations, adding confusion to the nomenclature of New and Old-World bats. Here we analyze novel morphological data to test the distinctiveness of *Histiotus* in relation to *Eptesicus*, provide evidence to treat both *Cnephaeus* and *Histiotus* at genus level, and describe a new genus to include Neotropical forms of *Eptesicus*; thus, resolving the paraphyly of New World *Eptesicus* and promoting stability in the nomenclature of the well-established genus *Histiotus*.

## MATERIAL AND METHODS

For qualitative and quantitative morphological analyses, we examined 673 specimens of *Eptesicus* and 144 specimens of *Histiotus* that include: *E. anatolicus* (N = 1), *E. andinus* (28), *E. brasiliensis* (94), *E. chiriquinus* (10), *E. diminutus* (37), *E. furinalis* (228), *E. fuscus* (196), *E. guadeloupensis* (2), *E. innoxius* (23), *E. taddeii* (2), *E. ulapesensis* (9), *E. bottae* (4), *E. gobiensis* (7), *E. isabellinus* (2), *E. nilssonii* (8), *E. pachyomus* (10), *E. serotinus* (10), *H. alienus* (1), *H. humboldti* (1), *H. laephotis* (21), *H. macrotus* (21), *H. magellanicus* (20), *H. colombiae* (11), *H. montanus* (26), and *H. velatus* (39).

The specimens examined are deposited in the following institutions: Colección Mamíferos Lillo, Universidad Nacional de Tucumán (CML, San Miguél, Tucumán, Argentina); Museo Argentino de Ciencias Naturales "Bernandino Rivadavia" (MACN, Buenos Aires, Buenos Aires Argentina); Coleção de Mamíferos "Alexandre Rodrigues Ferreira", Universidade Estadual de Santa Cruz (CMARF, Ilhéus, Bahia, Brazil); Coleção de Mamíferos da Universidade Federal de Lavras (CMUFLA, Lavras, Minas Gerais, Brazil); Coleção de Mamíferos da Universidade Federal de São Carlos (ANG, APC, FAU, ZSP, Sorocaba, São Paulo, Brazil); Coleção "Adriano Lúcio Peracchi", Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Rio de Janeiro, Brazil); Coleção do Laboratório de Diversidade de Morcegos, Universidade Federal Rural do Rio de Janeiro (LDM, Seropédica, Rio de Janeiro, Brazil); Museu Nacional (MN, Rio de Janeiro, Rio de Janeiro, Brazil); Muséum national d'Histoire naturelle (MNHM, Paris, France); American Museum of Natural History (AMNH, New York, New York, USA); Field Museum of Natural History (FMNH, Chicago, Illinois, USA); Louisiana State University, Museum of Natural Science (LSU, Baton Rouge, Louisiana, USA); National Museum of Natural History (USNM, Washington, D.C., USA); and Natural History Museum (BM, London, United Kingdom). See Appendix 1 for additional information about the examined specimens.

Species identification prior to morphological analyses was based on the available literature (eg. Davis and Gardner 2008, Feijó et al. 2015, Díaz et al. 2016, 2019, Sánchez et al. 2019), as well as by direct comparison with type specimens when possible (type specimens analyzed include: *Eptesicus andinus* Allen, 1914, *Eptesicus brasiliensis argentinus* Thomas, 1920, *Eptesicus brasiliensis thomasi* Davis, 1966, *Eptesicus chapmani* Allen, 1915, *Eptesicus chiralensis* Anthony, 1926, *Eptesicus chiriquinus* Thomas, 1920, *Eptesicus diminutus diminutus* Osgood, 1915, *Eptesicus diminutus fidelis* Thomas, 1920, *Eptesicus floweri* (de Winton, 1901), *Eptesicus fuscus carolinensis* É. Geoffroy St.-Hilaire, 1806, *Eptesicus fuscus dutertreus* (Gervais, 1836), *Eptesicus fuscus pelliceus* Thomas, 1920, *Eptesicus fuscus peninsulae* Thomas, 1898, *Eptesicus gaumeri* (Allen, 1897), *Eptesicus hilarii* (I. Geoffroy St.-Hilaire, 1824), *Eptesicus inca* Thomas, 1920, *Eptesicus innoxius* (Gervais, 1841), *Eptesicus montosus* Thomas, 1920, *Eptesicus punicus* Thomas, 1920, *Eptesicus ulapesensis* Sánchez et al., 2019, *Histiotus alienus* Thomas, 1916, *Histiotus colombiae* Thomas, 1916, *Histiotus inambarus* Anthony, 1920, *Histiotus laephotis* Thomas, 1916, *Histiotus mochica* Velazco et al., 2021, and *Histiotus velatus miotis* Thomas, 1916).

Qualitative and quantitative morphological external (N = 3) and skull (N = 16) characters (Tables 1 and 2) were selected following Davis (1966), Barquez et al. (1999), Miranda et al. (2006), Davis and Gardner (2008), Handley and Gardner (2008), Moratelli et al. (2013), Feijó et al. (2015), and Sánchez et al. (2019). We recorded qualitative and quantitative data from adults only, classified as such based on the closed epiphyses (q.v., Brunet-Rossini and Wilkinson 2009). Cranial measurements were taken under binocular microscopes with low magnification (usually 6×), to the nearest 0.01 mm, and their abbreviations are described in Table 1. A Multivariate Analysis of Variance (MANOVA) and subsequent pairwise Hotelling's tests were run in the software PAST 3.3 (Hammer et al. 2001) to test whether specimens representing the species we sampled of *Eptesicus* and *Histiotus* differ in skull dimensions. In all tests we calculated p-values with Bonferroni correction and considered them statistically significant for $\alpha \leq 0.001$.

**Table 1.** Skull dimensions used to perform principal component and canonical variate analyses. Measurements were taken in millimeters.

| Abbreviation | Measurement | Description |
|---|---|---|
| MAL | Mandibular Length | From the mandibular symphysis to the condyloid process |
| MAN | Mandibular Toothrow Length | From the lower canine to third molar |
| COH | Height of Coronoid Process | Perpendicular height from the tip of the coronoid process to the base of mandible |
| GLS | Greatest Length of Skull | From the apex of the upper internal incisors to the occiput |
| CCL | Condylo-canine Length | From the anterior surface of the upper canines to a line connecting the occipital condyles |
| CIL | Condylo-incisive Length | From the apex of upper internal incisors to a line connecting the occipital condyles |
| BAL | Basal Length | Least distance from the apex of upper internal incisors to the anterior margin of the foramen magnum |
| ZYG | Zygomatic Breadth | Greatest breadth across the outer margins of the zygomatic arches |
| MAB | Mastoid Breadth | Greatest breadth across the mastoid region |
| BCB | Braincase Breadth | Greatest breadth of the globular part of the braincase |
| POB | Postorbital Constriction | Least breadth across frontals posterior to the postorbital bulges |
| BAC | Breadth Across Canines | Greatest breadth across outer edges of the crowns of upper canines including cingulae |
| BAM | Breadth Across Molars | Greatest breadth across outer edges of the crowns of upper molars |
| MTL | Maxillary Toothrow Length | From the upper canine to third molar |
| M1M3 | Upper Molar Toothrow Length | From M1 to M3 |
| WFH | Width of Foramen Magnum | Greatest width between the internal margins of the foramen magnum, in a horizontal axis |

A Principal Component Analysis (PCA) was used to summarize patterns of size and shape variation, and to compare skull morphology among the species sampled of *Eptesicus* and *Histiotus*. Canonical Variate Analysis (CVA) was used to test the hypothesis that samples of *Eptesicus* and *Histiotus* are separated by morphological discontinuities that support their treatment as separate genera. PCA and CVAs were performed in R software (R Development Core Team 2012) using MASS (Venables and Ripley 2002) and Lattice (Sarkar 2008) packages. The Amelia II package (Honaker et al. 2011) was implemented in R software to estimate missing values (< 5% of total data set) from the existing raw data, by performing multiple iterations. A "size-free" Mosimann shape variables CVA (Mosimann 1970) was performed using the EnvStats (Milard 2013) package implemented in R software. Sixteen craniodental dimensions were used to perform the PCA and CVAs, and measurements (in mm) were taken as described in Table 1. A total of 176 specimens representing 23 species were selected for PCA and CVA (Appendix 1), that included *E. andinus* (N = 10), *E. brasiliensis* (10), *E. chiriquinus* (8), *E. diminutus* (10), *E. furinalis* (10), *E. fuscus* (8), *E. guadeloupensis* (2), *E. innoxius* (10), *E. ulapesensis* (9), *E. taddeii* (2), *E. bottae* (4), *E. gobiensis* (7), *E. isabellinus* (2), *E. nilssonii* (8), *E. pachyomus* (10), *E. serotinus* (10), *H. humboldti* (4), *H. laephotis* (10), *H. macrotus* (8), *H. magellanicus* (10), *H. montanus* (8), *H. colombiae* (6), and *H. velatus* (10). A further CVA was employed using only New World samples (N = 135) in order to better explore the morphometric variation within these lineages.

## RESULTS

### Morphological comparisons

New World *Eptesicus* (NWE) and Old World *Eptesicus* (OWE) are morphologically similar to each other when compared to *Histiotus*, which can be easily distinguished from NWE and OWE based on both external and skull qualitative and quantitative characters (Figs 1, 2, Table 2). Also, *Histiotus*, NWE, and OWE can be distinguished based on quantitative characters (Wilk's lambda = 3.10E-194; F = 5.65E97, p < 0.001). In NWE and OWE, ears are small, narrow, separated, and have a total length ranging from 7.0 to 24.0 mm, usually less than 20 mm (N = 398; Fig. 1, Table 2). Comparatively, the ears of *Histiotus* are greatly enlarged, wide, have a total length ranging from 21.0 to 39.1 mm, usually longer than 22 mm (N = 143), and are fully or partially connected across the head by a band of variable development (Fig. 1, Table 2). The tragus in NWE and OWE is small, blunt, and straight to strongly curved inward, with total length ranging from 4.8 to 12.0 mm (N = 129); in *Histiotus*, the tragus is long and slightly to strongly curved outward, with total length ranging from 8.5 to 20.0 mm (N = 123). The eyes in NWE and OWE are reduced, whereas in *Histiotus* they are larger—for comparative purposes, eyes are smaller or about the same size as nostrils and lower canines in the first two, and larger in *Histiotus*. The muzzle is strongly inflated in NWE and OWE, but not conspicuously inflated in *Histiotus* (Fig. 1). NWE and OWE have a robust and broad skull (mean value of GLS/BAM = 2.4; N = 389), and the jugal is relatively slender in comparison with *Histiotus*. *Histiotus* has a narrower skull

Figure 1. Representatives of New World *Eptesicus*: (A) *Eptesicus taddeii* and (B) *Eptesicus fuscus*; *Histiotus*: (C) *Histiotus velatus*; and Old World *Eptesicus*: (D) *Eptesicus serotinus*. Authorship of images: (B) Dr. Burton Lim and (D) Adrià López-Baucells, http://www.batmonitoring.org.

(mean value of GLS/BAM = 2.7; N = 94), with a well-developed postorbital process of the jugal. The auditory bullae are much larger in *Histiotus* than in NWE and OWE. The slope of the frontals is steeper than the nasals in NWE and OWE, but the nasal-frontal profile is relatively straight in *Histiotus* (Fig. 2), except in *H. humboldti*.

NWE can be separated into two distinct morphological groups; one includes the large species *E. fuscus* and *E. guadeloupensis* and can be differentiated from smaller congeners by a set of morphological characters: *fuscus* and *guadeloupensis* are large, with forearm length usually close to 50 mm and not overlapping with most congeners (usually less than 45 mm in other congeners); length of dorsal fur usually larger than 10 mm (most congeners have dorsal fur length less than 9 mm); tragus broader and rounded at the distal extremity when compared to congeners; robust skull, with a straight lateral profile of the braincase in lateral view (comparatively delicate in congeners, with a more domed shape); and well-developed sagittal and lambdoidal crests (crests absent to well developed in congeners, but comparatively smaller). A similar situation can be found within OWE, with distinct morphological groups in which *E. gobiensis* and *E. nilssonii* are smaller, with GLS < 16.5 mm and forearm length < 44 mm; *E. isabellinus*, *E. pachyomus*, and *E. serotinus* are larger, with GLS > 18 mm and forearm length > 44 mm; and *E. bottae* is intermediate in size, with differences between subspecies.
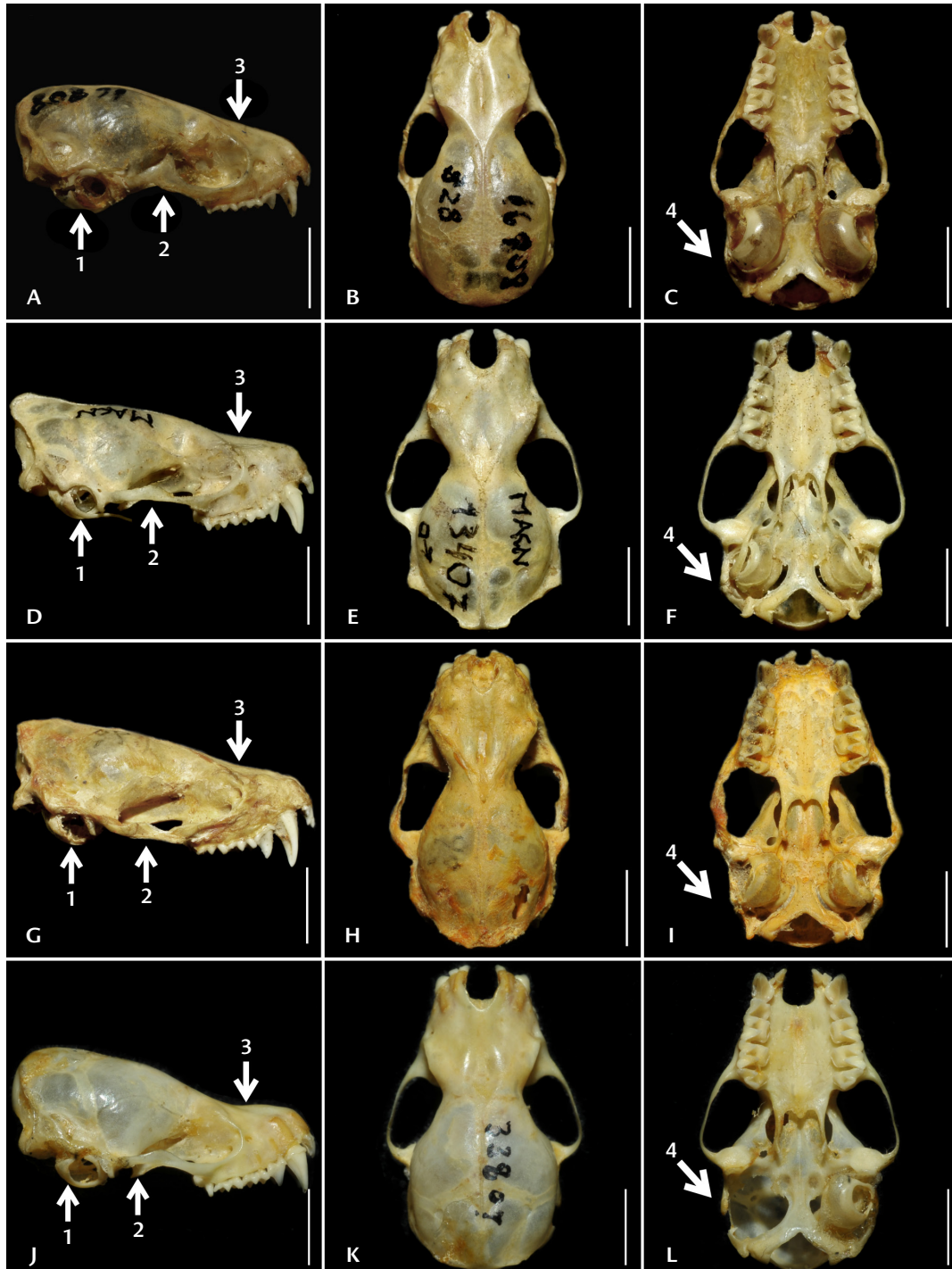
Figure 2. Lateral, dorsal, and ventral views of the skull of representatives of the type species of *Histiotus* (*H. velatus* [MACN 16808]; A, B, C), the type species of *Eptesicus* (*E. fuscus* [MACN 13407]; D, E, F), the first described Old World species of *Eptesicus* (*E. serotinus* [MACN 35.178]; G, H, I), and a representative of small Neotropical *Eptesicus* (*E. andinus* [AMNH 33807, holotype]; J, K, L). Arrows 1 and 4 indicate the auditory bullae; arrow 2 indicates the postorbital process of the jugal bone; arrow 3 indicates the frontal slope. Scale bars: 5 mm.

Table 2. Summary of diagnostic quantitative characters of external and skull morphology between New World *Eptesicus* (NWE), Old World *Eptesicus* (OWE), and *Histiotus* species. Mean values are presented in millimeters for "forearm length", "ear length", "tragus length", and the ratio between "greatest length of skull" (GLS) and "breadth across molars" (BAM). The number of specimens analyzed (N) for each measurement is provided in parentheses.

| Species | Length | | | GLS/BAM |
|---------|--------|-----|--------|---------|
| | Forearm | Ear | Tragus | |
| *Eptesicus andinus* (NWE) | 45.4 (22) | 18.1 (22) | 9.7 (22) | 2.3 (22) |
| *Eptesicus brasiliensis* (NWE) | 42.1 (74) | 14.0 (56) | 7.5 (29) | 2.3 (61) |
| *Eptesicus chiriquinus* (NWE) | 44.9 (7) | 14.0 (5) | 8.1 (2) | 2.3 (10) |
| *Eptesicus diminutus* (NWE) | 36.0 (31) | 13.1 (23) | 5.7 (6) | 2.3 (27) |
| *Eptesicus furinalis* (NWE) | 38.9 (142) | 13.7 (102) | 7.4 (15) | 2.3 (148) |
| *Eptesicus fuscus* (NWE) | 48.5 (37) | 17.1 (18) | 8.6 (11) | 2.4 (33) |
| *Eptesicus innoxius* (NWE) | 37.0 (20) | 13.7 (20) | 7.8 (4) | 2.4 (18) |
| *Eptesicus ulapesensis* (NWE) | 42.6 (9) | 15.3 (9) | – | 2.4 (9) |
| *Eptesicus taddeii* (NWE) | 47.1 (2) | 16.3 (2) | – | 2.3 (2) |
| *Histiotus alienus* | 44.5 (1) | 27.5 (1) | 12.8 (1) | 2.5 (1) |
| *Histiotus colombiae* | 48.8 (11) | 32.7 (11) | 12.0 (1) | 2.6 (4) |
| *Histiotus diaphanopterus* | 46.5 (2) | 29 (2) | 13.0 (2) | 2.8 (1) |
| *Histiotus humboldti* | 46.3 (4) | 28.7 (4) | 11.8 (4) | 2.8 (4) |
| *Histiotus laephotis* | 47.6 (16) | 33.5 (16) | 14.0 (16) | 2.7 (10) |
| *Histiotus macrotus* | 50.3 (18) | 34.4 (18) | 14.5 (17) | 2.6 (15) |
| *Histiotus magellanicus* | 46.8 (19) | 25.1 (20) | 10.7 (17) | 2.5 (15) |
| *Histiotus mochica* | 46.7 (1) | 32 (1) | 13.4 (1) | 2.9 (1) |
| *Histiotus montanus* | 46.8 (21) | 25.9 (21) | 11.6 (19) | 2.5 (14) |
| *Histiotus velatus* | 47.5 (36) | 28.4 (33) | 12.9 (35) | 2.7 (29) |
| *Eptesicus bottae* (OWE) | – | – | – | 2.4 (5) |
| *Eptesicus gobiensis* (OWE) | 40.9 (7) | 13.4 (7) | – | 2.4 (7) |
| *Eptesicus hottentotus* (OWE) | – | – | – | 2.2 (1) |
| *Eptesicus isabellinus* (OWE) | – | – | – | 2.3 (2) |
| *Eptesicus nilssonii* (OWE) | – | – | – | 2.4 (8) |
| *Eptesicus ognevi* (OWE) | – | – | – | 2.2 (1) |
| *Eptesicus pachyomus* (OWE) | 53.3 (9) | 18.5 (8) | 9.0 (3) | 2.3 (11) |
| *Eptesicus serotinus* (OWE) | 51.6 (7) | 19.4 (4) | – | 2.4 (23) |

## Morphometric analyses

Morphological differences between *Eptesicus* and *Histiotus* are summarized in the principal component and canonical variate analyses (Figs 3–6). In the PCA, the first principal component (PC1) accounts for 91% of the total variation (Fig. 3A) and is strongly influenced by size, as observed in the loadings of all variables (Fig. 3B). The plot of PC1 scores also reflects the differences in size variation in each genus, with NWE including a group of small forms (*E. diminutus*, *E. innoxius*, *E. furinalis*) that overlap only with *Histiotus humboldti*. *Eptesicus brasiliensis*, *E. ulapesensis*, *E. andinus*, and *E. taddeii* are intermediate in size and overlap with most species of *Histiotus*. The large species *Eptesicus*

*fuscus* and *E. guadeloupensis* do not overlap with *Histiotus* along PC1, except for a slight overlap between *E. fuscus* and *H. macrotus*. The plot of PC1 scores of OWE species also reflects size differences, with the small species *E. nilssonii* and *E. gobiensis* overlapping only with *H. humboldti*. The intermediate species *E. bottae* extensively overlaps with all the species of *Histiotus* except *H. humboldti*, and the large species *E. isabellinus*, *E. serotinus*, and *E. pachyomus* do not overlap with any of the *Histiotus* species along PC1.

The contrast between PC2 correlations, when the subset of measurements POB, BCB, WFH, GLS, CIL, CCL, MAB, and BAL is contrasted to those of ZYG, MAL, COH, BAM, BAC, MAN, and MAB suggests a differentiation pattern between most NWE, OWE, and *Histiotus* species when the effect of general size represented by PC1 is excluded. That contrast, except for the mandibular measurements MAL and COH, highlight differences related to cranial length and width that also characterize species of each genus. Exceptions to this pattern are *E. gobiensis* and *E. nilssonii*, which show similar relationships between these two subsets of measurements with those of most *Histiotus* species, despite the general size differences expressed along PC1; *Eptesicus andinus*, which extensively overlaps with *H. velatus* along PC2; and *E. fuscus* and *E. guadeloupensis*, which slightly overlap with *Histiotus* species along PC2, despite the general size differences expressed along PC1 (Fig. 3).

A similar pattern of differentiation between the two genera is revealed by the first CVA analysis (Fig. 4A). Representatives of *Histiotus* species are recovered as morphometrically distinct from representatives of NWE and OWE along the second axis (CV2), with scores for the last two widely distributed (Fig. 4A). CV1 accounts for 29% of the total variation and is clearly related to skull size, with the extremes of the CV1 continuum (Fig. 4) similar to those revealed along PC1 (Fig. 3A). Along the axis for CV2, which accounts for 18% of the variation between species, scores for representatives of all species of NWE and OWE, except *E. fuscus*, *E. guadeloupensis*, *E. nilssonii*, and *E. gobiensis*, do not overlap with those of *Histiotus* species. Nevertheless, despite the partial overlapping of scores in relation to either CV1 or CV2 axes, different trajectories of size-related differentiation along these two axes can be identified between the species samples of the genera. Because size alone does not permit clear characterization of each genus, we opted to conduct a "size-free" CVA in search of cranial patterns characterizing species distinctions between genera. In this analysis (Fig. 4B) almost all the species of NWE were retrieved in a single cluster, separate from the cluster for species of *Histiotus*, except
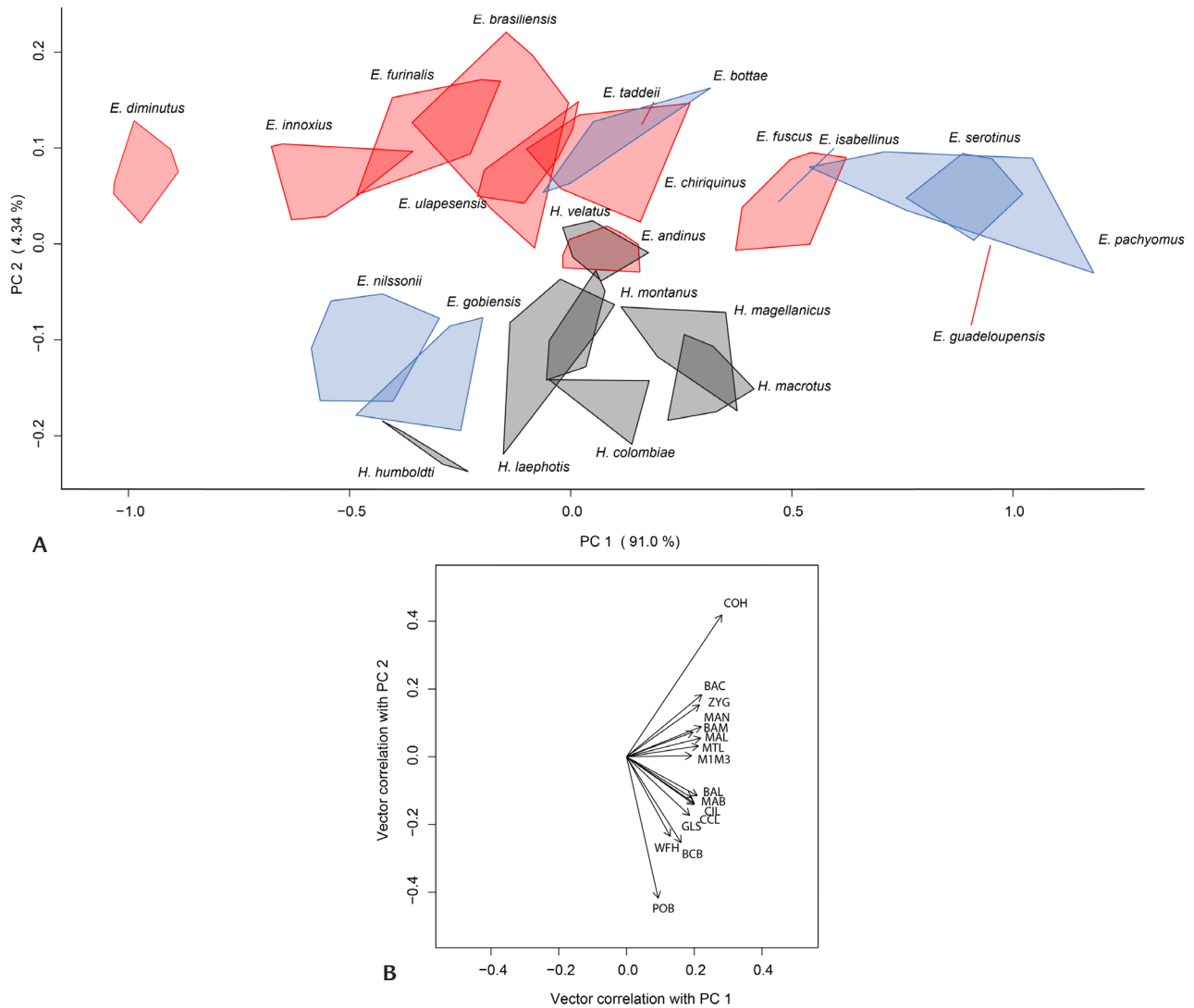
Figure 3. (A) Plot of multivariate individual scores of New World *Eptesicus* (Red), Old World *Eptesicus* (Blue), and *Histiotus* (Black) in the first two principal components. Analysis was performed using 16 cranial measurements. (B) Vector correlations of craniometric characters with the first two principal components eigenvectors. See Table 1 for abbreviations.

for *E. diminutus*, *E. innoxius*, and *E. andinus*, the three species that overlap extensively with *H. magellanicus*; *E. diminutus* and *E. innoxius* also slightly overlap with *H. montanus*, *H. macrotus*, and *H. velatus*. Species of OWE are grouped in two separate clusters, and do not overlap with *Histiotus*.

Vector correlations of original variables with the size-free CV1 (Fig. 5), which account for 23% of the size-independent variation among species, are like those revealed by the original variables and PC2, and summarize major craniometric differentiation patterns between NWE, OWE, and *Histiotus* species. Here again, the correlations of skull

length measurements GLS, CCL, CIL, and BAL contrast with BAM, ZYG, and MAN to separate content in the genera. In parallel to the scores of PC2, the exceptions are represented by *H. magellanicus*, *H. macrotus*, *H. velatus*, *E. gobiensis*, *E. nilssonii*, *E. diminutus*, and *E. innoxius*, species that overlap in this size-free canonical function. Also as noted with respect to the PC2 distribution of scores, these species are clearly distinguishable otherwise based on skull size, with *E. gobiensis*, *E. nilssonii*, *E. diminutus*, and *E. innoxius* being the smallest species of *Eptesicus*, and *H. magellanicus*, *H. macrotus*, and *H. velatus* being the largest *Histiotus*. Previously mentioned
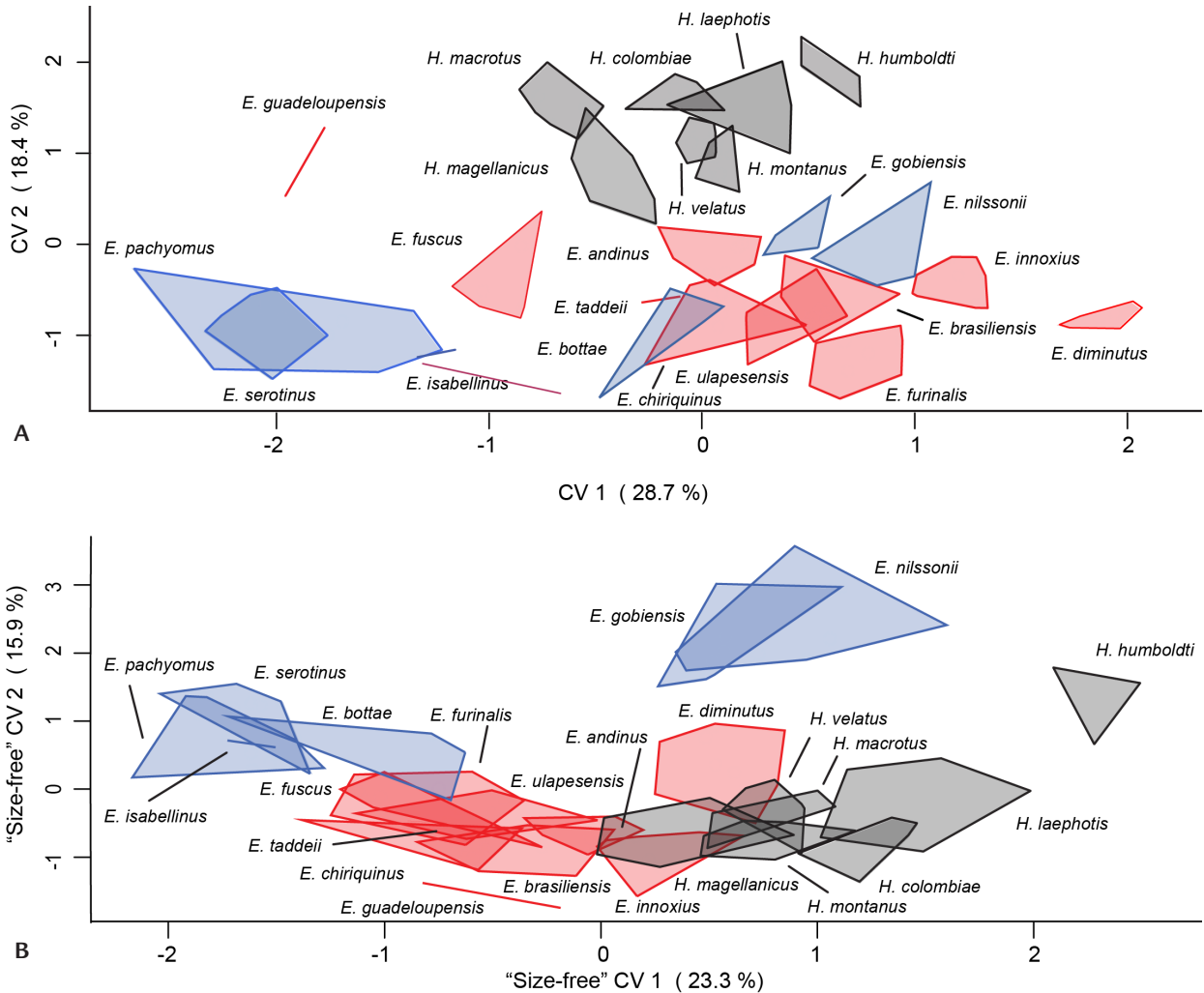
Figure 4. Plot of multivariate individual scores of New World *Eptesicus* (red), Old World *Eptesicus* (blue), and *Histiotus* (black) in the first two canonical variates: (A) canonical variates considering the effect of size; (B) "size-free" canonical variate using Mosimann shape variables. Analyses were performed using 16 cranial measurements.

qualitative and quantitative traits (Table 2) show these species to be morphologically distinct and easily assignable to their respective genus.

Patterns of distribution in the morphospace in the CVA that includes only New World species (Fig. 6A) are similar to that observed in Fig. 4A, with *Histiotus* species clustering together and not overlapping with any of the *Eptesicus* species included in the analysis. CV1 accounts for 34.1% of total variation, and, again, is strongly influenced by skull size, with species clusters located at the extremes of the axis reflecting the size variation within samples. Along CV1, *Histiotus* as a group overlaps only with *E. andinus*, *E. brasiliensis*, *E. chiriquinus*, *E. fuscus*, and *E. taddeii*. And the

large species, *E. fuscus* and *E. guadeloupensis*, do not overlap with any of the remaining *Eptesicus*. Along CV2, which accounts for 19.1% of the total variation, *Histiotus* spp. partially overlaps only with the cluster that includes small *Eptesicus*, and the large species *E. fuscus* and *E. guadeloupensis* also partially overlap with the cluster of small *Eptesicus*. Vector correlations (Fig. 6B) also show a strong influence of size, with a small contrast between the set of measurements POB, GLS, BCB, CIL, WFH, CCL, BAL, and MAB in relation to COH, ZYG, BAM, BAC, MAN, MTL, MAL, and M1M3, which also suggests a differentiation pattern between taxa included in the analysis. Here, again, the clusters of species clearly show different trajectories over the morphospace.
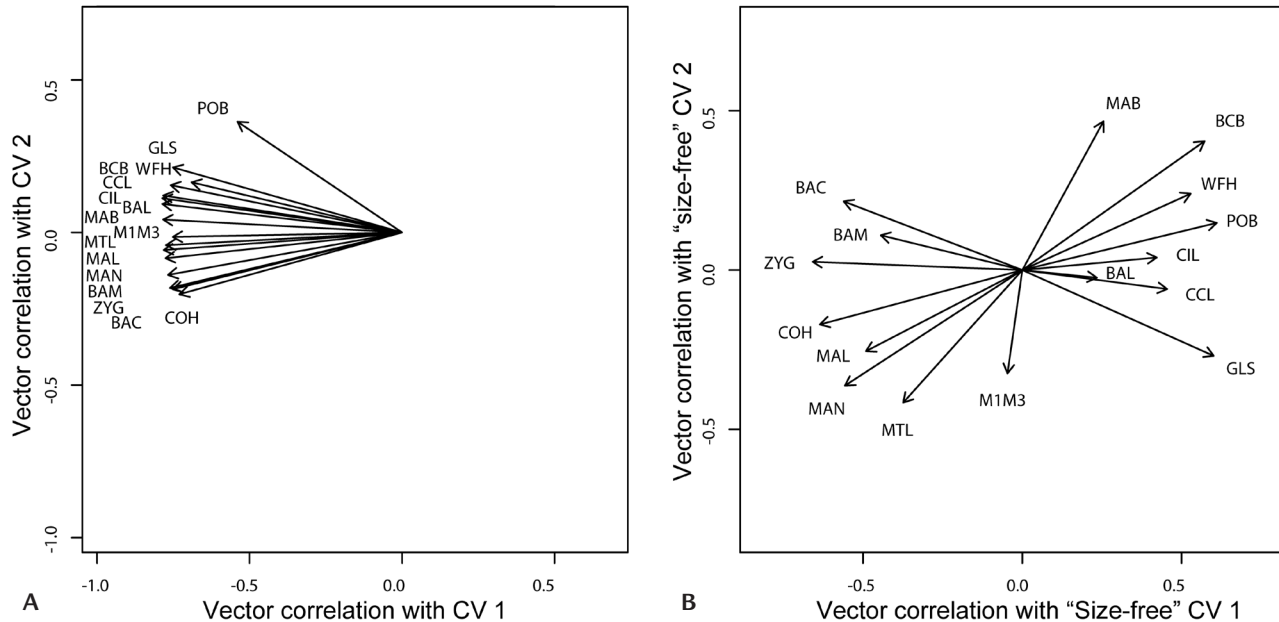
Figure 5. Vector correlations of craniometric characters with the first two eigenvectors of the canonical variates: (A) canonical variate considering the effect of size; (B) "size-free" canonical variate using Mosimann shape variables. See Table 1 for abbreviations.

## DISCUSSION

Taxonomic decisions at the generic level should consider phylogenetic relationships, synapomorphic character status, phenotypic distinctiveness, and ecological factors in the formal recognition of distinctiveness among clades (Isler et al. 2013, Garbino 2015). Also, the zoological nomenclature "should convey evolutionary relationships, diversity, divergence, and the potential to clarify conservation priorities" (Baird et al. 2021: 285).

Treating *Histiotus* as a subgenus to resolve the non-monophyly of *Eptesicus* is based mainly on the argument that it would "bring less turmoil to the taxonomy of the Palearctic forms" (Juste et al. 2013: 448). Earlier, Hoofer and Van Den Bussche (2003: 35) argued that this approach would "underscore cranial and dental similarities between *Histiotus* and *Eptesicus* (sensu stricto) and de-emphasize the assumption that large ears were gained secondarily in *Histiotus* after the divergence between New and Old World *Eptesicus*." Although this arrangement can be useful to avoid controversy in the taxonomy of Old World *Eptesicus*, it does not fully reflect other convergences observed in the phenotypes within Vespertilionidae (e.g., long, and wide ears in *Histiotus* and *Laephotis*; Hoofer and Van Den Bussche 2003), and the systematic history of the lineages involved.

Also, the decision to keep Old World forms within *Eptesicus* brings turmoil to the taxonomy of New World *Eptesicus* and *Histiotus*, since *Eptesicus* (sensu lato) must include *Histiotus* to keep *Eptesicus* monophyletic. *Histiotus* is morphologically distinct from *Eptesicus* and is a well-established genus that comprises a clade of easily recognizable Neotropical bats. Most authorities have treated *Histiotus* as separate from *Eptesicus* to avoid turmoil in the taxonomy of New World vesper bats (e.g., Davis and Gardner 2008, Handley and Gardner 2008, Moratelli et al. 2019). Moreover, three new species were described recently within *Histiotus*: *H. diaphanopterus*, *H. cadenai*, and *H. mochica* (Feijó et al. 2015, Rodríguez-Posada et al. 2021, Velazco et al. 2021), and two new species described within *Eptesicus*: *E. langeri* and *E. orinocensis* (Acosta et al. 2021, Ramírez-Chaves et al. 2021). Different generic arrangements were used by the different research groups, thus contributing to the nomenclatural instability of both *Eptesicus* and *Histiotus*.

A similar phylogenetic situation to that found within *Eptesicus* and *Histiotus* can be seen in the African genera *Laephotis* Thomas, 1901, and *Neoromicia* Roberts, 1926. *Neoromicia* was previously treated as a subgenus of *Eptesicus* but was raised to generic rank by Volleth et al. (2001). Subsequently, Kearney et al. (2002) suggested that *Laephotis* might nest within *Neoromicia* based on bacular structure.
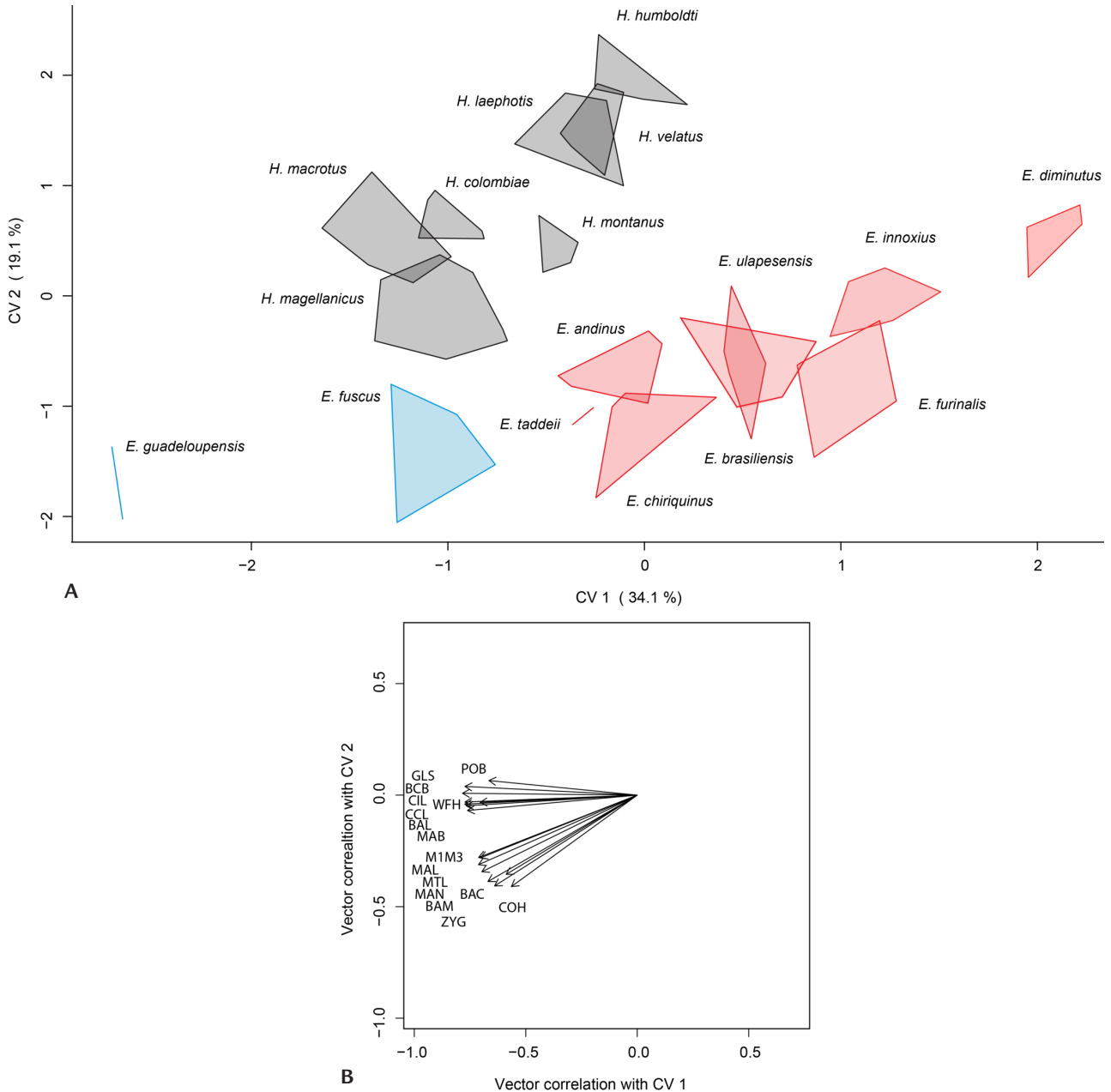
Figure 6. (A) plot of multivariate individual scores of New World *Eptesicus* (red and blue), and *Histiotus* (black) in the first two canonical variates; analysis was performed using 16 cranial measurements. (B) Vector correlations of craniometric characters with the first two canonical variates. See Table 1 for abbreviations.

Given this background, Hoofer and Van Den Bussche (2003) recommended restricting *Neoromicia* to its type species (thus sister to *Laephotis*); allocating taxa previously considered to be congeners to an unnamed genus. More recently, Monadjem et al. (2021) revised the diversity of pipistrelle-like bats in East Africa, resolving the paraphyly of *Neoromicia* by the

description of two new genera, and by the allocation of some species into *Laephotis*.

*Laephotis* is currently considered a full genus, with two sister groups: one that includes a long-eared specialized offshoot from an eptesicoid ancestor, closely related to *Neoromicia* based on molecular and morphological evidence,

with topologies like those retrieved for American *Eptesicus* and *Histiotus* (Hill and Harrison 1987, Hoofer and Van Den Bussche 2003, Roehrs et al. 2011, Monadjem et al. 2021); and another group including short-eared species previously considered as *Neoromicia* (Monadjem et al. 2021). The inclusion of short-eared species within *Laephotis*, according to the authors, suggests that the size of ears may not be a good diagnostic character at genus level, however, the integration of morphological, and molecular evidences still led to the split of *Neoromicia* into four genera rather than the treatment of *Laephotis* as a subgenus of *Neoromicia* (see Monadjem et al. 2021).

Also paralleling the case of *Laephotis* versus *Neoromicia*, morphological distinction in ear size and shape between *Histiotus* and *Eptesicus* likely reflect ecological and behavioral traits that can play a key role in niche differentiation, with ecomorphs adaptive to different prey or feeding strategies (Giménez and Giannini 2017, Yi and Latch 2022). According to Yi and Latch (2022), these differences in ear shape and size could also have allowed *Histiotus* to avoid competition and co-occur with *Eptesicus*.

These adaptations are reflected in the echolocation patterns of these taxa, which are variable within *Eptesicus* (sensu lato) and *Histiotus*. Most species of both genera have frequency modulated calls that often include quasi constant frequency components, and call structures are as follows: (1) Old World *Eptesicus* have calls that sweep from ca. 52.0 to 21.0 kHz, with peak frequency of 22.7–35.8 kHz, and call mean duration of 6.0–9.75 ms; (2) *Histiotus* have calls that sweep from ca. 53 to 15 kHz, with peak frequency of 22.4–32.1 kHz, and call mean duration of 1.3–5.0 ms; (3) New World *Eptesicus fuscus* and *Eptesicus guadeloupensis* have calls that sweep from ca. 50.0 to 25.0 kHz, with peak frequency of ca. 30 kHz, and call mean duration of 3.0–10.0 ms; and (4) New World small Neotropical *Eptesicus* have calls that sweep from ca. 80.0 to 33.0 kHz, with peak frequency of ca. 32.0 to 66.0 kHz, and call duration of ca. 3.0–9.4 ms (Rodríguez and Mora 2006, Papadatou et al. 2008, Ossa et al. 2014, Horta et al. 2015, Arias-Aguilar et al. 2018, Cláudio 2019, Rodríguez-Posada et al. 2021)

As previously discussed, and supported by our results, molecular data allow us to make two different taxonomic arrangements for *Eptesicus* (sensu lato) and *Histiotus*; but this approach alone was not sufficient to resolve the instability in the use of these names during the past two decades. The morphological data analyzed here provides robust additional evidence to resolve this issue in the light of a more integrative perspective. We considered the remarkable phenotypic discontinuity between *Eptesicus* (sensu lato) and *Histiotus*, allied to molecular data such as phylogenies, time of divergence and genetic distance between groups (see below), and echolocation data in deciding whether *Histiotus* and *Cnephaeus* should be treated at the generic or subgeneric rank (see Novaes et al. 2018); our evidence indicates that both should be treated as separate at the generic level, with *Cnephaeus* including Old World taxa previously treated as *Eptesicus* (adopted in the following paragraphs). In most phylogenetic reconstructions, *E. fuscus* has been recovered as sister to a clade including other American *Eptesicus* and *Histiotus* (Roehrs et al. 2010, 2011, Amador et al. 2018, Giménez et al. 2019). More recently, Yi and Latch (2022) conducted a broad phylogenetic study on *Eptesicus* and *Histiotus* based on UCEs, with extensive taxonomic and geographic sampling. Their findings indicate that *E. fuscus* and *E. guadeloupensis* are, in fact, more closely related to *Histiotus* than to remaining New World species of *Eptesicus*, which were recovered in a Neotropical clade sister to the *fuscus* + *Histiotus* clade. This suggests that the name *Eptesicus* should be restricted to *E. fuscus* and *E. guadeloupensis*, and the other New World species of *Eptesicus* allocated to a new genus. Additionally, we also recovered two distinct morphological groups within New World *Eptesicus* on both qualitative and morphometric analyses, which also support the split of New World species into two genera (Figs 4–6). Yi and Latch (2022) also recovered two clades within Neotropical *Eptesicus* (excluding *fuscus* and *guadeloupensis*), however, we did not find any morphological differences that support the split of this clade into two different genera.

Additional supporting evidence for this taxonomic arrangement is the time of divergence within *Eptesicus* (sensu lato) and *Histiotus* clades found by Yi and Latch (2022). According to Yi and Latch (2022), the split between Old and New World clades occurred around ca. 17 million years ago (mya), while the clade of *E. fuscus* and *Histiotus* diverged from the clade of Neotropical *Eptesicus* around ca. 14 mya (Fig. 7), which is similar to the time of divergence of other bat genera (see Amador et al. 2018, Baird et al. 2015, 2017, 2021). The intergeneric genetic distances between genera proposed here also support this arrangement; distances reported between the pairs of genera, based on cyt-b sequences, are: (1) *Cnephaeus* x *Histiotus* 18.1–19.9%; (2) *Cnephaeus* x *Eptesicus* 17.0–20.2%; (3) *Cnephaeus* x *Neoeptesicus* 19.4–23.2%; (4) *Histiotus* x *Eptesicus* 13.4–17.8%; (5) *Histiotus* x *Neoeptesicus* 9.3–17.1%; and (6) *Eptesicus* x *Neoeptesicus* 11.4–20.3% (Giménez et al. 2019, Acosta et al. 2021). Reported CO1 distances between genera pairs are: (1)
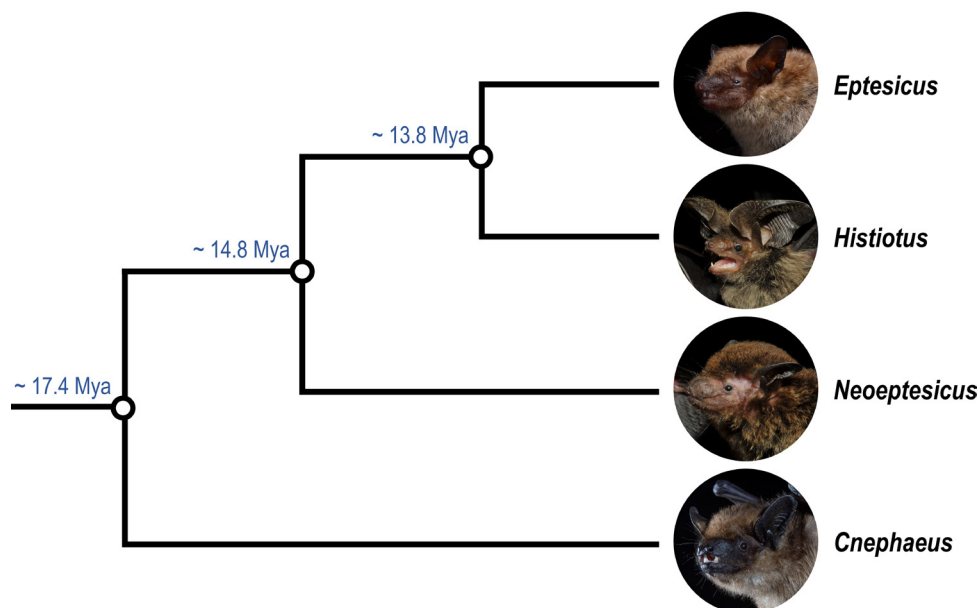
Figure 7. Simplified phylogeny of *Eptesicus*, *Cnephaeus*, *Histiotus*, and *Neoeptesicus*, modified from Yi and Latch (2022). Authorship of *Eptesicus* image: Dr. Burton Lim.

*Cnephaeus* x *Neoeptesicus* 12–16%; (2) *Eptesicus* x *Neoeptesicus* 14–19%; (3) *Cnephaeus* x *Eptesicus* 13–15%; and (4) outgroups (*Nyctalus*, *Tylonycteris*, and *Lasionycteris*) x *Eptesicus* (sensu lato) 15–19% (Sanchéz et al. 2019). For comparison purposes, Baker and Bradley (2006) stated that intergeneric distances between sister and non-sister bat taxa, considering the mitochondrial cyt-b gene, range from 3.3–14.7% and 8.4–15.7%, respectively. Moreover, cyt-b distances between seven Vespertilionidae genera studied by Monadjem et al. (2021) range from 14.8–20.3%, while intrageneric distances range from 4.2–14.2%.

Lastly, we recovered *Cnephaeus nilssonii* and *C. gobiensis* in a cluster separate from *C. isabellinus*, *C. pachyomus*, *C. serotinus*, and *C. bottae* in our morphometric analyses. This suggests robust divergence in skull morphology in both size and form, which could also be observed in our qualitative and quantitative results. *C. nilssonii* and *C. gobiensis* are included in the controversial subgenus *Amblyotus*, whose validity was questioned by recent molecular studies (see Artyushin et al. 2009, 2018). Moreover, Yi and Latch (2022) also recovered *Cnephaeus* as two paraphyletic clades that roughly resemble the divergence between Eurasian and South African species. Their sampling of *Cnephaeus* species was, however, limited and no further taxonomic decisions can be made now. Here we resolved the paraphyly of New World *Eptesicus*, which includes the type species and has no-

menclatural priority, and promoted the stability of *Histiotus*. Future studies including larger geographical and taxonomic samples of both morphological and molecular analyses are needed to solve the paraphyly within *Cnephaeus*, and to better evaluate the validity of *Amblyotus*.

## TAXONOMY

### *Neoeptesicus* gen. nov.

https://zoobank.org/1D855992-1B95-467D-93B4-3EC478240212

*Eptesicus* Rafinesque, 1820: 2; part.
*Adelonycteris* H. Allen, 1892: 466; part; replacement name for *Vesperus* Keyserling & Blasius, 1839, preoccupied.

Type species: *Vespertilio innoxius* Gervais, 1841.
Other species: *Neoeptesicus brasiliensis* (Desmarest, 1819); *N. furinalis* (d'Orbigny & Gervais, 1847); *N. andinus* (Allen, 1914); *N. diminutus* (Osgood, 1915); *N. chiriquinus* (Thomas, 1920); *N. taddeii* (Miranda, Bernardi & Passos, 2006); *N. ulapesensis* (Sánchez et al., 2019); *N. langeri* (Acosta et al., 2021); and *N. orinocensis* (Ramírez-Chaves et al., 2021).
Distribution: *Neoeptesicus* is a Neotropical genus, widely distributed across South America, and Central America. In Central America it is restricted to the southern mainland, with only the species *Neoeptesicus furinalis* and *N. brasiliensis* ranging northward into Mexico.

Diagnosis: *Neoeptesicus* can be distinguished by the following characters: ears short (<20 mm) and not connected; postorbital process of the jugal weakly developed; eyes comparatively small, with diameter smaller or about the same size as height of lower canines and diameter of nostrils (Fig. 1); auditory bullae small, basioccipital region is larger than the width of each auditory bullae; length of dorsal fur usually short (averaging 8 mm); length of forearm ranging from 31.4–48.8 mm (averaging 40.1 mm); tragus short and rounded, smooth and slender; GLS 12.9–18.0 mm (averaging 15.8 mm); and MTL 4.5–7.0 mm (averaging 5.8 mm).

Description: *Neoeptesicus* includes small-sized to medium species, with forearm length ranging from 31.4 to 48.8 mm. Dorsal fur usually short (LDF 4.5–13.1 mm), less than 10 mm for most species; hairs ranging from blackish and unicolored to strongly bicolored; dark basal color extending from 1/2 to almost the entire length of hairs; the contrast between bands ranges from faint to strong; tips of hairs ranging from blackish to golden orangish or yellowish. Ventral fur usually short (LVF 4.3–11.8 mm), less than 8 mm for most species; hairs bicolored with dark brown bases from 1/2 to about 4/5 of hairs length, tips of hairs ranging from dark brown to nearly white. Wing membranes naked, usually dark brown. Plagiopatagium attached to the base of the toe. Dorsal surface of the uropatagium somewhat paler than wing membranes, nearly naked with short sparse hairs that do not extend beyond the knees. Ventral surface of the uropatagium brown and sparsely haired near the base of the tail. Ears well separated, medium sized, usually dark brown, and with rounded tips; tragus wider at the base, straight to slightly curved, long and rounded. Muzzle broad and inflated.

Skull delicate to robust; rostrum short, wide, and flattened, weakly sloping upwards to the braincase; braincase slightly wider than the rostrum. Posterior region of the braincase ranging from rounded, regular to straight, slightly projected upwards. Nasal opening V- to U-shaped. Frontal expanded laterally towards the orbit. Sagittal and lambdoidal crests weakly to well developed, connected or not; occipital helmet weakly- to well developed. Triangular, flattened bony plate where the sagittal and lambdoidal crests connect ranging from absent to well developed, the region where crests connect may be enlarged. Zygomatic arches thin and slightly widened medially. Basisphenoid pits absent. Palate extends well beyond molars, ending in a concave posterior edge, with a weakly-developed to small medial spine.

Dental formula is I 2/3, C 1/1, P 1/2, M 3/3 (×2) = 32. $I^1$ separated, ranging from slender and weakly bilobed to spatulate and strongly bilobed; wide and short to long and narrow, with inner and outer cusps weakly- to well-developed. $I^1$ usually about three to four times the size of $I^2$. $I^1$ usually not aligned to $I^2$ on a transversal axis of the skull. $I^2$ and $C^1$ usually separated by a small gap, $C^1$ with two slightly concave faces on the lingual region, and one slightly concave face on the labial region. P1 well-developed, reaching 1/2 of $C^1$ in height; $P^1$ in contact with $C^1$ and molars. $M^1$ and $M^2$ about the same size, almost square shaped, with W-shaped cusps. $M^3$ reduced, triangular, with only 3 cusps. $I_1$ to $I_3$ reduced, trilobed, and fully occupying the space between canines. $P_2$ about three times $P_1$ in height. Molars have well-developed cusps and decrease in size from $M_1$ to $M_3$.

Comparisons: *Neoeptesicus* most resembles *Eptesicus*, and both can be distinguished from *Histiotus* based on several characters. Ears in *Histiotus* are greatly enlarged, > 21 mm (21–39 mm, usually > 25 mm); in *Neoeptesicus* and *Eptesicus* ears are comparatively reduced, < 20 mm (8–20 mm, usually < 18 mm); the tragus in *Histiotus* is notched and long, with total length > 10 mm (10–20 mm); in *Neoeptesicus* and *Eptesicus* the tragus is smooth and short, > 12 mm (4.8–12 mm); there is no overlap when the length of tragus is analyzed together with ear and forearm length. The ears in *Histiotus* are connected by a membrane of variable development, while in *Neoeptesicus* and *Eptesicus* this membrane is absent. Eyes in *Histiotus* are larger than nostrils and lower canines, and smaller or about the same size as nostrils or canines in *Neoeptesicus* and *Eptesicus.* The skull in *Histiotus* is narrow and long (mean value of GLS/BAM = 2.7) when compared to *Neoeptesicus* and *Eptesicus* (mean value of GLS/BAM = 2.3); the auditory bullae are comparatively twice as large in *Histiotus* than in *Neoeptesicus* and *Eptesicus*; and *Histiotus* has a well-developed postorbital process of the jugal, which is weakly developed in *Neoeptesicus* and *Eptesicus*.

The morphologically similar genera *Neoeptesicus* and *Eptesicus* can be distinguished using the following set of characters: length of dorsal fur, usually > 10 mm in *Eptesicus* and < 10 mm in *Neoeptesicus*; the only exceptions are *N. andinus* and *N. chiriquinus*, which can be differed from *Eptesicus* by the dark and nearly unicolored fur, with only the tips of dorsal hairs washed with lighter color. Length of ventral fur, usually > 8 mm in *Eptesicus* and < 8 mm in *Neoeptesicus*; the only exceptions, again, are *N. andinus* and *N. chiriquinus*. Color pattern, with strongly bicolored dorsal fur in *Eptesicus*, with the basal 1/2 of hairs dark brown and distal 1/2 brownish to golden brown; and ventral hairs also bicolored with the basal 2/3 of hairs dark brown, and distal 1/3 grayish yellow. In *Neoeptesicus* the pattern of dorsal and ventral fur color is highly variable, with most species present-

ing a different color combination than found in *Eptesicus*; dorsal fur can vary from unicolored to strongly bicolored and ventral fur can vary from dark brown to whitish, the few species that have the same pattern of color as *Eptesicus* can be easily differentiated based on other characters such as length of fur, length of forearm, and cranial characters. Length of forearm usually > 42 mm in *Eptesicus*, and usually < 45 mm in *Neoeptesicus*; species that overlap in size can be separated on other diagnostic characters; the only species of *Neoeptesicus* that overlap in both size and distribution with *Eptesicus* are *N. brasiliensis* and *N. chiriquinus*, two species that can be easily distinguished from *Eptesicus* based on length and color of dorsal fur. The skull in *Eptesicus* is robust, with well-developed crests and helmet, the crests are always connected and the triangular plate where lambdoidal and sagittal crests converge is always absent; in *Neoeptesicus* the shape of skull and development of these cranial features is highly variable, and only some of the largest species show the pattern seen in *Eptesicus*; again these species can be easily distinguished from *Eptesicus* by the combination of the characters described above. The length of skull is > 17 mm in *Eptesicus* and usually < 18 mm in *Neoeptesicus*, with no overlap when compared together with forearm length. *Eptesicus* is mainly distributed across North and Central Americas, overlapping in distribution only with *N. andinus*, *N. brasiliensis*, *N. chiriquinus*, and *N. furinalis*.

See Table 3 for additional comparisons.

## *Eptesicus* Rafinesque, 1820

*Vespertilio*: Schreber, 1774: pl. 53; part; not *Vespertilio* Linnaeus, 1758.

*Eptesicus* Rafinesque, 1820: 2; type species *Eptesicus melanops* Rafinesque, 1820 (= *Eptesicus fuscus* Palisot de Beau-

vois, 1796), by subsequent designation (Méhely 1900: 206).

*Vesperugo* Keyserling & Blasius, 1839: 312; part.

*Vesperus* Keyserling & Blasius, 1839: 313; part; proposed as a subgenus of *Vesperugo* Keyserling & Blasius, 1839; preoccupied by *Vesperus* Latreille, 1829 (Coleoptera, Cerambycidae).

*Adelonycteris* H. Allen, 1892: 466; part; replacement name for *Vesperus* Keyserling and Blasius, 1839, preoccupied.

Type species: *Vespertilio fuscus* Palisot de Beauvois, 1796.
Other species: *E. guadeloupensis* Genoways & Baker, 1975.

Distribution: *Eptesicus* is widely distributed across North and Central Americas, including the West Indies, and with a few records from northern South America, where it is restricted to Colombia, Ecuador, and Venezuela.

Diagnosis: *Eptesicus* can be distinguished by the following characters: ears short (<21 mm) and not connected; skull very robust, wide, and short; sagittal and lambdoidal crests well developed; postorbital process of the jugal weakly developed; eyes reduced, smaller or about the same size as lower canines and nostrils; auditory bullae small, the space between auditory bullae is larger than the width of each bullae; length of dorsal fur usually long (averaging 10.1 mm); length of forearm long, ranging from 40.1–54.0 mm (averaging 46.6 mm); tragus short and rounded, smooth and broad; GLS 16.9–20.8 mm (averaging 19.1 mm); and MTL 6.2–7.7 mm (averaging 7.1 mm).

Description: *Eptesicus* includes medium-sized to large bats. Dorsal fur long (LDF 8.1–13.7 mm) and woolly; hairs usually strongly bicolored with blackish bases extending about 1/2 of hair length, distal 1/2 of hairs golden to orangish brown; the juncture between bands is well marked. Ventral fur long (LVF 7.1–12.0 mm, averaging 8.8 mm) and woolly;

Table 3. Morphological differences between *Neoeptesicus* gen. nov., *Eptesicus*, and *Histiotus*.

| Character | *Neoeptesicus* gen. nov. | *Eptesicus* | *Histiotus* |
|---|---|---|---|
| Length of ears | < 20 mm | < 21 mm | > 21 mm |
| Connecting band between ears | Absent | Absent | Present, with variable development |
| Skull | Delicate to robust, wide and short | Very robust, wide and short | Delicate, long and narrow |
| Development of crests | Sagittal and lambdoidal crests weakly to well developed, united or not | Sagittal and lambdoidal crests well developed, united | Sagittal and lambdoidal crests weakly developed, separated |
| Postorbital process of the jugal | Weakly developed | Weakly developed | Well developed |
| Eyes | Small | Small | Large |
| Auditory bullae | Small | Small | Large |
| Length of dorsal fur (mean) | 4.5–13.1 mm (8.1 mm) | 8.1–13.7 mm (10.1 mm) | 8.0–14.5 mm (11.4 mm) |
| Length of forearm (mean) | 31.4–48.8 mm (40.1 mm) | 40.1–54.0 mm (46.6 mm) | 44.0–52.6 mm (47.8 mm) |
| Tragus | Wider at the base, short, rounded, smooth and slender | Wider at the base, short, rounded, smooth and broad | Wider at the base, long, pointed and notched |
| Occipital helmet | Absent to well developed | Well developed | Absent |
| GLS (mean) | 12.9–18.0 mm (15.8 mm) | 16.9–20.8 mm (19.1 mm) | 17.4–19.8 mm (18.4 mm) |
| MTL (mean) | 4.5–7.0 mm (5.8 mm) | 6.2–7.7 mm (7.1 mm) | 5.6–7.1 mm (6.3 mm) |

hairs bicolored with dark brown bases extending to about 2/3 of hairs length, distal 1/3 of hairs grayish yellow. Wing membranes naked, dark brown. Plagiopatagium attached to the base of the toe. Dorsal surface of the uropatagium almost naked, or with short sparse hairs that do not extend beyond the knees. Ventral surface of the uropatagium dark brown and sparsely haired along the base of the tail. Feet densely furred with short chestnut hairs. Ears well-separated, medium sized, dark brown, and with rounded tips; tragus wider at the base, straight to slightly curved, long, rounded, and broad. Muzzle broad and inflated.

Skull robust; rostrum short, wide, and flattened, and weakly sloping upwards to the braincase; braincase slightly wider than the rostrum. Posterior region of the braincase straight, slightly projected upwards. Nasal opening V-shaped. Frontal expanded laterally towards the orbit. Sagittal and lambdoidal crests well developed and connected; occipital helmet well-developed. Triangular, flattened bony plate where the sagittal and lambdoidal crests connect absent, the region where crests connect may be enlarged. Zygomatic arches thin and slightly widened medially. Basisphenoid pits absent. Palate extends well beyond molars, ending in a concave posterior edge, with a weakly- to moderately-developed medial spine.

Dental formula is I 2/3, C 1/1, P 1/2, M 3/3 (×2) = 32. $I^1$ separated, weakly to strongly bilobed; shape varies from narrow and long to broad and short, with outer cusps weakly to well developed. $I^1$ about three to four times the size of $I^2$. $I^2$ and $C^1$ separated by a small gap, $C^1$ with two slightly concave faces on the lingual region, and one slightly concave face on the labial region. P1 well developed, reaching 1/2 of $C^1$ in height; $P^1$ in contact with $C^1$ and molars. $M^1$ and $M^2$ about the same size, almost square shaped, with W-shaped cusps. $M^3$ reduced, triangular, with only 3 cusps. $I_1$ to $I_3$ reduced, trilobed, and filling all the space between canines. $P_2$ about three times $P_1$ in height. Molars have well developed cusps and decrease in size from $M_1$ to $M_3$.

See *Neoeptesicus* gen. nov. account and Table 3 for comparisons.

### *Histiotus* Gervais, 1856

*Plecotus*: I. Geoffroy St.-Hilaire, 1824: 446; part; not *Plecotus* É. Geoffroy St.-Hilaire, 1818.
*Vespertilio*: J. B. Fischer, 1829: 118; part; not *Vespertilio* Linnaeus, 1758.
*Nicticeius* Poeppig, 1830: column 218; incorrect subsequent spelling of, but not *Nycticeius* Rafinesque, 1819.
*Nycticeius*: Poeppig, 1835: 451; part; not *Nycticeius* Rafinesque.
*Nycticeus*: Lesson, 1836: 120; part; incorrect subsequent spelling of, but not *Nycticeius* Rafinesque.

*Nycticejus*: Lesson, 1842: 22; part; incorrect subsequent spelling of, but not *Nycticeius* Rafinesque.
*Histiotus* P. Gervais, 1856: 77, pl.13, fig. 6a and 6b (but not fig. 6 [= *Plecotus auritus*]); type species *Plecotus velatus* I. Geoffroy St.-Hilaire, 1824, by monotypy.
*Vesperus*: W. Peters, 1864: 383; part; not *Vesperus* Latreille, 1829 (Hymenoptera).
*Vesperugo*: Dobson, 1878: 188; part; not *Vesperugo* Keyserling and Blasius, 1839.
*Eptesicus*: Olrog, 1951: 508; part; not *Eptesicus* Rafinesque, 1820.
*Histictus* Ruschi and Bauer, 1957: 40; incorrect subsequent spelling of *Histiotus* P. Gervais.

Type species: *Plecotus velatus* I. Geoffroy St.-Hilaire, 1824.
Other species: *H. macrotus* (Poeppig, 1835); *H. montanus* (Philippi & Landbeck, 1861); *H. magellanicus* (Philippi, 1866); *H. colombiae* Thomas, 1916; *H. laephotis* Thomas, 1916; *H. alienus* Thomas, 1916; *H. humboldti* Handley, 1996; *H. diaphanopterus* Feijó et al., 2015; *H. cadenai* Rodríguez-Posada et al., 2021; and *H. mochica* Velazco et al., 2021.

Distribution: *Histiotus* is endemic to South America, where it has been recorded from almost every country, except from the Guianas and Trinidad and Tobago. Despite its wide distribution on the continent, most records from the genus are from cooler areas along the Andes, and also from southern, eastern and central Brazil, with only scattered records from the Amazon Basin.

Diagnosis: *Histiotus* can be distinguished by the following characters: ears long (>21 mm) and connected by a band of skin with variable development; skull delicate, narrow, and long; sagittal and lambdoidal crests weakly developed; postorbital process of the jugal well developed; eyes enlarged, larger than lower canines and nostrils; auditory bullae large, the space between auditory bullae is smaller than the width of each bullae; length of dorsal fur usually long (averaging 11.4 mm); length of forearm ranging from 44.0–52.6 mm (averaging 47.8 mm); tragus long, pointed and notched; GLS 17.4–19.8 mm (averaging 18.4 mm); and MTL 5.6–7.1 mm (averaging 6.3 mm).

Description: *Histiotus* includes medium-sized to large species. Dorsal fur long (LDF 8.0–14.5 mm), usually more than 10 mm; hairs ranging from almost unicolored to strongly bicolored; dark bases length from 1/2 to almost the entire length of hairs; the contrast between bands ranges from faint to very strong; distal portion of hairs ranging from dark brown to golden orangish or yellowish. Ventral fur long (LVF 6.0–12.6 mm), usually more than 8 mm; hairs bicolored with dark brown bases extending from 1/2 to about 3/4 of hairs length, distal portion of hairs ranging from dark brown to nearly white. Wing membranes naked, usually dark brown.

Plagiopatagium attached to the base of the toe. Dorsal surface of the uropatagium somewhat paler than wing membranes, almost naked, with scarce hairs that do not extend beyond the knees. Ventral surface of the uropatagium usually brown, with scarce hairs close to the base of the tail. Ears greatly enlarged, connected by a band of skin of variable development, varying from oval to triangular; tragus wider at the base, straight to slightly curved, very long, notched and pointed. Muzzle broad and slightly inflated.

Skull delicate; rostrum short and flattened, usually straight in lateral profile; braincase slightly wider than the rostrum. Posterior region of the braincase rounded, regular. Nasal opening V- to U-shaped. Frontal expanded laterally towards the orbit. Sagittal and lambdoidal crests weakly developed, not connected, occipital helmet absent. Triangular, flattened bony plate where the sagittal and lambdoidal crests connect ranging from absent to well developed. Zygomatic arches thin and greatly widened medially. Basisphenoid pits absent. Palate extends well beyond molars, ending in a concave posterior edge, with a weakly- to mid-developed medial spine.

Dental formula is I 2/3, C 1/1, P 1/2, M 3/3 (×2) = 32. $I^1$ separated, spatulate and strongly bilobed; wide and short, with inner and outer cusps well-developed. $I^1$ usually about three to four times the size of $I^2$. $I^1$ usually not aligned to $I^2$ on a transversal axis of the skull. $I^2$ and $C^1$ usually separated by a small gap, $C^1$ with two slightly concave faces on the lingual region, and one slightly concave face on the labial region. P1 well-developed, reaching 1/2 of $C^1$ in height; $P^1$ in contact with $C^1$ and molars. $M^1$ and $M^2$ about the same size, almost square shaped, with W-shaped cusps. $M^3$ reduced, triangular, with only 3 cusps. $I_1$ to $I_3$ reduced, trilobed, and occupying all the space between canines. $P_2$ about three times $P_1$ in height. Molars have well developed cusps and decrease in size from $M_1$ to $M_3$.

See *Neoeptesicus* gen. nov. account, and Table 3 for comparisons.

## ACKNOWLEDGEMENTS

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**Competing Interests**

**How to cite this article**

**Published by**

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# APPENDIX

Appendix 1. List of specimens included in morphological and morphometric analyses. Voucher material consists of stuffed skins, fluid preserved specimens, and skulls, deposited in the collections mentioned in Material and Methods section. Localities are arranged alphabetically by species and major political units. Specimens marked with asterisks were included in the principal component and canonical variate analyses.

*Cnephaeus anatolicus*.—EGYPT (N = 1): Cairo (BM 1998.16).

*Cnephaeus bottae*.—IRAN (N = 1): Mala-i-mir (BM 50.10.4.1*). IRAQ (N = 3): Baghdad (FMNH 42471*, BM 21.3.1.1*, 21.3.1.2*).

*Cnephaeus gobiensis*.—IRAN (N = 1): Mazandaran, Sama (FMNH 96763*). MONGOLIA (N = 6): Bayan Hongor, Kholobolchi Nor, Orog Nuur, 25 mi N (FMNH 33900*, 33901*, 33902*, 33903*, 33904*, 33905*).

*Cnephaeus isabellinus*.—ALGERIA (N = 2): Laghorial (BM 19.7.7.1160*, 19.7.7.2408*).

*Cnephaeus nilssonii*.— GERMANY (N = 2): Buchenberg (BM 0.2.8.3*, 0.2.8.4*). NORWAY (N = 3): Surendal, Moen (BM 25.11.3. 2*, 25.11.3.3*, 25.11.3.4*). SWEDEN (N = 3): Upsala (BM 11.1.1.40*, 11.1.1.41*, 11.1.1.42*).

*Cnephaeus pachyomus*.—AFGHANISTAN (N = 3): Nangarhar, 3 mi N Jalalabad (FMNH 102499*, 102500*, 102501*). CHINA (N = 3): Fujian, Futsing, Ling Sioh (FMNH 33927*, 33928*, 33930*). INDIA (N = 2): Nagaland, Naka Hills, Takubama (FMNH 76031*, 76032*). NEPAL (N = 1): Sankhuwasabha, Tumlingtar (FMNH 114246*). PAKISTAN (N = 1): Malakand, Swat District, Karakar Pass (FMNH 140422*).

*Cnephaeus serotinus*.—GREECE (N = 8): Near Athens (BM 8.10.2.10*); Patras (BM 8.10.2.1*, 8.10.2.2*, 8.10.2.3*, 8.10.2.4*, 8.10.2.7*, 8.10.2.9*, 8.10.2.11*). RUSSIA (N = 2): Locality not informed (BM 65.3773*, 65.3774*).

*Eptesicus fuscus*.—BAHAMAS (N = 6): Acklins Island, cave between Snug Corner and Spring Point (LSU 17088); Crooked Island, cave between Turtle Sound and Cripple Hill (LSU 17083–17087); Long Island, Mc Kinno's Cave, Whalehead (FMNH 44663–44669, 44672, 44675, 44676); Nassau (BM 3.10.3.1–3.10.3.5); New Providence (BM 15070–15072, 43321–43323). BARBADOS (N = 1): Locality unknown (BM 75.568). BELIZE (N = 1): Toledo (FMNH 129693). CANADA (N = 2): Alberta, Banff (FMNH 41304); Ontario, Toronto (FMNH 7306). COLOMBIA (N = 5): Cundinamarca, Bogotá (FMNH 49154); Bogotá, Pacho (BM 21.5.2.2, 21.5.2.3); Bogotá, Paine (BM 23.11.13.2); Medellín (BM 21.7.1.2). COSTA RICA (N = 6): San José, División (LSU 28346); San José, Río Corrogres, ca. 2 km NW Santa Ana (LSU 12976–12980). CUBA (N = 1): Santo Domingo (BM 97.12.15.1); Locality unknown (MNHN-ZM-MO 1997-1832). GUATEMALA (N = 5): Dueñas (BM 45.2.24.41, 45.2.24.42); Guatemala, 8 mi SE Guatemala, Finca Sta. Lucia (FMNH 73368); Locality unknown (BM 63.1735; MNHN-ZM-MO 1887-850). JAMAICA (N = 1): Chinchona (FMNH 63932). MEXICO (N = 25): Baja California, La Grulla, San Pedro

Martir Mts. (FMNH 10865); Baja California, Parral (FMNH 10868–10877); Baja California, Rosarito (FMNH 15864); Baja California, San Antonio (FMNH 10867); Baja California, Santa Eulalia (FMNH 10866); Baja California Sur, Sierra Laguna (BM 98.3.1.3); Durango, Coyotes (FMNH 14600, 15922); Oaxaca, Campamento Río Molino (LSU 11932); San Luis Potosí, Cañada Grande, Mts. SE of Cañada Grande, 6 mi SE (LSU 4039, 4040); San Luis Potosí, Villa Del Reyes (LSU 2780); San Luis Potosí, 3 km SW San Isidro (LSU 4932); Sonora, Providentia Mines (FMNH 11773, 11774); Locality unknown (BM 56.8.1.9). PANAMA (N = 1): Darién, ca. 6 km NW Cana, E slope Cerro Pirre (LSU 25508). UNITED STATES OF AMERICA (N = 118): Arizona, Apache Co., White Mts. (FMNH 1058, 1059); Arizona, Cochise Co., Chiricahua Mts. (FMNH 1040–1046, 1049–1055, 15068, 15069); Arizona, Cochise Co., SW Research Station, near portal (FMNH 172508–172511); Arizona, Pima Co., Tucson (LSU 10128, 10129, 10419); Arkansas, Clay Co., Green Way (FMNH 5833*); Arkansas, Independence Co., Bone Cave (FMNH 64027*, 64028*); Arkansas, Independence Co., Bat Cave 1.2 mi SE Lock + Dam #3 on White River (LSU 15180, 17807); California, Butte Co., 4 mi E Chica (LSU 6777–6779); California, Inyo Co., Lone Pine (FMNH 13332–13337); California, Mendocino Co., Gualala River (FMNH 48181); California, Tulare Co., Mt. Whitney (FMNH 13323,13324, 13326–13330); Georgia, Decatur Co., Bainbridge (FMNH 74847, 74848, 74850); Illinois, Cook Co., Chicago (FMNH 166992); Illinois, Du Page Co. (FMNH 152064*, 152065, 175324*, 175325, 175326*, 175327*, 175328, 178148, 178149, 178151,178152, 167065*, 235421); Illinois, Kane Co. (FMNH 90541, 178151); Illinois, La Salle Co., Peru (FMNH 53115, 53120); Illinois, Lake Co., Zion (FMNH 166993); Illinois, Sangamon Co., Springfield (FMNH 134397); Kentucky, Carter (MACN 13407); Louisiana, Natchitoches Parish, Natchitoches (LSU 1108); Louisiana, Ouachita Parish, Monroe (LSU 26305); Louisiana, Lincoln Parish, Ruston (LSU 47, 50); Louisiana, Sabine Parish, W Many (LSU 11602, 11603); Louisiana, Santa Elena Parish, 5 mi NNE Chipola (LSU 11604); Louisiana, Tangipahoa Parish (LSU 186); Massachusetts, Hampden Co., Montgomery (FMNH 199518–199520); Michigan, Washtenaw Co., Ann Arbor (LSU 462); Michigan, Washtenaw Co. (FMNH 54650); Minnesota, Becker Co. (FMNH 165372); Minnesota, Crow Wing Co., Brainerd (FMNH 165347); Missouri, Lawrence Co., Miller, 2 mi S, 0.5 mi W Iberia (FMNH 58596, 58597); Montana, Yellowstone Co. (FMNH 5663); Nebraska, Cass Co., 1.5 mi NE Louisville (FMNH 79828, 79829); New Jersey, Essex Co., Montclaire (FMNH 124191); New Jersey, Morris Co., Hibernia (FMNH 124192); Oklahoma, Woodward, Alabaster Cav. (FMNH 83345); South Carolina, Charleston Co., Charleston (MNHN-ZM-MO 1997-1822); Tennessee, Davidson Co., Nashville (LSU 19503); Tennessee, Hickman Co. (FMNH 5106); Tennessee, Warren Co., 12 mi S Mc Minniville Bat Cave (LSU 19502); Vermont (locality unknown, LSU 580); Washington, Island Co., Whidbey Island (LSU 37155); Washington, Klickitat Co. (LSU 37182–37185); West Virginia, Greenbrier Co., Job Knob (FMNH 5610); West Virginia, Greenbrier Co., White Sulphur Spgs. (FMNH 5611, 5709, 5895–5897); Wisconsin, Brow Co., Green Bay (FMNH 154653–154658); Wisconsin, Marinette Co., Pound (FMNH 178029); Wisconsin, Milwaukee Co., Milwaukee, University of Wisconsin (FMNH 58594); Wisconsin, Milwaukee Co., Shorewood (FMNH 58595). VENEZUELA (N = 2): Mérida (BM 27.11.197); Mérida, Culata (BM 98.7.1.28).

*Eptesicus guadeloupensis*.—GUADELOUPE (N = 2): Sainte-Rose (MNHN 2015-2085); Locality unknown (MNHN 2015-282).

*Histiotus alienus*.—BRAZIL (N = 1): Santa Catarina, Joinville (BM 9.11.19.1).

*Histiotus diaphanopterus*.—BRAZIL (N = 1): Maranhão, Tranqueira (FMNH 26466); BOLIVIA (N = 1): Santa Cruz, 5.5 km NNW of Valle Grande (AMNH 264086).

*Histiotus humboldti*.—VENEZUELA (N = 4): Amazonas, Cerro Neblina, 2.8 km NE Pico Phelps (USNM 560627); Distrito Federal, Caracas, 5 mi N of Caracas (USNM 370967); Distrito Federal, Caracas, 9.4 km N of Caracas, Hotel Humboldti (USNM 370970); Mérida (MNHN-ZM-MO 1972-762).

*Histiotus laephotis*.—ARGENTINA (N = 12): Catamarca, Cuesta del Clavillo (CML 5253*); Catamarca, Paclin (CML 10833*); Jujuy, Cueva del Tigre (MACN 16811); Jujuy, San Pedro (CML 7058*); Salta, La Vina, Iglesia (MACN 16810); Salta, Río das Piedras (BM 34.11.4.1, 34.11.4.2); Tucumán, Tucumán (BM 2.1.5.1*, 4.10.2.1*); Tucumán, Burruyacú, El Naranjo (MACN 16814); Tucumán, Horco Molle (CML 4515*); Tucumán, Yerba Buena (CML 6103*). BOLIVIA (N = 7): Cochabamba, Pocana (BM 34.9.2.20); Pilcomayo, San Francisco Misiones (BM 97.2.25.3); Caiza (BM 97.2.25.1*, 97.2.25.2, 97.2.25.4*); Locality unknown (BM 45.11.18.1, 45.11.18.2). PERU (N = 2): Cuzco, Huasampilla (BM 73.7.3.4); Huancavelica (locality unknown, BM 38.9.26.3*).

*Histiotus macrotus*.—ARGENTINA (N = 6): Catamarca, 5 km NW Chumbicha (CML 7894); Catamarca, Dique el Potrero (CML 6061); Neuquén, Parque Nacional Nahuel Huapi (CML 9884); Salta, 20 km N Cafayate (CML 5406); Tucumán, Chicligasta (CML 6185); Tucumán, Pueblo Viejo (CML 6059). CHILE (N = 13): Santiago (BM 35.11.10.1*, 35.11.10.3*, 35.11.10.4, 35.11.10.5*, 35.11.10.6*, 35.11.10.9, 35.11.10.13*, 35.11.10.14*, 35.11.10.16*, 35.11.10.17*, 35.11.10.18, 35.11.10.19); Locality unknown (MNHN-ZM-MO 1999-962). PERU (N = 2): Ancash, Huari, 1 Km W of Picheu, mouth of coal mine (FMNH 129207); Huanuco, E slope Cordillera Carpish, Carretera Central (LSU 12587).

*Histiotus magellanicus*.—ARGENTINA (N = 8): Chubut, Río Turbio (MACN 16505); Neuquén (CML 3231); Neuquén, Los Lagos (CML 10853, 10854); Neuquén, Parque Nacional Nahuel Huapi (CML 9887); Río Negro, Bariloche (MACN 23650); Río Negro, El Bolson (LSU 16784); Tierra del Fuego, Viamonte (BM 30.10.9.1). CHILE (N = 12): Aisen, Almirante Simpson, Isla Gran Guaiteca (FMNH 127477*, 127478*, 127479*, 127480*); La Araucania, Cautin, Lake Gualletue (FMNH

23624*); La Araucania, Malleco, Curacautín (FMNH 23622, 23623*); Los Lagos, Chiloé, Río Inio (FMNH 23619*, 23620*); Los Lagos, Valdivia, Mafil (FMNH 23621*); Maquehue (BM 8.3.1.1*); Patagonia, Last Hope Inlet (BM 7.4.5.1).

*Histiotus colombiae*.—COLOMBIA (N = 11): Cundinamarca, Bogotá (FMNH 72165*, 72166*, 72167*, 72168*, 72169, 72170*, 72171*, 72172–72174); Cundinamarca, Coachi (BM 99.11.4.1).

*Histiotus mochica*.—PERU (N = 1): Piura, Talara, Quebrada Pariñas, 9.6 km NE of Talara (AMNH 278521).

*Histiotus montanus*.—ARGENTINA (N = 11): Catamarca, Las Estarcias (CML 1758); Chubut, Pico Salamanca (28.12.11.1*); Cordoba, El Carrizal (BM 16.1.6.1*, 16.1.6.2*); Neuquén, Catán, Las Coloradas (MACN 13844); San Luis (locality unknown, MACN 16809); San Juan, Jachal (CML 5568*); Santa Cruz, Punta Loyola (BM 20.11.29.1*); Tucumán, Burruyacú, Anta Mapu (MACN 16813); Tucumán, Burruyacú, El Naranjo (MACN 16815); Tucumán, Nareu (BM 4.10.2.2*). CHILE (N = 5): Santiago, Punta Alta (BM 3.7.3.2*); Locality unknown (BM 49.12.4.26, 43.12.16.15, 73.12.16.14; MNHN-ZM-MO 1874-53*). ECUADOR (N = 1): Pichincha, Quito (MNHN-ZM-MO 1904-1179). PERU (N = 6): Arequipa, Islay, Chucarapi (FMNH 50780, 50781); Cuzco, ca 14 km NE Alba Malaga on Ollantaitambo-Quillabamba (LSU 19215); Huancavelica, Angaraes, Lircay (FMNH 75149); San Martín, Puerta del Monte, ca 30 km NE Los Alisos (LSU 27260); Western coast (BM 68.4.29.7). URUGUAY (N = 3): Riviera, Riviera (FMNH 65634, 65635); Soriano (locality unknown, BM 94.1.24.8).

*Histiotus velatus*.—ARGENTINA (N = 9): Corrientes, Virasoro (MACN 18055); Jujuy, Manuel Belgrano (CML 7059, 11916); Misiones, Oberá (MACN 18053, 18054, 18055, 18056–18059). BRAZIL (N = 22): Maranhão, Tranqueira (FMNH 26466); Mato Grosso, Chapada (BM 3.7.7.17); Minas Gerais, Lagoa Santa (FMNH 20744; MN 6516); Minas Gerais, Viçosa (MN 3395); Rio de Janeiro, Ilha Grande (MN 23071, 23072); Rio de Janeiro, Itaguaí (MACN 16812); Rio de Janeiro, Rio de Janeiro, Quinta da Boa Vista (MN 3547, 23049); Rio de Janeiro, Seropédica (ALP 1522, 1579, 1581, 2096, 2349, 2350, 4845, 4942, 5088, 5595); São Paulo, Pirassununga (MN 23048); Santa Teresa (MNHN-ZM-MO 1999-963). PARAGUAY (N = 1): Colonia Asunción (MACN 16808). PERU (N = 11): Cuzco, Quispicanchi (FMNH 66389, 66391, 66393, 68496–68502, 68504, 68504).

*Neoeptesicus andinus*.—BOLIVIA (N = 2): Cochabamba, Calahuasi (CML 1330); Cochabamba, Choro (BM 2.1.1.1). ECUADOR (N = 5): Mirador (BM 99.9.9.1, 99.9.9.2); Pastaza, Sarayacu (BM 54.375); Pastaza, Canelos (BM 54.373, 54.374). PERU (N = 21): Junín, Chanchamayo (BM 9.7.5.3, 7.6.15.2); Huanuco, E slope of Cordillera Carpish, Carretera Central (LSU 12581*, 14289*, 14290*, 14291*, 14292*, 14294*, 14295*, 14296*, 14297*, 14298*, 14299–14305); San Martín, Puerta del Monte, ca. 50 km NE Los Alisos (LSU 27261, 27262).

*Neoeptesicus brasiliensis*.—ARGENTINA (N = 10): Córdova, Cruz Del Eje (BM 2.2.5.1); Corrientes, Goya (98.3.4.3–98.3.4.8); Entre Ríos, La Paz (CML 11965); Jujuy (BM 20.1.7.1); Locality unknown (MNHN-ZM-MO 1911–615). BOLIVIA (N = 1): Santa Cruz, Buena Vista (BM 26.12.4.20). BRAZIL (N = 33): Goyar (MNHN-ZM-MO 1997-1807–1997-1810); Minas Gerais, Caeté, Mina Apolo (CMUFLA 2445); Minas Gerais, Igarapé (CMUFLA 2359); Minas Gerais, João Monlevade, RPPN Belgo Mineira (CMUFLA 956, 968–971); Minas Gerais, Lavras, Parque Ecológico Quedas do Rio Bonito (CMUFLA 177, 178); Minas Gerais, Lima Duarte, Parque Estadual do Ibitipoca (CMUFLA 1026, 1040); Minas Gerais, Mariana (CMUFLA 1422, 1428, 3131, 3121); Minas Gerais, Marliéria, Parque Estadual do Rio Doce (CMUFLA 1892); Minas Gerais, Minduri, Mata Triste (CMUFLA 142); Pará (BM 5.1.25.8); Pará, Juruti (APC 2254); Pará, Tauari (FMNH 42737); Rio Grande do Sul, São Lorenzo (BM 88.11.30.2); Rio de Janeiro, Rio de Janeiro (BM 52.8.27.9); Santa Catarina (BM 7.1.1.364, 7.1.1.365); São Paulo, Iperó, FLONA Ipanema (APC 2101); São Paulo, Piquete (CMUFLA 2916); Locality unknown (MN 3191, 3192; BM 44.3.7.25). COLOMBIA (N = 14): Boca Del Cauca (BM 99.9.6.3); Cundinamarca, Bogotá (BM 99.11.4.3); Cundinamarca, Bogotá, Cueva Del Hermitano (BM 99.11.4.2); Santa Fé de Bogotá (BM 7.1.1.368); Bolívar, Catival (FMNH 69523*, 69524*); Santana, near Honda (BM 10.9.23.8–10.9.23.10); Villavicencio, Finca el Buque (FMNH 121263*, 121265*, 121266*). COSTA RICA (N = 1): Guanacaste, Volcán Cacao (BM 1988.510). ECUADOR (N = 10): Napo, San José de Payamino (FMNH 125001*, 125002); Pastaza (FMNH 43146*); Pastaza, Canelos (BM 54.382); Pastaza, Río Solis (MNHN-ZM-MO 1984-1943, 1984-1944); Morona-Santiago, Gualaquiza (BM 7.1.1.369–7.1.1.372). GUYANA (N = 1): Demerara (BM 8.3.7.17). PANAMA (N = 1) Boca Del Toro (BM 99.9.6.1, 99.9.6.2). PERU (N = 24): Amazonas, Utcubamba (FMNH 106756); Ayacucho, Huanhuachayo (LSU 16634); Cuzco, Paucartambo (FMNH 123953, 123954, 170271*, 170273*, 174917*); Huanuco, Santa Elena, 35 km NE Tingo María (LSU 12582–12586, 14306–14308, 17714); Ucayali, Maynas (CML 12025); Ucayali, Balta, Río Curanja (LSU 12280, 12281); Ucayali, Yarinacocha (LSU 14309, 14310); Madre de Dios, Pampas de Heath (LSU 22128–22130).

*Neoeptesicus chiriquinus*.—ARGENTINA (N = 2): Jujuy, Arroyo Los Matos, Finca las Capillas (CML 7541*); Jujuy, Manuel Belgrano (CML 9901*). BRAZIL (N = 2): Minas Gerais, Lavras, Valos (CMUFLA 510*); São Paulo, Angatuba, Estação Ecológica de Angatuba (ANG 01M*). COLOMBIA (N = 1): Valdira (BM 98.10.3.32*). FRENCH GUIANA (N = 1): Sant-Elie (MNHN 2016-945*). PANAMA (N = 1): Chiriquí, Boquete (BM 3.3.3.1*). (PERU (N = 3): Cuzco, Chanchamayo (BM 94.8.6.1); Cuzco, Paucartambo (FMNH 174921); Río Chinchao, Hacienda Vista Alegre (FMNH 24884*).

*Neoeptesicus diminutus*.—ARGENTINA (N = 23): Buenos Aires (CML 1820; MACN 18051); Catamarca, El Durazno (CML 7738*, 7741); Corrientes, Itati (BM 24.6.6.4); Jujuy, Laguna La Brea, 25 km W Palma Sola (CML 3084*, 3086); Misiones

(MACN 5131, 16790, 22418, 24868); Salta, Aguaray (MACN 30289); Salta, Anta (CML 6050*, 7336*, 7337*); Salta, Cerillos (CML 7682*); Salta, José de San Martín (CML 6139*, 6140, 10950*); Salta, Metán (CML 7742*); Santa Fé, Esperanza (BM 1.2.4.1); Tucumán, Burruyacú (CML 9840, 11906*). BRAZIL (N = 10): Bahia, São Marcello (FMNH 20971 [holotype]); Goiás, Niquelândia (CMUFLA 2034); Maranhão, Alto Parnaíba (FMNH 26452); Minas Gerais (FMNH 20743); Minas Gerais, Belo Horizonte (CMUFLA 1131); Minas Gerais, Lavras (CMUFLA 173, 2175); Minas Gerais, Mariana (CMUFLA 3117); Pará, Almeirin (MN 3261); São Paulo, Valparaíso (FMNH 41630). URUGUAY (N = 3): Balneario las Cañas, Río Negro (CML 1859); Quebracho, Paysandu (FMNH 72813, 72814).

*Neoeptesicus furinalis*.—ARGENTINA (N = 102): Buenos Aires (MACN 44.1, 19206); Catamarca, El Durazno (CML 8937); Catamarca, Paclín (CML 10831); Catamarca, San Antonio de la Falda (CML 1023); Chaco, Almirante Brown (CML 3220, 3221, 3225, 3226, 3850, 3854); Chaco, Río Teuco (CML 5397); Córdova, Los Cisnes (BM 20.3.14.20, 20.3.14.21); Corrientes, Ituzaingo (MACN 16784, 18037; BM 69.1246); Corrientes, P. N. Mburucuyá (MACN 20917); Corrientes, Paso de la Patria (MACN 18052); Corrientes, Laguna Gelarza (CML 3697); Entre Ríos (MACN 21091–21093, 19386–19389, 16801–16803, 16805–16807); Formosa (MACN 20874); Formosa, Cassinera (MACN 20933, 20936, 20940); Formosa, Estero Poi, Algarroba (MACN 4672); Formosa, Lo Bermejo (CML 3855, 3856, 5411); Formosa, Pilcomayo (CML 4670; MACN 16778, 20876, 20879); Formosa, Río Porteño (CML 2047, 2047); Formosa, P.N. Pilcomayo (MACN 20879); Jujuy, El Carmen (CML 7876); Jujuy, Ledesma (CML 5223; MACN 13162, 13163); Jujuy, Manuel Belgrano (CML 4313, 11908); La Rioja, San Blas de Los Sauces (CML 5445); Locality unknown (CML 5430); Misiones (CML 2157; MACN 17903); Misiones, Capital (MACN 44.1, 16781–16782, 18043, 18046, 18048, 18049); Misiones, Guarani (CML 3857); Orán, Santa María (CML 5221); P. N. Chaco (MACN 20861, 20865); Salta, 8km W Piquirenda (CML 5222); Salta, Aguaray (MACN 30290); Salta, Generel José de San Marten (CML 10959, 10961); Salta, La Candelaria (CML 7882); Salta, Metáu (CML 11910); Salta, Orán (CML 4331, 5142, 10972; MACN 16793); Salta, Río Ftiyuro (CML 5372); San Luis, Santa Rosa de Conlapa (MACN 21696); Santiago del Estero, Jiménez (MACN 16792); Tucumán (CML 9883*; BM 1.6.3.1); Tucumán, Alberdi (CML 10829*, 10832*); Tucumán, Burruyacú (CML 9881, 11911, 11912*); Tucumán, Concepción (BM 25.3.1.1–25.3.1.3); Tucumán, Cruz Alta (CML 9882*); Tucumán, Leales (CML 10992*, 10993*); Tucumán, Reserva Provincial Aguas Chiquitas (CML 5225*, 5226*, 5227*); Tucumán, Tafí Viejo (CML 7087); Tucumán, Trancas las Mesadas (CML 1193); Tucumán, San Miguel de Tucumán (CML 5657, 5984). BELIZE (N = 37): Belize District, Belize city (FMNH 121087); Belize District (FMNH 129690, 129691); Cayo (FMNH 121092, 121103); Cayo, Tea Kettle (FMNH 58487); Cayo, Central Farm (FMNH 58481–58483, 121088–121091, 121093–121101, 121104); Cayo, Ontario Village (FMNH 121102); Corozal, Santa Clara (FMNH 58488); Corozal, 2.5 km W Patchakan (FMNH 121107, 121108); Orange Walk (FMNH 58489–58494, 121106); Stann Creek, Melinda Agricultural Station (FMNH 58484–58486). BOLIVIA (N = 4): Caiza (BM 97.2.25.8); Santa Cruz, Buena Vista (BM 26.12.4.21); Santa Cruz, Parapetí (BM 21.11.6.2); Sierra Santa Rosa (BM 25.2.1.4). BRAZIL (N = 35): Bahia, Brejinho das Ametistas (CMARF FIOLCT18M); Bahia, Lamarão (BM 3.9.5.16); Espírito Santo (ALP 9286, 9287, 9544, 9547, 9559, 9847); Minas Gerais (locality unknown, MN 3297; ALP 11, 5546, 5671–5673); Minas Gerais, Caeté (CMUFLA 2345); Minas Gerais, Conceição do Mato Dentro (CMUFLA 1629); Minas Gerais, Lavras (CMUFLA 175, 176, 468, 470, 472, 481, 509, 534, 2172, 2173, 2174); Minas Gerais, Mariana (CMUFLA 3114, 3132, 3133); Minas Gerais, Minduri (CMUFLA 247); Minas Gerais, Monte Belo (CMUFLA 2077); Minas Gerais, Muzambinho (CMUFLA 2484, 3087); Minas Gerais, Salinas (CMUFLA 1385); Minas Gerais, São Roque de Minas (CMUFLA 20); São Paulo, Cruzeiro (BM 1.2.7.2, 1.2.7.3); São Paulo, Iperó, FLONA Ipanema (APC 1740, 1749, 1959, 1960, 1963); São Paulo, Mairinque (FAU 27); Tocantins, Mateiros (CMUFLA 1015). COLOMBIA (N = 2):Tolima, Guamo (FMNH 86721); Meta, Villavicencio, Finca El Buque (FMNH 121264). COSTA RICA (N = 3): Limon, Cariari (LSU 12982, 12983); San José, Río Corrogres (LSU 12981). FRENCH GUIANA (N = 8): Cayenne (MNHN 2016-948, 2016-949); Guiana (MNHN 2016-953); Kourau (MNHN 2016-958–2016-960); Paracou (MNHN-ZM-MO 1995-890); Sant-Elie (MNHN 2016-950). GUYANA (N = 2): Demerara, Georgetown (BM 5.11.1.1, 7.6.20.1). HONDURAS (N = 1): Atlantida, Tela (FMNH 41366). MEXICO (N = 9): Chiapas, ca. 40 km N Huixtla (LSU 11930); San Luis Potosí, 1 km W Huichihuayan (LSU 4933, 4934); San Luis Potosí, El Salto (LSU 4935); Tabasco, 0.8 km W Miramar (LSU 8423–8425, 8427); Vera Cruz, Achotal (FMNH 14150). PARAGUAY (N = 8): Canindeyú,17 km SE Igotiní (CML 5467); Paraguarí, Sapucay (BM 0.6.7.3, 1.8.1.2, 1.11.1.1–1.11.1.5). PERU (N = 4): Loreto, Maynas (CML 1554, 2624); Loreto, Río Curanja (LSU 12282, 12283). SURINAME (N = 1): Zandevig (BM 52.1025). URUGUAY (N = 1): Montevideo, Manga (MACN 16775).

*Neoeptesicus innoxius*.—ECUADOR (N = 10): El Oro, Zaruma (BM 0.2.9.1*); Gulf of Guayaquil, Puná (BM 99.8.1.1, 99.8.1.2); Santa Rosa (BM 0.2.9.3*, 0.2.9.4*, 0.2.9.5*, 0.2.9.6*, 0.2.9.7*, 0.2.9.8*, 0.2.9.9*). PERU (N = 13): Lambayeque, Etén (BM 0.3.1.104, 0.3.1.105*, 0.3.1.106, 0.3.1.107*, 0.3.1.108, 0.3.1.109); Lambayeque, Motupe (FMNH 81033); Lambayeque, 44 km N Olmos then ca. 20 km E (LSU 21309,21310); Lambayeque, 12 km N Olmos (LSU 27258, 27259); Piura, Amotape (MNHN-ZM-AC A6987); Piura, Piura (BM 0.3.1.1).

*Neoeptesicus taddeii*.—BRAZIL (N = 2): São Paulo, São Miguel Arcanjo, Parque Estadual Carlos Botelho (ZSP 17*, 48*).

*Neoeptesicus ulapesensis*.—ARGENTINA (N = 9): La Rioja, General Belgrano (CML 11888*, 11889*, 11990*, 11991*, 11992*); La Rioja, San Martín, Ulapes (CML 11884*, 11885*, 11886*, 11887*).