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Systematics and biogeography of tube-nosed bats, *Murina* (Mammalia, Chiroptera, Vespertilionidae), from the Philippines with descriptions of six new species

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Abstract

Murina is a wide-ranging genus of insectivorous bats that occurs throughout Asia whose known diversity has recently been increasing with the description of 26 new species in the past 20 years. The Philippine archipelago—mostly comprised of islands with oceanic origin and thus a history of isolation—has produced a fauna rich in endemic species, including bats. Here, we describe the morphological and genetic diversity among *Murina* specimens collected from across the Philippine islands and compare them to representatives from the Southeast Asian mainland and adjacent islands. Our results show that the wide-spread *M. cyclotis* represents a radiation, beginning around 11 mya, of five distinct *Murina* species endemic to the Philippines, including three single-island endemics. These five new *M. cyclotis* group species are mostly allopatric in distribution, except for two species—the smallest and largest that occur in the Philippines—that co-occur on Mindanao Island. Our study documents *Murina suilla*, a species occurring in Indonesia, Malaysia and Thailand, and only occurring on Mindoro and Palawan Islands within the Philippines. Additionally, we describe a new species that is sister to *M. suilla* and is widespread across the Philippine archipelago. Overall, our study has increased the number of Philippine *Murina* species from two to seven. As the first phylogeographic analysis of a laryngeal echolocating bat genus within the Philippines, our study provides evidence that the diversification of understory insectivorous bats largely echoes that of fruit bats (Pteropodidae), which is characterized by endemic Philippine lineages that are primarily confined to known biogeographic regions that constitute sets of modern islands that were connected during the last ice age, or to individual oceanic islands. We hypothesize that subsequent phylogeographic investigations of other bat taxa may reveal similar, previously unrecognized, endemic radiations within the highly biodiverse Philippines.

Key words: diversification, endemism, Miocene, phylogeny, oceanic islands, species limits, Southeast Asia

Introduction

Species of tube-nosed bats in the genus *Murina* are found over a wide geographic area from north-east Pakistan to China and Siberia in the east and south through Japan, Korea, the Philippines, Indonesia and into Australia (Hill 1992). Simmons & Cirranello (2024) recognized 39 species of *Murina*, an increase of 23 species over 19 years. Since the publication of this list, three new species have been described: *M. yuanyang* (Mou *et al.* 2024), *M. yushuensis* (Wang *et al.* 2024) and *M. lvchun* (Mou *et al.* 2025). It should be noted that three species described, *M. lvchun* (Mou *et al.* 2025), *M. fanjingshanensis* (He *et al.* 2015), and *M. rongjiangensis* (Chen *et al.* 2017) were described in online-only journals that do not meet ICZN standards of registration in Zoobank and are technically considered unpublished until the authors redescribe them. Simmons & Cirranello 2024 and Mammal Diversity Database 2025, treated *M. rongjiangensis* as conspecific with *M. shuipuensis*. However, we consider *M. rongjiangensis* may represent a different species that requires a more thorough analysis. Thus, we recognize 43 species in the genus.

The Philippines bat fauna is notably diverse, with 79 currently recognized species (Heaney *et al.* 2010, 2012).

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Several authors have suggested that some of these individual taxa represent multiple species, some of which are genetically distinct but morphologically cryptic and awaiting description (Ingle & Heaney 1992; Heaney & Roberts 2009; Sedlock & Weyandt 2009; Esselstyn *et al.* 2012; Heaney *et al.* 2012, 2016b). If added to the new species described here, we estimate that these might bring the current count to potentially 100 species for the Philippines.

Subsequent to the description of the first endemic Philippine bat, *Desmalopex leucopterus*, by Temminck (1853), progress towards unraveling these evolutionary puzzles was hindered for decades by lack of specimens with sufficient geographic and population-level representation. Beginning with efforts to conduct comprehensive field inventories in the middle 1980s using mist nets (e.g., Heaney *et al.* 1989; Heaney *et al.* 1991; Rickart *et al.* 1993; Esselstyn *et al.* 2004), many new Philippine records were obtained (e.g., Heaney *et al.* 2016b) and new species endemic to the Philippines have been described (Esselstyn 2007; Helgen *et al.* 2007; Esselstyn *et al.* 2008). Robust molecular phylogenetic and population genetic studies investigating potential diversification among and within Philippine islands thus far have been limited to a few bat taxa, including four pteropodid species (Peterson & Heaney 1993; Heaney & Roberts 2009; Roberts 2006 a,b) and two taxonomically broad phylogenetic studies (e.g., Jones *et al*. 2002; Giannini & Simmons 2003; Nesi *et al*. 2021). Patterns of diversification within most Philippine bats have been little studied; however, recent phylogenetic studies of *Hipposideros* (Esselstyn *et al.* 2012) and *Kerivoula* (Sedlock *et al.* 2020) have begun to fill in this gap.

Up to about a decade ago, only three species of *Murina* were reported as coming from the Philippines. *Murina cyclotis*, as defined at the time, was first collected in the Philippines in 1988 with one specimen from Catanduanes Island (Heaney *et al.* 1991) and another from Mt. Isarog in southeastern Luzon (Heaney *et al.* 1999). In the following years small numbers were collected during surveys throughout the Philippines, for example, Sibuyan Island (Goodman & Ingle 1993) and Mt. Kitanglad, both captured in 1992 (Heaney *et al.* 2006), Mt. Makiling in 1999 (Sedlock 2001b), Kalinga Province in northern Luzon in 2001, and Mindanao in 2006 (Heaney *et al.* 2010). *Murina suilla*, as defined at the time, was not captured in the Philippines until 2005, when collected by D. S. Balete in Davao Oriental Province on Mindanao Island (Balete *et al.* 2006). In subsequent years, and with the deployment of harp traps to complement mist nets, individuals reported as *M. suilla* were captured across the archipelago from Mindanao to the Visayas in the central islands and to northern Luzon (Heaney *et al.* 2010; Balete *et al.* 2011, 2013). *Murina tubinaris* has been reported only from Palawan Island (Esselstyn *et al.* 2004); however as noted below, it probably represented what is currently called *M. suilla*.

The geological history of the Philippines makes it an interesting place to examine the extent of diversification within *Murina* and other bats. The archipelago consists of oceanic islands that have not had dry-land connections to mainland areas or adjacent larger islands, with the possible exception of the Palawan chain of islands, which might have been connected to Borneo during one or more of the Pleistocene periods of low sea level (Heaney 1986, 1991; Hall 1998, 2012). Though isolated from the mainland and other islands, those areas are relatively near, so dispersal to the Philippines from the southwest (Borneo), south and southeast (Sulawesi and New Guinea), and north (Taiwan) by bats is conceivable. Moreover, the oceanic islands merged into a fewer number of larger but still isolated islands during periods of low sea level that occurred repeatedly during the Pleistocene (Fig. 1), likely impacting gene flow and speciation (Heaney & Roberts 2009; Sedlock *et al.* 2020). Thus, we studied *Murina* to provide a relatively detailed assessment of this long history of varying geological isolation to understand the direct impact on species diversity in this genus, but also the evolution of all Philippine fauna, as discussed below.

In this paper we summarize and examine the Philippine specimens in the genus *Murina*. We provide information on the identification and distribution of all species, including *M. suilla*, and the description of six new species of *Murina* from the Philippines of which all but one are part of the *M. cyclotis* species group. We also place our results into a broader biogeographic context within Southeast Asia.

Materials and Methods

Field and Museum Methods

Specimens of *Murina* obtained and examined for this study are listed in Appendix 1 and in the descriptions of the new species. Nearly all Philippine specimens are currently housed at the Field Museum of Natural History, Chicago (FMNH), but half of the specimens of the new species, including the holotypes, will be returned to the National

Museum of the Philippines, Manila (PNM). Specimens of *Murina* had muscle tissue sampled from the left thigh or pectoral muscle of all fresh, intact specimens and preserved in either 95% ethanol or liquid nitrogen. After the tissues were returned to the museum, all were preserved in liquid nitrogen. Most bodies were fixed in formalin in the field and subsequently transferred to 70% ethanol (with most skulls subsequently removed and cleaned). We followed all relevant Philippine laws and regulations in the capture and handling of animals in the field, and in exporting specimens. We also followed guidelines for animal care and use as established by the American Society of Mammalogy (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists 2016).

Specimen data

For the morphometric analysis we included 45 specimens of *Murina* from the Philippines (Appendix 1) catalogued by the Field Museum of Natural History, Chicago, FMNH (the six holotypes were subsequently given National Museum of the Philippines numbers, PNM), seven specimens of *M. suilla* from the Naturalis Biodiversity Center, Leiden (RMNH), and six specimens of *M. suilla* at the Royal Ontario Museum, Toronto (ROM). We note that Esselstyn *et al.* (2004) tentatively referred to a single specimen from Palawan Island as *M. tubinaris*, but based on geography and craniodental characters, we here tentatively refer it to *M. suilla*.

Sequence data

The molecular dataset for the mitochondrial DNA gene cytochrome *b* (Cytb) consisted of 213 specimens representing 26 of 42 currently recognized species of *Murina*, one of two species of *Harpiola*, the monotypic genus *Harpiocephalus*, and *Kerivoula hardwickii* and *Myotis ikonnokovi* as outgroup taxa (Appendix 2). We downloaded 64 of these sequences from GenBank. For the 149 new sequences deposited in GenBank, DNA extraction was done primarily from muscle tissue (FMNH) and liver (ROM) initially frozen in liquid nitrogen with a phenol-chloroform procedure followed by elution in 50 µl of TE buffer as outlined in Lim *et al.* (2008). In summary, PCR amplification of the 1,140 base pairs (bp) of Cytb used forward primer LGL 765 and reverse primer LGL 766 (Bickham *et al.* 1995). The thermocycling conditions were 36 cycles of denaturation at 94 °C for 45 s, annealing at 50 °C for 30 s, and extension at 72 °C for 2 min 30 s. Nucleotide sequencing was done on an ABI 3730 DNA analyzer in the Laboratory of Molecular Systematics at the Royal Ontario Museum. Sequences were verified and aligned with Sequencher v4.8 (Gene Codes Corporation 2007).

The nuclear Y-chromosome intron 7 (Dead Box RNA helicase Y; DBY) was also sequenced from a subset of 55 male specimens representing 17 currently recognized species of *Murina*, one species of *Harpiola*, one species of *Harpiocephalus*, and *Kerivoula hardwickii* and *Myotis ikonnokovi* as outgroup taxa (Appendix 3). All sequences for DBY were newly generated and deposited in Genbank. DNA extraction, nucleotide sequencing, and sequence alignment was similar to the Cytb protocol. PCR amplification of the approximately 400 bp of DBY used forward primer HDBY7F and reverse primer HDBY7R (Hellborg & Ellegren 2003). The thermocycling conditions were 36 cycles of denaturation at 94 °C for 45 s, annealing at 54 °C for 30 s, and extension at 72 °C for 2 min 30 s (Lim *et al.* 2008).

Phylogenetic analyses

A maximum likelihood approach was used to estimate the phylogenetic relationships within *Murina* as implemented in MEGA 7 (Kumar *et al.* 2016). The best-fit nucleotide substitution model was assessed by the lowest Bayesian Information Criterion score. For Cytb, it was the General Time Reversible model with Gamma distribution and Invariable sites. Branch support was summarized by using 1,000 bootstrap replications. The number of variable sites was low for DBY, which did not facilitate bootstrap resampling, so these characters were mapped onto the Cytb gene tree.

FIGURE 1. Map of the Philippines with the collecting localities of species of *Murina* and *Harpiocephalus harpia.* Current islands are shown in dark green. The estimated extent of islands that existed during the period of low sea level during the last glacial maximum, estimated at -120 m below current sea level, is shown in light green. Names of late Pleistocene islands used in the text are shown in capital letters. Modified from Heaney 1986, 1991, and Heaney *et al*. 2016b.

Molecular dating analyses

Divergence times within *Murina* were estimated using the Cytb data by the RelTime maximum likelihood method which does not require assumptions for lineage rate variations (Tamura *et al.* 2012). Because there are no fossils of *Murina*, a calibration point based on the average estimated divergence of 16.4 mya for the split of *Harpiocephalus* and *Murina* was used (Ruedi *et al.* 2013).

Morphological analysis

External body measurements were recorded in the field to the nearest mm and body mass (Mass) was recorded to the nearest g using a Pesola 50 g scale. In the lab, JLE measured cranial and external wing characters to the nearest 0.01 mm using Mitutoyo digital calipers and a stereoscope.

External measurements recorded include, TL: total length—from the tip of the face/chin to the tip of the tail; TV: tail vertebrae length—from the tip of the tail to the base of the tail vertebrae; HF: hind foot length—from the heel to the tip of the longest toe, including the claw; Ear: ear length—from the notch at the base of the ear to the tip of the pinna; FA: forearm length—from the elbow to the wrist with both joints folded; 3DM, 4DM, and 5DM: and length of 3rd, 4th and 5th metacarpals—from the wrist to the end of the respective metacarpals.

Cranial measurements include, GLS: greatest length of skull—from the posterior edge of the skull to the front of the incisors; CIL: condyloincisive length—from the occipital condyles to the front of the incisors; PAL: palatal length—from the anterior palatal emargination to the midpoint of the posterior palatal emargination; ROSD: depth of the rostrum—measured from the top of the palate to the top of the rostrum at the distal end of the nasals; ZB: zygomatic breadth—greatest width across the zygoma; MAST: mastoid width—greatest width across the mastoids; BBC: braincase width—greatest width across the braincase; POC: postorbital constriction—the least width of the constriction posterior to the orbits; LORW: least orbital width—least distance between the orbits measured at the zygoma; CM^3U: length of maxillary toothrow—from the front of the canine to the posterior edge of the 3rd upper molar; M^2M^2: greatest width across upper molars measured across second upper molars; CC:—width across the upper canines; GLM: greatest length of mandible—greatest length measured from the posterior edge of the mandibular condyles to the front of the lower incisors; CM_3L: length of mandibular toothrow—from the front of the canine to the posterior edge of the 3rd lower molar; HCP: height of coronoid process—measured from the inferior surface of the angular process of the ramus to the tip of the coronoid process.

We used Principal Components Analysis (PCA) of wing and skull measurements to describe morphological clustering among specimens using the multivariate program NTSYSpc 2.2 (Rohlf 2009). The sexes were analyzed separately because *Murina* females are larger than males as noted by Eger & Lim (2011). Specimens of Philippine *Murina* and specimens of M. *suilla* from Java, Sabah and Sarawak were included in this analysis. Selected morphometric characters used were FA, 3DM, 4DM, 5DM, GLS, CIL, PAL, ROSD, ZB, MAST, BBC, POC, LORW, CM^3U, M^2M^2, CC, GLM, CM_3L and HCP and these data were standardized to avoid giving more weight to larger variables.

Echolocation call analysis

Variation in the acoustic structure of bat echolocation calls can often provide sufficient information for reliable and efficient species identification. We recorded echolocation calls from 10 individuals, identified at the time as *M. cyclotis* and *M. suilla* from free-flying bats in either a mobile flight cage (3 × 3 × 2 m), or a small room (approx. 4 × 4 × 2.5 m). *Murina* calls were recorded from bats in flight in Cebu (five females, two males) and Siquijor (one female, two males) Islands. Calls were recorded using an Ultrasoundgate 116 (Avisoft Bioacoustics, Inc.) detector with a sampling rate of 375 or 500 kHz and stored onto a laptop computer. SASLabPro (version 5.2.12, Avisoft Bioacoustics, Inc.) was used to collect measurements from spectrograms generated with a fast Fourier transform (FFT) length of 256 kHz and a Hann window. The automatic measurement function was used to measure the duration, start frequency, and terminal frequency at -25 dB from peak amplitude. Peak frequency was measured as the frequency with the highest energy across the entire call. Bandwidth was calculated as the difference between the start and terminal (peak) frequency. We measured up to seven calls from each individual and calculated the mean peak frequency and duration, the maximum bandwidth and start frequency, and the minimum terminal frequency for each individual. These values were used in subsequent summary statistics by species.

Photography

Skulls of four holotype specimens were photographed using a Scanning Electron Microscope (SEM) at the FMNH, and two species were photographed using a digital stereoscopic microscope at the ROM.

Results

Molecular phylogeny

For Cytb, the aligned sequences of 213 specimens had a length of 1,140 bp with 576 bp (50%) that were invariable, 510 bp (45%) that were potentially parsimony informative, and 54 bp (5%) that were variable for only a single specimen. The resultant phylogenetic tree from the maximum likelihood analysis recovered a monophyletic ingroup of Murininae with 82% bootstrap support (Fig. 2). Although most basal relationships within Murininae are poorly resolved and supported, species-level clades have > 85% bootstrap support. Of the previously recognized species of murinines in the Philippines, *Harpiocephalus harpia* is monophyletic with populations from the islands of Luzon, Mindanao, and Mindoro in a well-supported clade with about 10% sequence divergence from mainland Southeast Asia and Taiwan.

Within Philippine *Murina* there is a well-supported clade for *Murina suilla*, but also intraspecific phylogeographic structuring with the Philippine Island of Mindoro about 5 % divergent from Java and Borneo (Fig. 2). In addition, *Murina suilla*-like specimens from Cebu, Luzon, and Mindanao form a clade that is sister to a clade that contains *Murina florium* in Sulawesi and Papua New Guinea and *M. suilla* (from Mindoro, Borneo, and Java). Based on the specimens we examined, *Murina suilla*, *M. florium* and the specimens from the Philippines share four distinct morphological characters: the mesostyle on M^1 is long and not reduced as in the *M. cyclotis* group (Fig. 3A); the anterior upper premolar is half the height of the posterior premolar (Fig. 8F); on the lower molars, the talonid is almost equal in size to the trigonid, in contrast to the *M. cyclotis* group which has a reduced talonid (Fig. 3B); and dorsal hairs are distinctly dark at the base and dark tipped (Fig. 3C), contrasting with pale banding at the base. It should be noted that *M. aenea* which is within the *M. suilla-florium* clade and has banded fur, shares dental characters with the *M. cyclotis* group. More broadly, *M. walstoni, M. philippinensis, M. florium,* and *M. suilla* share one DBY nucleotide polymorphism (Fig. 2).

The phylogenetic relationships within the *Murina cyclotis* group (defined here as including *M. cyclotis*, *M. fionae*, *M. lorelieae*, *M. peninsularis* and five previously undescribed lineages from the Philippines) are even more diverse with the five lineages in the Philippines having about 20% sequence divergence. All five share morphological characters of reduced M^1 mesostyles, (upper, Fig. 3A), the anterior upper premolar is slightly smaller than the posterior premolar (Fig. 8A–E), reduced talonids (Fig. 3B) and dorsal fur with pale base and red grey colour tones (Fig. 3C).

Although not the focus of this paper, the Cytb tree suggests that the taxonomic status of *Harpiola* needs further study as it is embedded within *Murina* as found in other studies (e.g., Eger & Lim 2011; Son *et al*. 2015). However, a recent study (Wang *et al*. 2024) using nuclear data, shows *Harpiola* phylogenetically distinct from *Murina* and sister to *Harpiocephalus*. Additionally, *Harpiocephalus harpia* from the Philippines represents a well-supported clade (99%) distinct from mainland and Taiwanese *Harpiocephalus harpia* specimens. Further study is needed to discern whether the Philippine clade constitutes a unique species.

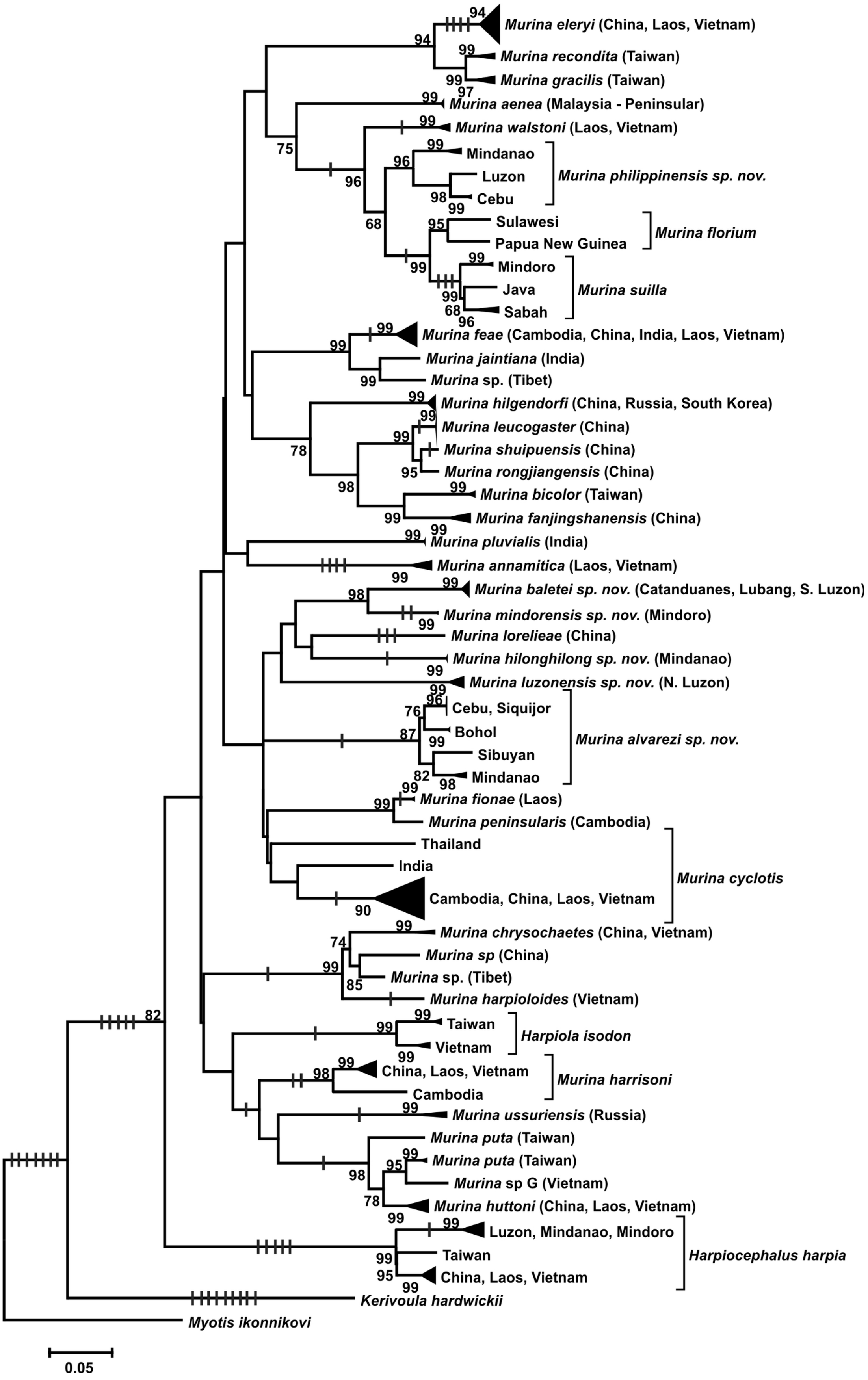

FIGURE 2. Maximum likelihood tree of *Murina* from Cytb gene. Bootstrap support is indicated for greater than 50%.

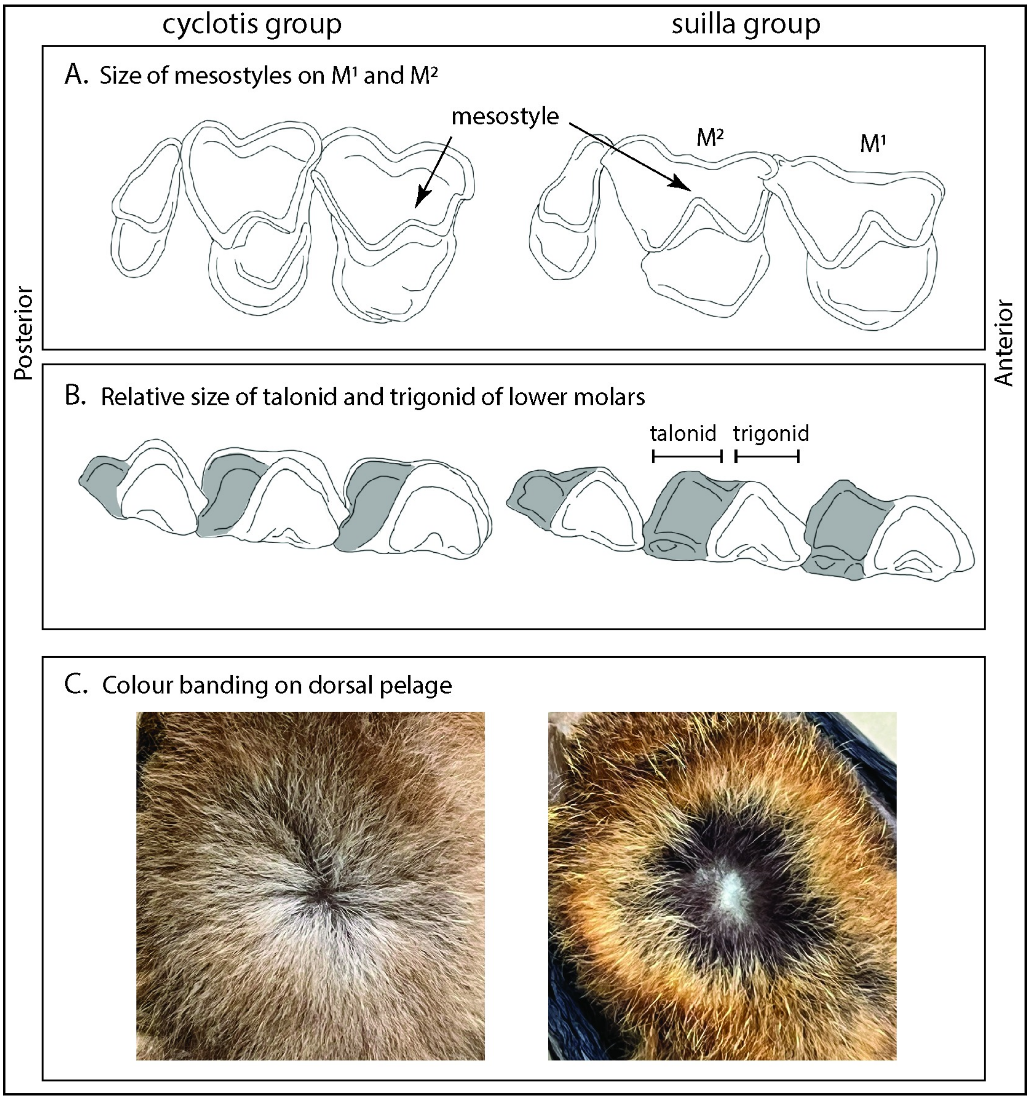

FIGURE 3. Comparison of selected traits that distinguish *Murina* species within the *cyclotis* and *suilla* groups. A. The mesostyle on M^1 and M^2 is reduced in the *cyclotis* group compared to the *suilla* group; B the talonid and trigonid of the lower molars are equal in proportion to each other in the *suilla* group, but not in the *cyclotis* group (the talonid portion of the molars are shaded to emphasis this difference); and C, the dorsal pelage of *suilla* group species has a dark base that is lacking in *cyclotis* group species. Molar illustrations of *cyclotis* group based on *M. hilonghilong* (FMNH 190118; Fig. 9A), and *suilla* group based on *M. philippinensis* (FMNH 205834; Fig. 9F). Pelage photographs are of *M. luzonensis* (FMNH 190766; *cyclotis* group) and *M. philippinensis* (FMNH 205834; *suilla* group).

For DBY, the aligned sequences of 55 specimens had a length of 418 bp with 349 bp (83%) that were invariable, 33 bp (8%) that were potentially parsimony informative, 33 bp (8%) that were variable for only a single specimen, and 3 bp (1%) that were single nucleotide insertions or deletions. The resultant phylogenetic tree from a neighbor-joining analysis recovered a monophyletic ingroup of Murininae with 89% bootstrap support (Fig. S1). However, several species clades were poorly resolved or supported because of the low number of variable sites typically found in nuclear genes as compared to mitochondrial genes. Nonetheless, mapping of these nucleotide polymorphisms in DBY supports the Cytb gene tree (Fig. 2). For example, five DBY sites support the monophyly of Murininae, five sites support the monophyly of *Harpiocephalus*, one site supports the monophyly of *Harpiola*, and three of the divergent lineages from the Philippines that are closely related to *Murina cyclotis* from mainland Asia are supported by DBY data.

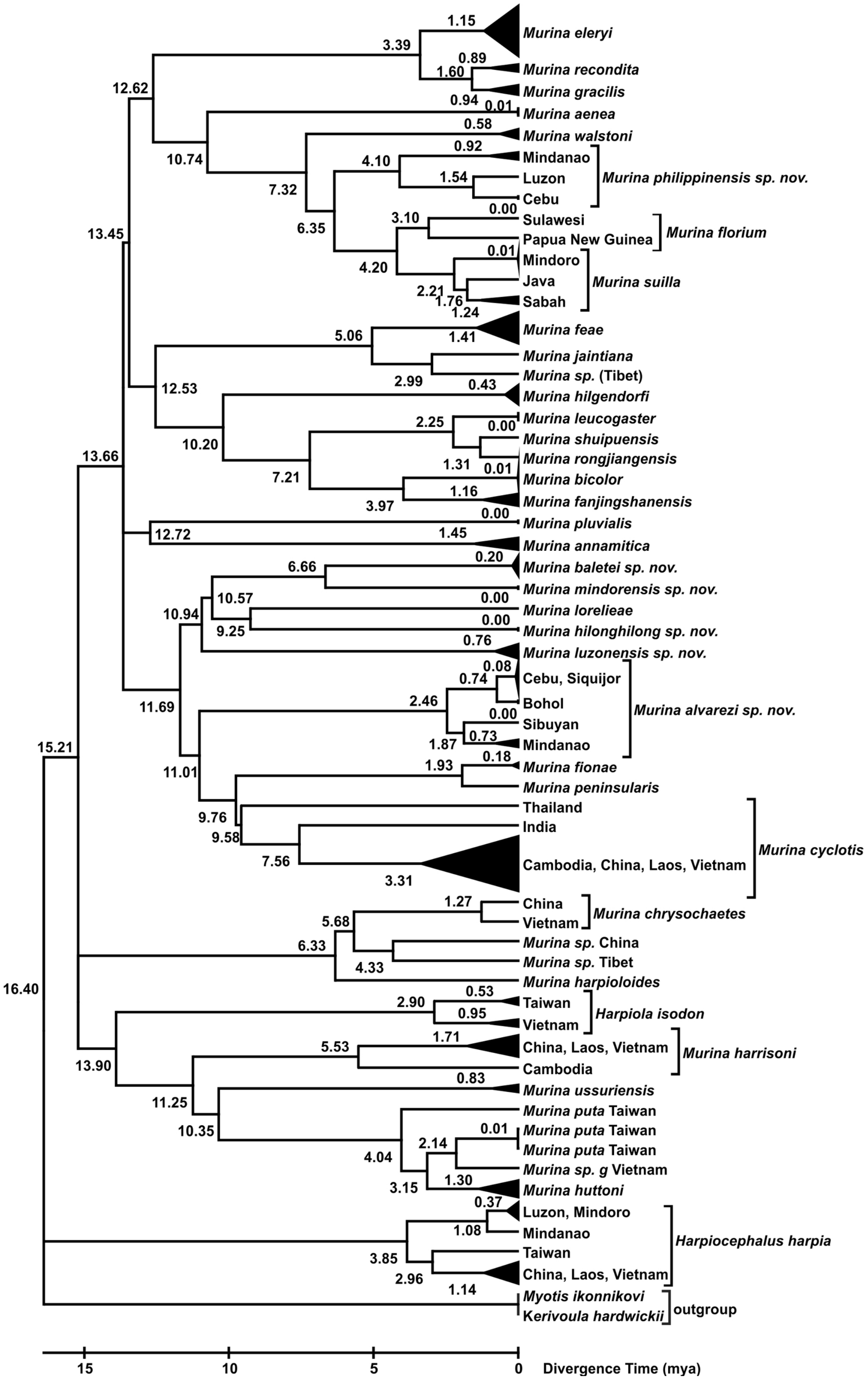

FIGURE 4. *Murina* molecular-dated tree using the RelTime method (Tamura *et al*. 2012).

Molecular dating

Based on the split of *Harpiocephalus* and *Murina* at 16.4 mya (Ruedi *et al.* 2013), the RelTime maximum likelihood analysis of molecular dating using Cytb data estimated the divergence of *Harpiocephalus harpia* populations from the Philippines and continental Asia at about 3.85 mya (Fig. 4).

The most recent common ancestor of the *Murina suilla* group diverged about 7.32 mya, including lineages that range from Borneo and Java to the Philippines and Papua New Guinea (Fig. 4). Within this group are two lineages that occur in the Philippines. One includes populations currently distributed in Luzon, Cebu, and Mindanao that shared a common ancestor at about 4.10 mya. They are part of a larger clade that diverged about 6.35 mya and includes a lineage from Sulawesi and Papua New Guinea (*M. florium*), as well as one from Borneo, Java, and Mindoro that we consider represents *M. suilla* because the type locality is on Java and that shared a common ancestor at 2.21 mya.

The divergence of the *Murina cyclotis* group, as defined above, began about 13.66 mya with basal relationships that are poorly resolved but imply rapid dispersal and speciation within continental Southeast Asia and the Philippines at about 11.69 mya (Fig. 4). One clade includes *Murina cyclotis*, *Murina fionae*, and *Murina peninsularis,* all from continental Southeast Asia that shared a common ancestor at about 9.76 mya. A second major clade includes four species from the Philippines and a continental species, *Murina lorelieae,* currently known from China and Vietnam that diverged about 10.94 mya. A third clade represents a fifth species from the Philippines but its placement in the phylogeny (Fig. 2) is ambiguous, relative to the two other clades in the *M. cyclotis* group.

The genetic and morphological analyses (see below) indicate that the specimens of *Murina* collected in the Philippines and examined in this study represent six distinctive undescribed species of *Murina* and one known species, *Murina suilla* found on Mindoro and (tentatively) Palawan islands. Five of these species share pelage and skull characteristics with *Murina cyclotis*: reddish, bicoloured dorsal pelage; reduced mesostyle on M^1 (Fig. 3A); and talonid of M_1 about 1/3 the size of the trigonid (Fig. 3B). The sixth species shares pelage and skull characteristics with *M. suilla*. In the following species accounts we describe six new species of *Murina* from the Philippines and review *M. suilla* in the Philippines.

Systematic descriptions and species accounts

Murina alvarezi **sp. nov.**

(Figs. 1, 6, 7, 8E, 9E, 10A; Tables 1, 2A, 2B)

Murina cyclotis: Kitangland: Heaney *et al*. 1998: 27; Heaney *et al*. 2006: 30, 35, 36. Bohol Island: Sedlock *et al.* 2014: 205, 207; Siquijor Island: Heaney *et al*. 1998:27

Holotype. FMNH 205831, field number JLS 738, young adult female, specimen stored in alcohol, skull extracted, collected by J. L. Sedlock, 7 August 2009. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila before the end of 2025, where it has been assigned PNM 9670. The nucleotide sequence as deposited in GenBank of Cytb mitochondrial gene is PV659290.

Type locality. Sitio Bulalacao, Brgy Nug-as, Alcoy Municipality, Cebu Province, Cebu Island, Philippines, 9.7205 N 123.4594 E, elevation 763 m.

Paratypes. All seven paratypes were collected at the type locality: FMNH 205826, field number JLS 666, ♀, collected 25 July 2009; FMNH 205827, field number JLS 706, ♂, collected 3 August 2009; FMNH 205828, field number JLS 722, ♀, collected 3 August 2009; FMNH 205829, field number JLS 723, ♀, collected 3 August 2009; FMNH 205830, field number JLS 735, ♂, collected 3 August, 2009; FMNH 205832, field number JLS 739, ♀, collected 7 August 2009; and FMNH 205833, field number JLS 740, ♀, collected 7 August 2009.

Etymology. This species is named in honor of James Alvarez, a remarkably devoted, young Filipino wildlife biologist with a passion for studying and conserving Philippine bats. A graduate student and biologist at the University of the Philippines—Los Baños Museum of Natural History, his unexpected death on Mount Apo in 2018 cut short a promising career of exploring Philippine biodiversity and inspiring future generations of Filipino biologists. The suggested English common name is Alvarez's tube-nosed bat.

Measurements of holotype (in mm) and body mass (in g): total length, 97; tail vertebrae, 37; hind foot, 10.5; ear, 17, forearm, 35.6; and mass, 6.4.

Referred Material. FMNH 146890, field number SMG 5001, ♂, collected 21 February 1992, NW slope Mt. Guitingguitlin, 4.5 km S, 4 km E Magdiwang, Romblon Province, Sibuyan Island, Philippines, (12 27 N, 122 33 E, elevation 325 m); FMNH 202815, field number SEW 112, ♂, collected 11 July 2008 at Nan-od Brgy, Sierra Bullones Munic., Bohol Province, Bohol Island, Philippines (9.7469 N, 124.2638 E, elevation 586 m); FMNH 202816, field number JLS 590, ♂, collected 3 July 2008 at Sitio Libertad, Bugsoc Brgy, Sierra Bullones Munic. Bohol Province, Bohol Island, Philippines (9.7641 N, 124.2658 E, elevation 336 m); FMNH 209658, field number JLS 808, ♀, collected 6 km E of San Juan town centre, Siquijor Province, Siquijor Island, Philippines (9.1410 N 123.5472 E, elevation 170 m); FMNH 209659, field number JLS 809, ♂, collected 5 July 2010, same locality as previous; FMNH 209660, field number JLS 784, ♂, collected 23 June 2010 same locality as previous, 9.18706 N, 123.58040 E, elevation 550m.; FMNH147078, field number LRH 4639, ♂, collected 18 April 1992 Mt. Kitanglad Range, 115 km S, 6 km E Baungon, Bukidnon Province, Mindanao, Philippines (8 11 N, 124 44.5 E, elevation 1100 m); FMNH 147079, field number LRH 4665, ♀, collected 21 April 1992, same locality; FMNH 190119, RKSG 80, ♂, collected Hilong-hilong Range Carrasacal Munic., Suragio del Sur Prov. Mindanao; and FMNH 186817, field number DSB 3656, ♀, collected 19 May 2005 at Mt. Hamiguitan, San Isidro Munic., Davao Oriental Province, Mindanao, Philippines (6 43 56.3 N 126 09 03.2 E).

Diagnosis. A medium sized *Murina* similar to *Murina cyclotis* (as defined by Francis & Eger 2012) but with a larger, heavier skull and genetically different at greater than 18% average sequence divergence in Cytb from other species in the genus (Table 3). Among the Philippine species of the *M. cyclotis* species group described here, *M. alvarezi* is the smallest (FA females = 35.8 mm, males = 33.7 mm; GLS females = 18.3, males = 17.5 mm); wing membrane attaches close to the claw of the toe; and penis narrow (1.5 mm). Similar to *M. cyclotis*, with all upper premolars similar in height; anterior upper molars with reduced mesostyles; and lower molars with reduced talonids (Figs. 8E, 9E). The sagittal and lambdoidal crests are clearly defined.

Description. In the holotype and paratype series of specimens from Cebu, the dorsal fur is bicoloured, grey buff at the base with reddish brown tips (Fig. 10A); the fur is 10–11 mm at the shoulder. On the underside, the throat is unicoloured, varying from white to buff; the ventrum is unicoloured white to buff in the centre and weakly bicoloured laterally, buff-grey to buff base and reddish brown to brown tips. The forearm, lower leg, interfemoral membrane, and foot are hairy. There is some colour variation within the species, with females from Siquijor and Mindanao paler than Cebu specimens. The ear is round and notched on the posterior edge (Fig. 10A). The skull has a moderately inflated braincase, shallow rostral depression, and small but defined sagittal and lambdoid crests. The upper toothrows are parallel to each other; the inner upper incisors are bicuspidate and longer than the outer; and the canines are large and heavy. The upper premolars are well developed, of similar height, and 2/3 the height of the canines (Fig. 8E). The mesostyles of the first (M^1) and second upper molars (M^2) are greatly reduced. The talonids (posterior section of the first, M_1 and second lower molars, M_2) are also greatly reduced relative to the trigonids (anterior section), about 1/3 the size of the trigonid (Fig. 9E). Penis of males is narrow (1.5 mm). See Tables 1 and 2A, 2B for selected external and skull measurements.

TABLE 1. Selected external measurements and body mass (g), [(mean); (min-max in mm.)] for eight species of Philippine Murininae.

	n	FA	TL	TV	HF	Ear	Mass
Murina alvarezi ♀	7	35.8; 35.2–36.3	97.6; 93.0–100.0	35.9; 33.0–39.0	10.3; 9.0–11.0	17.0; 16.0–18.0	7.5; 6.4–8.5
Murina alvarezi ♂	10	33.7; 32.2–34.9	91.8; 80.0–98.0	34.2; 27.0–39.0	9.6; 7.0–11.0	15.6; 13.0–18.0	6.5; 6.0–7.0
FMNH 205831 holotype *M. alvarezi* ♀	1	35.6	97.0	37.0	10.5	17.0	6.4
Murina baletei ♀	6	37.8; 36.6–39.3	96.3; 93.0–102.0	38.5; 34.0–42.0	9.2; 8.0–10.0	15.5; 15.0–16.0	10.6; 9.5–11.0
Murina baletei ♂	3	35.5; 34.8–36.1	89.3; 88.0–90.0	34.7; 32.0–38.0	8.7; 8.0–9.0	14.8; 14.0–15.5	8.0; 7.6–8.5

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TABLE 1. (Continued)

	n	FA	TL	TV	HF	Ear	Mass
FMNH 205411 holotype *M. baletei* ♂	1	34.8	88.0	34.0	8.0	15.0	8.0
Murina hilonghilong ♀	1	43.3	91.0	36.0	12.0	14.0	13.5
FMNH 190118 holotype *M. hilonghilong* ♂	1	39.3	91.0	31.0	9.0	15.0	10.0
Murina luzonensis ♀	3	36.6; 35.5–38.2	92.7; 91.0–96.0	36.8; 35.0–38.2	9.5; 9.0–10.0	15.7; 13.9–18.0	8.6; 7.5–9.6
Murina luzonensis ♂	3	35.6; 35.2–35.9	86.0; 82.0–91.0	34.3; 31.0–37.0	9.0; 9.0–9.0	15.0; 15.0–15.0	7.8; 7.5–8.0
FMNH 190764 holotype *M. luzonensis* ♂	1	35.2	82.0	31.0	9.0	15.0	7.5
Murina mindorensis ♀	1	39.0	99.0	41.0	9.0	17.0	12.0
FMNH 228475 holotype *Murina mindorensis* ♂	1	36.9	91.0	34.0	9.0	16.0	8.7
M. philippinensis ♀	3	32.4; 31.1–33.4	76.3; 72.0–80.0	30.7; 30.0–32.0	8.2; 7.0–9.5	15.0; 14.0–16.0	4.8; 4.0–6.1
M. philippinensis ♂	3	31.9; 30.8–32.8	74.7; 68.0–80.0	25.7; 25.0–26.0	8.3; 8.0–9.0	14.0; 12.0–16.0	4.5; 4.0–5.0
FMNH 205834 holotype *M. philippinensis* ♂	1	32.8	80.0	26.0	9.0	16.0	4.4
FMNH 230353–54 *Murina suilla* ♀	2	34.1; 33.5–34.6	78.5; 77.0–80.0	31.0; 29.0–33.0	6.5; 6.0–7.0	13.5; 13.0–14.0	6.6; 6.0–7.2
Harpiocephalus harpia ♀	5	49.1; 48.2–50.5	119.6; 109.0–132.0	46.0; 41.0–61.0	12.2; 11.0–13.0	16.4; 15.0–18.0	20.9; 17.5–24.0
Harpiocephalus harpia ♂	8	46.5; 44.8–48.8	107.8; 103.0–114.0	42.5; 40.0–49.0	11.4; 9.5–13.0	16.5; 15.0–18.0	13.8; 11.5–19.0

Ecology. This species has a broad elevational range, occurring from 85 m elevation to 1100 m (Fig. 5) in a diversity of forest types and levels of disturbance. A single individual was captured in regenerating logged dipterocarp forest growing on ultramafic soils in southeastern Mindanao, characterized by stunted trees and an understory dominated by Malabayabas (*Tristaniopsis* spp.) (Balete *et al.* 2006). Another individual was captured in northeastern Mindanao in a lowland Magkuno or ironwood (*Xanthostemon verdugonianus*) forest. Several individuals were captured in second-growth dipterocarp forest on limestone in the Visayas, in small forest patches surrounded by corn and vegetable crops (Cebu, Siquijor and Bohol Islands; Sedlock *et al*. 2014); a mahogany plantation also on limestone; and within disturbed old-growth dipterocarp forest at 1100 m on Mt. Kitanglad (Heaney *et al.* 2006). Post-lactating females were captured in May in southeastern Mindanao (Mt. Hamiguitan), and in August on Cebu Island, along with three immature females. All individuals were captured in harp traps set along forest trails, except for two mist net captures on Mt. Kitanglad in central Mindanao, and one on Mt. Hamiguitan.

Distribution. Widespread within the southern and central Philippines, collected on Mindanao, Siquijor, Bohol, Cebu, and Sibuyan Islands (Fig. 1).

Genetic Analyses. Cytb and Dby sequences are available on GenBank for specimens listed in Appendices 2 and 3. *Murina alvarezi* is one of five divergent Cytb lineages from the Philippines that is related to *M. cyclotis* from mainland Asia and is supported by DBY data (one site, Fig. 2). Relative divergences among Philippine species are discussed below.

Murina baletei sp. nov.

(Figs. 1, 8C, 9C, 10B; Tables 1, 2A, 2B)

M. cyclotis: Catanduanes: Heaney *et al*. 1991: 406, 408; Heaney *et al*. 1998: 27; Mt. Isarog, Luzon Island: Heaney *et al*. 1999: 29, 30, 32; Sedlock *et al*. 2008: 352, 354; Mt. Makiling, Luzon Island: Sedlock 2001a: 182, 183, 193, 196; Sedlock 2001b: 167, 168, 173, 174. Mt. Irid, Luzon Island: Balete *et al*. 2013: 21; Heaney *et al*. 2016b: 243.

Holotype. FMNH 205411, field number DSB 5990, adult male, specimen in alcohol with skull removed, collected by D. S. Balete, 8 June 2009. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines before the end of 2025, where it has been assigned PNM 9673. The nucleotide sequence as deposited in GenBank of Cytb mitochondrial gene is PV659284 and DBY nuclear gene is PV659294.

Type locality. 1.3 km S, 0.8 km W Mount Irid peak, elevation 775 m, Rodriguez Municipality, Rizal Province, Luzon Island, Philippines (14.779 N, 121.318 E).

Paratype. FMNH 205410, field number DSB 5989, adult female, collected same date and same locality as the holotype.

Etymology. This species is named in honour of Danilo S. Balete, a Filipino biologist whose passion for and knowledge of Philippine biodiversity inspires young scientists even after his unexpected death in 2017. The species distribution includes the Bicol Peninsula of southern Luzon where Balete was born, as well as Mt. Makiling where he studied the diet of *Megaderma spasma* as an undergraduate student at the University of the Philippines, Los Baños (Balete 2010), and Mt. Isarog—the site of his master's research on native rodent ecology (Balete & Heaney 1997). The suggested English common name is "Balete's tube-nosed bat."

Measurements of holotype. (in mm) and body mass (in g): total length, 88; tail vertebrae, 34; hind foot, 8; ear, 15, forearm, 34.8; and mass, 8.

Referred Material. FMNH 166428, field number JLS 142, ♀, collected 29 March, 1999 and FMNH 166429, field number JLS 163, ♂, collected 14 July, 1999 at Mount Makiling, (14 09 N, 121 13 E, elevation 400 m and 300 m respectively, Laguna Province, Luzon Island (14.1499996 N, 121.216667 E); FMNH 177471, field number JLS 186, ♀, collected 4 July 2003 (co-ordinates not recorded in the field and subsequently estimated from Google Earth as 14.150 N, 121.217 E) and FMNH 177472, field number JLS194, ♀, collected 15 July, 2003 (co-ordinates not recorded in the field and subsequently estimated from Google Earth as 14.132 N, 121.210 E) at Los Baños, Mount Makiling, Laguna Province, Luzon Island, Philippines; USNM 573774, field number EAR 1685, ♂, collected 22 February 1988, 1 km N, 8.5 km W Gigmoto, elevation 200 m, Buadan R., Catanduanes Province, Catanduanes Island, Philippines (13 49 N, 124 19 E); USNM 573776, field number EAR 1788, ♀, collected 9 May 1988, Mt. Isarog, 4.5 km N, 20.5 km E Naga, elevation 475 m, Camarines Sur Province, Luzon Island, Philippines (13 40 N, 123 20 E); USNM 573777, field number EAR 1839, ♀, collected 25 March 1988, Mt. Isarog, 4.5 km N, 20.5 km E Naga, Camarines Sur Province, Luzon Island, Philippines (13 40 N, 123 21 E); and FMNH 218203, field number DSB 9183, ♀, collected 27 May 2012 at Ambulong Peak, Lubang municipality, Lubang, Philippines (13.79226 N 120.14645 E).

Diagnosis. A medium sized *Murina* similar to *Murina cyclotis* (as defined by Francis and Eger 2012) but larger, with a more robust skull, and sagittal and lambdoidal crests that are well defined. Although dorsal fur is bicoloured as in *M. cyclotis*, this species has pale basal bands blending to greyish-brown tips. It differs genetically by >12% average sequence divergence in Cytb from other species in the genus (Table 3).

Description. Dorsal fur is bicoloured with a grey base blending to reddish brown/greyish brown tips. Hair measures 9–10 mm at the shoulders. The ventral hair is also bicoloured but paler than on the dorsum, with pale grey bases blending to pale brown or reddish-brown tips. The posterior border of the ear is notched. The forearm is hairy and the uropatagium is covered with long hairs. This species appears to be sexually dimorphic in colour with tips of fur slightly redder in colour for females than males (photo of holotype live, Fig. 10B).

The skull is robust, somewhat like *M. cyclotis* but much larger (Tables 1 and 2A, 2B), has well developed sagittal and lambdoidal crests which clearly define the posterior of the skull where they meet, producing a helmet shape. The rostrum is heavy and slopes gradually to the forehead (Fig. 8C). Similar to *M. cyclotis*, the molars have reduced mesostyles (Figs. 3A, 9C), but the teeth are very heavy and substantial looking. The canine is short but greater in length than P^2 and P^4 (Fig. 8C). The lower incisors are tricuspidate and the remaining teeth heavy. The talonid is ½ size of the trigonid (Figs. 3B, 9C). Penis of males is short and wide (3 mm. at widest point) relative to *M. alvarezi*. See Tables 1 and 2A, 2B for selected external and skull measurements.

Ecology. This species has been captured from a broad range of elevations (200–1125 m, Fig. 5) and habitat types. On Luzon Island, it was recorded in remnant primary, lowland forest and montane forest on Mt. Isarog (Heaney *et al.* 1999); in second growth lowland dipterocarp forest (e.g., *Shorea* spp.) on Mt. Makiling (Sedlock 2001b; a), and in regenerating lowland forest on Mt. Irid (Balete *et al.* 2013). On Catanduanes Island, it was captured in primary forest on a small plateau between two rivers (Heaney *et al.* 1991). Bats were captured in harp traps set across trails, as well as in mist nets set along trails, intercepting bats flying low through the forest understory. Pregnant females were captured in March on Luzon Island and in May on Catanduanes Island; the latter female was primiparous with two embryos measuring 15 mm. Lactating females were captured on Luzon Island in June (Mt. Irid; FMNH 205410, DSB 5989) and July (Mt. Makiling; FMNH 177471, JLS 186). Reproductively active males with scrotal testes were captured in June and July on Luzon Island. Notably, one of these males, with a black gland below its scrotum, was captured with a lactating female in the same net.

Distribution. Lubang, southern Luzon and Catanduanes islands (Fig.1).

Genetic Analyses. Cytochrome *b* and DBY sequences are available on GenBank for specimens listed in Appendices 2 and 3. *Murina baletei* is one of the divergent lineages from the Philippines that is closely related to *M. cyclotis* from mainland Asia. Relative divergences among Philippine species are discussed below. The standard karyotype was described by Rickart *et al.* (1999) as representing *M. cyclotis*.

***Murina hilonghilong* sp. nov.**

(Figs. 1, 8A, 9A; Tables 1, 2A, 2B).

Holotype. FMNH 190118, field number RKSG 82, adult male, alcohol specimen with skull extracted, collected in a harp trap by R. K. S. Gomez, 30 July 2006. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila before the end of 2025 where it has been assigned PNM 9674. The nucleotide sequence as deposited in Genbank of Cytb mitochondrial gene is PV659272 and DBY nuclear gene is PV659349.

Type locality. Barangay (Brgy.) Adlay, Carrascal Municipality, Surigao del Sur Province, Hilong-hilong Range, Mindanao Is., Philippines (coordinates not recorded in the field, subsequently estimated from topographic maps as 9.088 N, 125.73 E); elevation 85 m.

Paratype. FMNH 191407 female, (RKSG 198) collected 17 October 2006 at Brgy San Antonio, Mt Hilong-hilong, Agusan del Norte Province, Mindanao Is. Philippines (coordinates not recorded in the field, subsequently estimated from topographic maps as 9.087 N, 125.70 E; elevation 1400 m).

Etymology. This species is named after the mountain range where it was captured, Mt. Hilong-hilong, which stretches across two provinces—Agusan del Norte and Surigao del Sur in northeastern Mindanao. We use the name of the mountain as a noun in apposition.

Measurements of holotype. (in mm) and body mass (in g): total length, 91; tail vertebrae, 31; hind foot, 9; ear, 15, forearm, 41; and mass, 10.

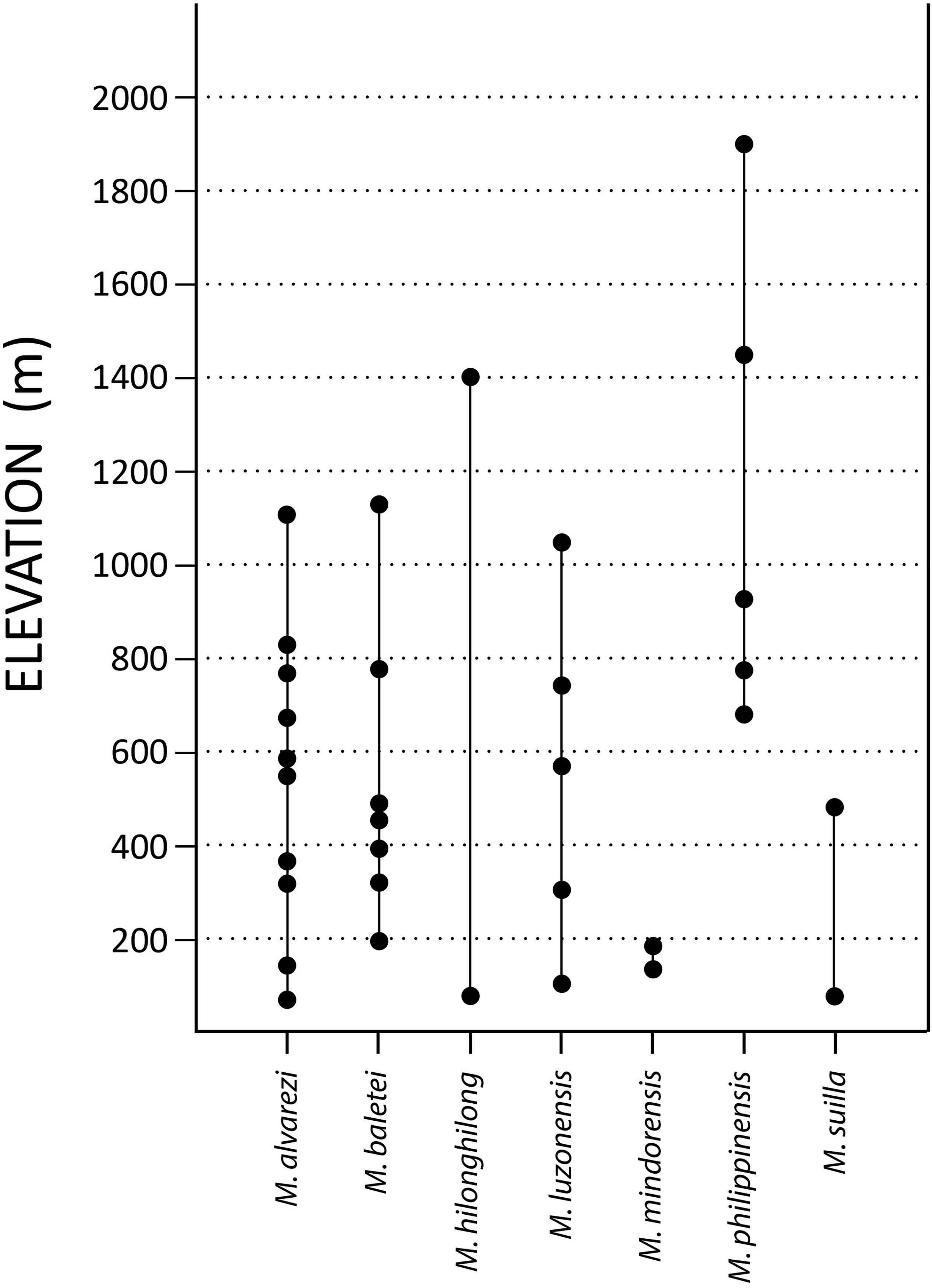

FIGURE 5. *Murina* species elevations in Philippines. Solid dots represent localities documented in the text, with vertical lines connecting all elevational records for a given species.

Diagnosis. This is the largest species of *Murina* in the Philippines, and the largest of all species of *Murina*. *Murina hilonghilong* has dentition like *Murina cyclotis* with upper premolars similar in size to each other, with reduced mesostyles on M^1 and M^2 (Fig. 9A) and reduced talonids on the lower molars (M_1 and M_2; Fig. 9A) but is larger in body size and skull size, with a white ventrum and a large difference in Cytb sequence (>17%). The sagittal and lambdoidal crests are well defined.

Description. The dorsal fur is tricoloured, with pale grey bases changing to buff with pale reddish-brown tips; guard hairs also have reddish brown tips. The ventrum is unicoloured white from the throat to the centre of the abdomen. On the sides of the abdomen the hairs are white at the base blending to buff tips. The guard hairs on the belly are long, white, and shiny, more obvious in the mid ventrum than along the sides. The uropatagium is hairy (pale orange) with long hairs covering the proximal half. Likewise, the feet are covered with long hairs extending beyond the claws. The forearm and thumb are also quite hairy, but the hairs are short and pale in colour.

The ears are relatively short with a notch on the posterior border. The tragus is long and typical of *Murina* species. The calcar is long, and the wing membrane is inserted on the side of the toe at the base of the claw.

The skull is robust with a deep rostrum which has a well-marked rostral depression, and heavy, well developed sagittal and clearly defined lambdoid crests (Fig. 8A). The upper toothrows are parallel and the teeth are heavy in appearance. The inner upper incisor is simple in shape with a bicuspidate tip that may not be obvious in a worn tooth, and the tooth is mostly obscured by the larger outer incisor. The upper canine is large and heavy, P^2 and P^4 are similar in shape with P^4 slightly larger than P^2. The first and second upper molars are similar in size and shape with greatly reduced mesostyles. As in other species of *Murina*, M^3 is greatly reduced. The basisphenoid pits are well defined and tear drop in shape (Fig. 9A). On the mandible, the incisors are tricuspidate, and the remaining teeth are heavy in appearance. The canine is short but slightly longer than the premolars in both sexes; P_4 is larger than P_2 and both premolars on the male specimen are worn. M_1 is larger than M_2 and the talonid on M_1 is approximately ¼ the size of the trigonid but on M2 it is closer to 1/3 the size of the trigonid. The male holotype is significantly smaller in skull and external measurements than the female paratype (PC1) and they differ in shape (PC2, Fig. 6). The coronoid process is distinctly shorter in the male relative to the female accounting for their difference in shape (Fig. 6) (HCP 6.3 mm (♂) and 7.6 (♀). See Tables 1 and 2A, 2B for selected external and skull measurements.

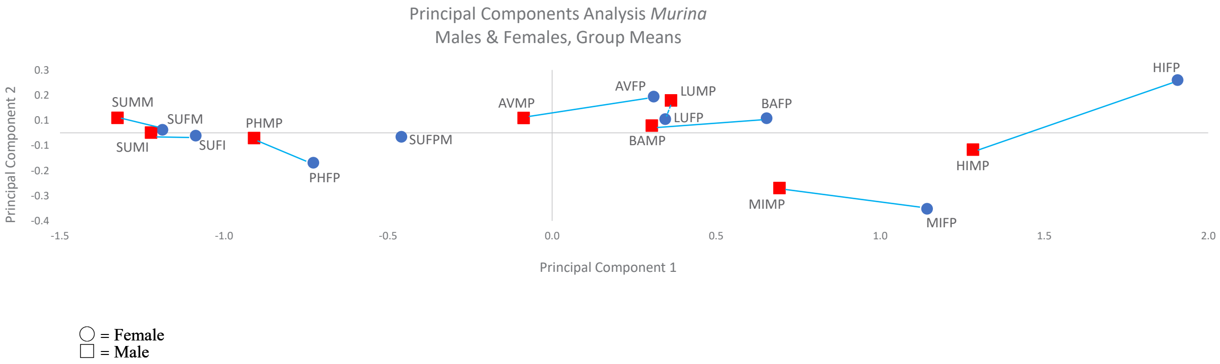

FIGURE 6. *Murina* males and females Principal Components projections. SUMM *M. suilla* ♂ Sabah; SUFM *M. suilla* ♀ Sabah; SUMI *M. suilla* ♂ Java; SUFI *M. suilla* ♀ Java; PHMP *M. philippinensis* ♂ Philippines; PHFP *M. philippinensis* ♀ Philippines; SUFPM *M. suilla* ♀ Mindoro; AVMP *M. alvarezi* ♂ Philippines; AVFP *M. alvarezi* ♀ Philippines; LUMP *M. luzonensis* ♂ Philippines; LUFP *M. luzonensis* ♀ Philippines; BAMP *M. baletei* ♂ Philippines; BAFP *M. baletei* ♀ Philippines; MIMP *M. mindorensis* ♂ Philippines; MIFP *M. mindorensis* ♀ Philippines; HIMP *M. hilonghilong* ♂ Philippines; HIFP *M. hilonghilong* ♀ Philippines.

Ecology. The only two specimens representing this species were captured at 85 m elevation in *magkono* (ironwood) forest (*Xanthostemon verdugonianus*) and in regenerating transitional lowland-montane forest at 1400 m on Mt. Hilong-hilong, the highest mountain in northeastern Mindanao and a Key Biodiversity Area (Mallari *et al.* 2001). Home to endemic birds, mammals, and amphibians (Plaza & Sanguila 2015, Gracia *et al.* 2021), Mt. Hilong-hilong was identified in 2014 by Bird Life International as an Important Bird and Biodiversity Area in Danger.

Distribution. Currently known only from two localities in NE Mindanao, associated with the Hilong-hilong Mountain Range (Fig.1). They probably occur elsewhere in this area.

Genetic Analyses. Cytochrome *b* and Dby sequences are available on GenBank for specimens listed in Appendices 2 and 3. *Murina hilonghilong* is one of three divergent lineages supported by Dby data (one site, Fig. 2) from the Philippines that is closely related to *M. cyclotis* from mainland Asia. Relative divergences among Philippine species are discussed below.

TABLE 2A. Selected skull measurements, [(mean+/- sd); (min-max in mm.)] for eight species of Philippine Murininae including holotypes of six new species.

	n	GLS	CIL	PAL	ROSD	ZB	MAST	BBC	POC
Murina alvarezi ♀	7	18.33+/-0.23	16.57+/-0.22	7.72+/-0.24	2.35+/-0.12	10.45+/-0.18	8.61+/-0.20	7.99+/-0.18	4.59+/-0.16
		17.9–18.6	16.2–16.9	7.4–8.0	2.2–2.6	10.1–10.7	8.2–8.8	7.6–8.1	4.3–4.7
M. alvarezi ♂	10	17.47+/-0.25	15.74+/-0.24	7.30+/-0.29	2.27+/-0.12	9.85+/-0.19	8.32+/-0.12	7.89+/-0.10	4.50+/-0.13
		17.2–17.9	15.4–16.2	7.0–7.9	2.1–2.5	9.6–10.1	8.2–8.5	7.7–8.1	4.3–4.7
Holotype *M. alvarezi* ♀	1	17.9	16.2	7.4	2.3	10.3	8.6	8.0	4.7
M. baletei ♀	6	18.84+/-0.28	17.01+/-0.28	7.70+/-0.27	2.45+/-0.06	10.66+/-0.18	8.99+/-0.14	8.33+/-0.18	4.72+/-0.12
		18.4–19.2	16.5–17.3	7.4–8.1	2.4–2.5	10.5–11.0	8.8–9.2	8.1–8.6	4.6–4.9
M. baletei ♂	3	18.16+/-0.28	16.33+/-0.21	7.65+/-0.24	2.32+/-0.03	10.33+/-0.38	8.69+/-0.20	8.25+/-0.15	4.63+/-0.07
		17.9–18.4	16.1–16.5	7.4–7.9	2.3–2.3	10.0–10.7	8.5–8.9	8.1–8.4	4.6–4.7
Holotype *M. baletei* ♂	1	18.2	16.4	7.9	2.3	10.3	8.5	8.1	4.7
M. hilonghilong ♀	1	21.3	19.0	9.1	2.8	12.1	10.0	8.8	5.3
Holotype *M. hilonghilong* ♂	1	19.9	17.8	8.1	2.8	11.7	9.4	8.8	5.1
M. luzonensis ♀	4	18.18+/-0.32	16.60+/-0.31	7.56+/-0.37	2.44+/-0.04	10.45+/-0.29	8.57+/-0.19	8.05+/-0.15	4.61+/-0.09
		17.8–18.4	16.3–16.9	7.3–8.1	2.4–2.5	10.1–10.6	8.3–8.7	7.8–8.2	4.5–4.7
M. luzonensis ♂	2	18.12+/-0.25	16.49+/-0.36	8.02+/-0.13	2.38+/-0.17	10.27+/-0.26	8.73+/-0.13	8.17+/-0.07	4.57+/-0.08
		17.9–18.3	16.2–16.7	7.9–8.1	2.3–2.5	10.1–10.5	8.6–8.8	8.1–8.2	4.5–4.6
Holotype *M. luzonensis* ♂	1	17.9	16.2	7.9	2.5	10.1	8.6	8.1	4.6
M. mindorensis ♀	1	19.7	18.2	7.8	2.7	11.4	9.5	8.8	5.3
Holotype *M. mindorensis* ♂	1	19.2	17.6	7.6	2.5	11.2	9.3	8.6	4.9
M. philippinensis ♀	2	15.87+/-0.60	14.33+/-0.47	6.72+/-0.41	2.01+/-0.18	8.87+/-0.34	7.77+/-0.25	7.60+/-0.33	4.52+/-0.09
		15.4–16.3	14.0–14.7	6.4–7.0	1.9–2.1	8.6–9.1	7.6–7.9	7.4–7.8	4.5–4.6

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TABLE 2A. (Continued)

	n	GLS	CIL	PAL	ROSD	ZB	MAST	BBC	POC
M. philippinensis ♂	3	15.64+/-0.40 15.3–16.1	14.11+/-0.34 13.7–14.4	6.73+/-0.39 6.4–7.2	1.94+/-0.04 1.9–2.0	8.67+/-0.24 8.4–8.9	7.56+/-0.09 7.5–7.7	7.55+/-0.11 7.5–7.7	4.33+/-0.15 4.2–4.5
Holotype *M. philippinensis* ♂	1	15.6	14.2	6.6	1.9	8.4	7.5	7.5	4.5
M. suilla Mindoro ♀	2	16.21	14.75	5.75	2.17	9.16	8.02	7.89	4.48
Harpiocephalus harpia ♀	3	22.88+/-0.32 22.5–23.2	20.76+/-0.36 20.4–21.1	9.06+/-0.60 8.4–9.6	3.60+/-0.34 3.2–3.9	14.22+/-0.76 13.4–14.8	11.69+/-0.64 11.0–12.1	9.97+/-0.71 9.5–10.8	5.73+/-0.36 5.4–6.1
Harpiocephalus harpia ♂	7	21.56+/-0.73 20.8–22.6	19.37+/-0.72 18.5–20.6	8.94+/-0.38 8.4–9.6	3.41+/-0.16 3.2–3.6	12.98+/-0.76 12.4–14.5	10.70+/-0.68 9.8–11.9	9.43+/-0.37 9.0–10.0	5.46+/-0.18 5.2–5.6

TABLE 2B. Selected skull measurements, [(mean+/- sd); (min-max in mm.)] for eight species of Philippine Murininae including holotypes of six new species.

	n	LORW	CM3U	M2M2	CC	GLM	CM3L	H CP
Murina alvarezi ♀	7	5.72+/-0.08 5.6–5.9	5.78+/-0.09 5.6–5.9	5.74+/-0.15 5.5–5.9	4.57+/-0.07 4.4–4.6	11.64+/-0.19 11.4–11.9	6.31+/-0.09 6.2–6.4	5.36+/-0.19 5.2–5.6
M. alvarezi ♂	10	5.53+/-0.15 5.3–5.8	5.54+/-0.15 5.3–5.8	5.56+/-0.12 5.4–5.8	4.36+/-0.10 4.2–4.5	10.99+/-0.19 10.7–11.3	6.01+/-0.19 5.6–6.3	4.78+/-0.17 4.5–5.0
Holotype *M. alvarezi* ♀	1	5.7	5.8	5.5	4.6	11.4	6.2	5.2
M. baletei ♀	6	6.06+/-0.12 6.0–6.3	5.94+/-0.09 5.8–6.1	6.05+/-0.10 6.0–6.2	4.92+/-0.11 4.8–5.1	12.18+/-0.33 11.6–12.5	6.38+/-0.35 5.7–6.7	5.39+/-0.08 5.3–5.5
M. baletei ♂	3	5.92+/-0.21 5.8–6.2	5.65+/-0.09 5.6–5.8	5.88+/-0.10 5.8–6.0	4.72+/-0.23 4.5–5.0	11.45+/-0.25 11.2–11.6	6.25+/-0.40 5.8–6.5	5.09+/-0.18 4.9–5.3
Holotype *M. baletei* ♂	1	5.8	5.8	5.8	4.5	11.6	6.5	4.9
M. hilonghilong ♀	1	6.2	6.9	6.9	5.7	13.7	7.5	7.6
Holotype *M. hilonghilong* ♂	1	6.6	6.4	6.5	5.4	12.7	7.0	6.3

......continued on the next page

TABLE 2B. (Continued)

	n	LORW	CM3U	M2M2	CC	GLM	CM3L	H CP
M. luzonensis ♀	4	5.69+/-0.17 5.5–5.8	5.91+/-0.03 5.9–5.9	5.97+/-0.11 5.8–6.1	4.67+/-0.14 4.5–4.8	11.67+/-0.14 11.5–11.8	6.48+/-0.08 6.4–6.6	5.17+/-0.09 5.1–5.3
M. luzonensis ♂	2	5.95+/-0.17 5.8–6.1	5.97+/-0.02 6.0–6.0	5.76+/-0.04 5.7–5.8	4.56+/-0.16 4.5–4.7	11.75+/-0.08 11.7–11.8	6.69+/-0.16 6.6–6.8	5.05+/-0.33 4.8–5.3
Holotype *M. luzonensis* ♂	1	5.8	6.0	5.7	4.5	11.7	6.6	4.8
M. mindorensis ♀	1	6.0	6.4	6.8	5.5	12.8	6.6	5.6
Holotype *M. mindorensis* ♂	1	5.9	6.0	6.4	4.9	12.1	6.4	5.1
M. philippinensis ♀	2	5.16+/-0.04 5.1–5.2	5.23+/-0.22 5.1–5.4	5.37+/-0.28 5.2–5.6	3.85+/-0.25 3.7–4.0	10.20+/-0.48 9.9–10.5	5.51+/-0.42 5.2–5.8	3.43+/-0.33 3.2–3.7
M. philippinensis ♂	3	5.09+/-0.10 5.0–5.2	4.99+/-0.10 4.9–5.1	5.13+/-0.10 5.0–5.2	3.69+/-0.10 3.6–3.8	9.79+/-0.44 9.3–10.2	5.51+/-0.24 5.3–5.8	3.54+/-0.33 3.3–3.9
Holotype *M. philippinensis* ♂	1	5.1	4.9	5.0	3.6	9.9	5.5	3.4
M. suilla Mindoro ♀	2	5.07	5.19	5.47	3.92	10.31	4.75	4.0
Harpiocephalus harpia ♀	3	8.14+/-0.31 7.9–8.5	6.66+/-0.14 6.5–6.8	7.55+/-0.34 7.3–7.9	7.05+/-0.33 6.7–7.2	15.15+/-0.47 14.7–15.6	7.68+/-0.63 7.0–8.2	9.21+/-1.21 7.9–10.3
Harpiocephalus harpia ♂	7	7.57+/-0.26 7.2–8.0	6.37+/-0.21 6.0–6.6	7.03+/-0.26 6.7–7.4	6.37+/-0.39 5.8–6.8	13.98+/-0.61 13.1–15.0	7.32+/-0.61 6.1–7.9	8.25+/-0.48 7.6–9.1

***Murina luzonensis* sp. nov.**

(Figs. 1, 8D, 9D, 10C; Tables 1, 2A, 2B)

Murina cyclotis: Mt. Mingan: Balete *et al*. 2011: 79; Balbalasang, Heaney *et al*. 2005: 58; Mt. Twin Peaks, Mungiao Mts: Duya *et al*. 2007: 50, 56; Penablanca, Heaney *et al*. 2016b: 243 (but note that *M. baletei* is also referred to as *M. cyclotis* in this book); also referenced as *M. cyclotis* in Heaney *et al*. 2010).

Holotype. FMNH 190764, field number DSB 4348, young adult male, alcohol specimen with skull extracted, collected by D. S. Balete 24 June 2006. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila before the end of 2025, where it has been assigned PNM 9672.

Type locality. Dingalan Munic, 2.6 km S, 3.5 km W Mingan Peak, Aurora Province, Luzon Island, Philippines

(15.45902 N 121.37114 E), elevation 559 m. The nucleotide sequence as deposited in Genbank of Cytb mitochondrial gene is PV659250 and DBY nuclear gene is PV659355.

Paratype. FMNH 190765, field number DSB 4349, ♂, same date and locality as the holotype; and FMNH 190766, field number DSB 4362, ♂, collected 25 June 2006, 2.25 km S, 3.25 km W Mingan peak, elevation 733 m, Aurora Province, Luzon Island, Philippines (15.4609 N 121.3732 E).

Etymology. This species name reflects its currently known distribution, which is based on specimens collected across northern Luzon Island. The suggested English common name is "Luzon tube-nosed bat".

Measurements of holotype. (in mm) and body mass (in g): total length, 86; tail vertebrae, 31; hind foot, 9; ear, 15, forearm, 35.2; and mass, 7.5.

Referred Material. FMNH 169020 ♀ (field number LRH 6320) collected 13 March, 2001, Mapga, elevation 1050 m, Balbalasang Brgy, Balbalan Munic., Kalinga Province, Luzon Island, Philippines (17 27 N 121 09 E); FMNH 176550 ♂ (field number Twin Peaks 136) collected 6 May 2003 at Twin Peaks, elevation 300 m, Sitio Matulang, Brgy Sta Margarita, Baggao Munic., Cagayan Province, Luzon Island, Philippines (18 N 121 E); FMNH 180287 ♀ (field number PAA 495) collected 5 June 2004 at Mungiao Mts., elevation 450 m, Sitio Mangitagud, Brgy Matmad, Nagtipunan Munic., Quirino Province, Luzon Island, Philippines (16 03 22.5 N 121 28 39.7E); and FMNH 214117 ♀ (DSB 8159) collected 15 June 2011, 19 km NE Peñablanca, elevation 100 m, Cagayan Prov. Luzon, Philippines (17.8 N 121.87 E).

Diagnosis. Like *Murina cyclotis* but larger, more robust skull and genetically different with >18% average sequence divergence in Cytb from other species in the genus (Table 3). Similar to *M. baletei*, but teeth are heavier, especially the premolars; the post-palate is longer than *M. baletei*; a lateral view of the skull shows a brow ridge; the posterior sagittal crest is not well developed; the sagittal/lambdoid junction is not well defined with the distance from this junction to the foramen magnum greater than in *M. baletei*. Basisphenoid septum on *M. luzonensis* is wider than *M. baletei* (Figs. 8D, 9D).

Description. Dorsum almost unicoloured, with buff coloured hairs and light brown tips. The hairs at the shoulders are 6–7 mm long. The ventrum is unicoloured, light buff at the throat changing to grey buff along the sides and abdomen. The uropatagium is uniformly covered with long hair. The forearms and thumbs are covered with short dense fur buff in colour. The ear is notched on its posterior border (Fig. 10C).

TABLE 3. *Murina* sp. Philippines: Estimates of evolutionary divergence based on Tamura-Nei model for cytochrome *b* between species (lower triangle) and within species (diagonal).

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) *M. baletei*	0.007						
(2) *M. alvarezi*	0.211	0.031					
(3) *M. hilonghilong*	0.175	0.183	0.001				
(4) *M. luzonensis*	0.191	0.199	0.182	0.016			
(5) *M. mindorensis*	0.122	0.205	0.170	0.181	0		
(6) *M. philippinensis*	0.221	0.236	0.237	0.232	0.209	0.063	
(7) *M. suilla*	0.234	0.252	0.242	0.255	0.243	0.137	0.045

Skull is relatively robust but sagittal and lambdoidal crests are not well developed; the back of the braincase is rounded and low (relative to *M. baletei*) (Fig. 8D); teeth are heavy looking and mesostyles on upper molars are reduced (Fig. 9D). The basisphenoid septum is wider than in *M. baletei*. On the lower molars, the talonid is approximately ½ the size of the trigonid (Fig. 9D). Penis of male is short and wide compared to *M. alvarezi*. See Tables 1 and 2A, 2B for selected external and skull measurements.

Ecology. This species was captured across a broad range of elevation (200–1050 m; Fig. 4), including intact lowland dipterocarp forest on Mount Mingan (Balete *et al.* 2011); disturbed lowland forest within the Mungiao mountain range and Mount Twin Peaks; regenerating forest over limestone near the Cagayan River (Balete *et al.* 2020); and within disturbed lower mossy forest at 1050 m near the village of Balbalasang in Kalinga Province (Rickart *et al.* 2011). One lactating female was captured in June; and two post-lactating females were captured, in March and May.

Distribution. The central Cordillera and northern Sierra Madre range in northern Luzon Island from Mt. Twin Peaks to the Mingan mountains (Fig.1).

Genetic Analyses. Cytochrome *b* and DBY sequences are available on GenBank for specimens listed in Appendices 2 and 3. Relative divergences among Philippine species are discussed below.

Murina mindorensis sp. nov.

Figs. 1, 8B, 9B; Tables 1, 2A, 2B.

Holotype. FMNH 228475, field number DSB 11094, adult male, alcohol specimen with skull extracted, collected by D. S. Balete, 3 April 2015. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila before the end of 2025, where it has been assigned PNM 9675. The nucleotide sequence as deposited in Genbank of Cytb mitochondrial gene is PV659308 and DBY nuclear gene is PV659361.

Type locality. 4.0 km S., 5.0 km W. Mt. Tallulah peak, Sablayan Municipality, Occidental Mindoro Province, Mindoro Island, Philippines (12.82673 N 120.94919 E, elevation 140 m).

Paratype. FMNH 228476, field number DSB 11055, adult female, collected by D. S. Balete, 31 March 2015 at 5.6 km N., 4.6 km W. Mt. Tallulah peak, Sablayan Municipality, Occidental Mindoro Province, Mindoro Island, Philippines (12.84097 N 121.94526 E, elevation 180 m).

Etymology. This species name reflects its distribution which is restricted to Mindoro Island. The suggested English common name is "Mindoro tube-nosed bat."

Measurements of holotype. (in mm) and body mass (in g): total length, 91; tail vertebrae, 34; hind foot, 9; ear, 16, forearm, 36.9; and mass, 8.7.

Diagnosis. A large *Murina* similar to *Murina cyclotis* (as defined by Francis & Eger 2012) but larger (FA = 36.9–39.0 mm; Table 1) with a longer, more robust skull (GLS = 19.2–19.7 mm; Tables 2A, 2B) and genetically different by about 12% average sequence divergence in Cytb from its sister species *M. baletei* (Figs. 2 and 4, Table 3).

Description. Dorsal fur of the holotype is reddish in colour, buff at the base, blending to brownish red tips. The ventrum is unicolour dark buff. The female paratype is pale reddish buff at the base dorsally and unicolour buff on the ventrum.

The skull (Figs. 8B, 9B) is large with a heavy rostrum, with modest sagittal and lambdoidal crests, and lacks an elevated ridge where the two meet. The upper toothrows are parallel. The upper incisors are bicuspidate and simple in shape and the inner are longer but slighter than the outer incisors. The upper premolars are similar in size. The mesostyles of M^1 and M^2 are reduced, and the labial face of these molars is V-shaped. The upper canines are long and robust. The basisphenoid pits are relatively well developed with a medium width septum. On the mandible, the incisors are tricuspidate; the canines are heavy and well worn. P_2 is smaller than P_4; the talonids on the lower molars are about ½ the trigonids. See Tables 1 and 2A, 2B for selected external and skull measurements.

Ecology. This species was captured within regenerating lowland dipterocarp forest (140–180 m) with a dense ground cover of ferns, gingers, orchids, and *Begonia*. In March, a pregnant female was captured in a "V-net" (i.e., two ground mist nets arranged in a V-shape) (embryo crown rump length = 17 mm). A male was captured in a net set at ground level.

Distribution. This species is endemic to Mindoro Island where two individuals were captured at two netting sites near the base of Mt. Tallulah.

Genetic Analyses. Cytochrome *b* and DBY sequences are available on GenBank for specimens listed in Appendices 2 and 3. *Murina mindorensis* is one of three divergent lineages that is supported by DBY data (two sites, Fig. 2) from the Philippines that is closely related to *M. cyclotis* from mainland Asia. Relative divergence among Philippine species is discussed below.

Murina philippinensis sp. nov.

Figs. 1, 7B, 8F, 9F, 10D; Tables 1, 2A, 2B.

Murina suilla: Balete *et al.* 2013: 15, 21; Heaney *et al*. 2016b: 244

Holotype. FMNH 205834, field number JLS 726, adult male, alcohol specimen with skull extracted, collected by J. L. Sedlock, 5 August 2009. The holotype is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila before the end of 2025, where it has been assigned PNM 9671. The nucleotide sequence of Cytb mitochondrial gene is PV659294 and DBY nuclear gene is PV659358.

Type locality. Sitio Bulalacao, Brgy Nug-as, Alcoy Municipality, Cebu Province, Cebu Island, Philippines (9.7205 N 123.4594 E, elevation 763 m)

Paratype. FMNH 205835, field number JLS 741, adult female, collected 8 August 2009, same locality as holotype.

Etymology. The most widespread of the Philippine endemic *Murina* species, this species name reflects its broad distribution across oceanic portions of the Philippine archipelago, from Luzon in the north to Mindanao in the south. The suggested English common name is "Philippine tube-nosed bat."

Measurements of holotype (in mm) and body mass (in g): total length, 80; tail vertebrae, 26; hind foot, 9; ear, 16, forearm, 32.8; and mass, 4.4.

Referred Material. FMNH 186818, field number DSB 3657, ♂, collected 18 September 2005, San Isidro Municipality, Mt. Hamiguitan, Davao Oriental Province, Mindanao Island, Philippines (06 43 56.3 N 126 09 3.2 E elevation 670 m); FMNH 195493, field number GBI 18, ♂, collected 25 May 2007, Maragusan Municipality, Mt. Kampalili, Compostella Valley Province, Mindanao Island, Philippines (7 17 11.7 N 126 16 30.9 E, elevation 1900 m); FMNH 206220, field number DSB 5721, ♀, collected 12 October 2008, Polomoc Municipality, 1.4 km S, 0.55 km E Mt. Matutum peak, South Cotabato Province, Mindanao Island, Philippines (6.3482 N 125.07867 E, elevation 1450 m); and FMNH 205412, field number DSB 5983, ♀, collected 8 June 2009, Rodriguez Munic., 1.25 km S, 0.5 km W Mt Irid peak, Rizal Province, Luzon Island, Philippines (14.7800 N 121.32116 E, elevation 920 m).

Diagnosis. The smallest species of *Murina* in the Philippines and a member of the *M. suilla* group as defined by Hill and Francis (1984). *Murina philippinensis* is generally similar in size, colour and tooth formation to *M. suilla* from Mindoro but differs by having light brown wings and less hairy tail membrane and is smaller (FA = 30.8–33.4 mm vs. 33.5–34.6 mm; GLS = 15.3–16.3 mm vs. 16.1–16.3 mm). Externally *M. philippinensis* differs from the *M. cyclotis* group with its tricoloured fur, which is dark at the base, unique among the Philippine species, and it is much smaller (Table 1). The mesostyle on M^1 and M^2 is not reduced (compare ventral skull images Fig. 9F with A–E), and the talonid on lower molars is more than ½ the size of the trigonid (compare mandible images 9F with A–E).

Description. The dorsal pelage of the holotype is bright reddish brown (chestnut) in colour. The dorsal fur is tri-coloured, dark greyish brown at the base, a narrow band of light brown in the middle section grading into overall bright reddish-brown tips, some of which have dark brown tips (Fig. 3C). The ventrum is bi-coloured, dark grey at the base with buffy tips, including the chin, belly, abdomen and along the wings. The fur on the uropatagium is reddish brown and the uropatagium is heavily furred along the tail vertebrae, tibia and feet. The ear is notched on the posterior side.

The dorsal colour of the Luzon specimen (FMNH 205412) is similar to the holotype; ventrally, the basal band is a lighter grey with buff tips. Banding is more obvious at the throat, along the wings and on the chest; and the abdomen is unicolour buff. A specimen from Mindanao (FMNH 1865818) has shorter fur dorsally and ventrally and the dorsum is a yellow brown colour rather than reddish brown of the more northern specimens. The dorsal fur has some dark brown tips, giving it a mottled appearance.

The braincase of the skull (Fig. 8F) is elevated, the anterior upper premolar (P^2) is small, about half the height of the posterior (P^4); the inner upper incisor (I^2) is about the same height but smaller than and anterior to the outer incisor (I^3). The upper molars (M^1, M^2) have well developed cusps with a distinct W-shape (Figs. 3A, 9F). The toothrows are convergent and the basisphenoid pits are teardrop in shape. On the mandible the incisors are tricuspidate, the anterior premolar (P_2) is smaller than the posterior (P_4), and the talonids of the first two molars are equal in size to the trigonids (Figs. 3B, 9F). See Tables 1 and 2A, 2B for selected external and skull measurements.

Ecology. This species was captured across the archipelago from Luzon to Mindanao, and across a broad elevational range (670–1450 m), although seemingly absent below about 650 m (Fig. 5). On Cebu Island, it was captured in a small, isolated patch of second-growth forest on limestone surrounded by corn and vegetable crops. On Luzon it was captured in disturbed lowland dipterocarp-lower montane forest on limestone (Balete *et al.* 2013), and on Mindanao Island it was recorded in second-growth lowland forest on ultramafic soils (670 m), and in primary transitional montane forest dominated by tree ferns, rattan and thick moss-cover (1450 m). Bats were captured using harp traps and nets set across forest trails, as well as a mist net set across a river. A lactating female was captured in June on Luzon Island, and a post-lactating female was captured on Cebu Island in August.

Distribution. The most widespread of the Philippine *Murina* species, *M. philippinensis* occurs from Luzon south to Mindanao, apparently excluding only the Palawan region, the Babuyan and Batanes Islands north of Luzon, and the islands between Mindanao and Borneo (including Jolo and Tawitawi; Fig. 1).

Genetic Analysis. Cytochrome *b* and DBY sequences are available on GenBank for specimens listed in Appendices 2 and 3. Estimates of evolutionary divergence based on Cytb indicate that *M. philippinensis* differs by 14% from *M. suilla,* represented in this analysis by specimens from Mindoro, Java and Sabah and by 23% or more from other species of *Murina* from the Philippines (Table 3).

Murina suilla **(Temminck, 1840).**

Tables 1, 2A, 2B

Murina tubinaris: Palawan: Esselstyn *et al*. 2004: 271, 278, 288, 289, 296.

Specimens examined from Philippines. FMNH 230253, field number DSB 11108, ♀; FMNH 230254, field number DSB 11170, ♀, collected 1.40 km N, 2.75 km W. Mt Tallulah peak on Mindoro Island, Sablayan Municipality, Occidental Mindoro Prov., Mindoro Island (12.80287 N, 120.96232 E, elevation 490 m) (Fig.1).

Description. Fur on the dorsum is grey at the base with pale mid band and dark brown tips. Ventrally this species is unicolour buff on the mid-belly and bicoloured laterally with grey-based hairs and dark brown tips. Wings are dark brown in colour. Tail membrane is hairy, especially along the tail vertebrae. Conformation of upper and lower molars typical of *M. suilla* without reduced mesostyles on M^1 and M^2 and large talonids on M_1 and M_2 (Figs. 3A, B). See Tables 1 and 2A, 2B for selected external and skull measurements.

Comparison with *M. philippinensis*. *M. suilla* from Mindoro has darker wings, more hairy tail membrane, and differs in colour, having dark brown tips dorsally and dark tips on the lateral portions of the belly. *M. philippinensis* is reddish brown dorsally and buff coloured ventrally. Although the two species differ in colour, they share the dorsal tri-coloured banding pattern and tooth morphology. Size comparisons given above.

Other Records. *Murina cf. suilla* Palawan: (9 27 48 N, 118 32 16 E) was caught at the "rain forestation" site in Sitio Kandis, Aborlan Municipality, in forest/grassland mosaic at ca. 40 m, about seven km away from the next good secondary forest in the foothills of the Victoria Range (Esselstyn *et al.* 2004). Esselstyn *et al.* (2004) recorded this specimen (Staatliches Museum fur Naturkunde Stuttgart SMNS 49238) as *Murina cf tubinaris* from Palawan and although the identification of this specimen cannot be confirmed, it is more likely to be *M. suilla* than *M. tubinaris*. *M. tubinaris* is now referred to as *M. feae* (see Francis & Eger 2012; holotype from Myanmar). Records of *M. feae* are restricted to mainland SE Asia, from India to China. Similar to *M. suilla*, *M. feae* has tricoloured fur dorsally and bicoloured fur ventrally. The holotype of *M. suilla* is from Java. Specimens from Java and Borneo are small (FA 29–30 range), whereas the two Mindoro specimens are larger (FA 33–34), similar in size to the Palawan specimen. Identification of the specimen from Palawan should be regarded as provisional. We make the species assignment primarily based on the presence of *M. suilla* on Borneo and Mindoro, which lie at either end of Palawan. Also, it should be noted that Palawan has none of the endemic species of pteropodids that are otherwise restricted to the oceanic islands of the Philippines (Heaney, 1991; Esselstyn *et al.* 2004), so that finding *M. philippinensis* on Palawan would be surprising. Further investigation is warranted.

Ecology. *M. suilla* was captured on Mindoro Island in regenerating lowland dipterocarp forest (490 m) with a dense ground cover of ferns, gingers, and giant taro (*Alocasia sp.*). Two females were captured in February, and one was pregnant. Both were captured in mist nets.

Genetic Analyses. Cytochrome *b* and DBY sequences are available on GenBank for specimens listed in Appendices 2 and 3. Relative divergences among Philippine species is discussed below.

Comparison of Philippine *Murina cyclotis* group species

We describe five *M. cyclotis*-like species from the Philippines: *M. alvarezi, M. baletei, M. luzonensis, M. mindorensis and M. hilonghilong* in order of size from smallest to largest. These members of the *Murina cyclotis* species group share similar tooth characteristics including upper premolars similar in size to each other, reduced mesostyles on M^1

and M^2 (Fig. 3A) and reduced talonids on the lower molars, M_1 and M_2 (Fig. 3B). Differences in morphology and distribution are summarized in Table 4.

The five members of the *M. cyclotis* group differ from the small *Murina philippinensis* and *M. suilla* in tooth morphology and pelage colour. More broadly, *M. walstoni, M. philippinensis, M. florium,* and *M. suilla*, which are supported by a single nucleotide polymorphism in DBY (Fig. 2), share two tooth characters: 1) mesostyle on M^1 not reduced, and 2) trigonid is equal in size to or larger than the talonid on the lower molars. Dorsal fur colouration is shared by *M. philippinensis* and *M. suilla*, with dark bases, pale mid-band. and dark tips; *M. florium* is bicoloured dorsally with pale base/middle and greyish brown tips. *M. walstoni* is unicoloured with pale grey brown fur that is slightly fuzzy and sparse.

TABLE 4. Morphological Comparison of Philippine *Murina cyclotis* group species. All measurements in mm. Sample sizes in parentheses.

Character	*M. alvarezi*	*M. baletei*	*M. hilonghilong*	*M. luzonensis*	*M. mindorensis*
FA ♀	35.2-36.3 (7)	36.6-39.3 (6)	43.3 (1)	35.5-38.2 (3)	39.0 (1)
FA ♂	32.2-34.9 (10)	34.8-36.1 (3)	39.3 (1)	35.2-35.9 (3)	36.9 (1)
GLS ♀	17.9-18.6 (7)	18.4-19.2 (6)	21.3 (1)	17.8-18.4 (4)	19.7 (1)
GLS ♂	17.2-17.9 (10)	17.9-18.4 (3)	19.1 (1)	17.9-18.3 (2)	19.2 (1)
Dorsal fur	Weakly bicoloured, grey buff base, reddish brown tips	Bicoloured, grey base blending to reddish brown or greyish brown tips	Tricoloured, pale grey base, buff mid band, pale reddish brown tips	Almost unicoloured, buff coloured hair, light brown tips	Buff at base blending to reddish brown tips
Distribution	Southern and central Philippines, Mindanao, Siquijor, Bohol, Cebu, Sibuyan	Lubang, southern Luzon, Catanduanes	Mindanao	Northern Luzon	Mindoro

Genetic Divergence

Estimates of evolutionary divergence (Table 3) based on the Tamura-Nei model for Cytochrome *b* indicate that within the Philippine species, *M. mindorensis* and M. *baletei* are the sister-taxa that are least divergent (12%); *M. philippinensis* and *M. suilla* are next at 14% and these latter two species are the most divergent from the *M. cyclotis* species group (21–25%). Within the latter group, *M. alvarezi* is most divergent from *M. baletei* (21%).

Echolocation

Murina alvarezi and *M. philippinensis* both emitted frequency-modulated (FM) calls (Fig. 7) that were broadband, short duration, and high frequency—attributes that may allow them to detect and take stationary prey from substrates (Schmieder *et al.* 2012). The mean peak frequency of *M. alvarezi* calls (79.7 kHz, Table 5) was within the range of *M. cyclotis* peak frequencies recorded from peninsular Malaysia (54–136 kHz; Kingston *et al.* 1999) and Vietnam (72–158 kHz; Győrössy *et al.* 2024). Similarly, the peak frequency of the single *M. philippinensis* in this study (82 kHz, Table 5) was within the range of *M. suilla* recorded in peninsular Malaysia (44–127 kHz, Kingston *et al.* 1999). Nevertheless, peak frequency, which is the most repeatable measurement of echolocation pulses (e.g., duration and bandwidth are dependent on context, distance, and angle from sound source to microphone, etc.) is extremely variable within *Murina* species resulting in broad overlap among species. Large signal bandwidths facilitate highly accurate target localization in terms of both range and angle estimation and can thus be interpreted as an adaptation to foraging in the highly cluttered environment of the forest understorey (Kingston *et al.* 1999).

TABLE 5. Duration, bandwidth, peak echolocation frequency of two Philippine *Murina* species.

Species	N	Duration (ms)	Bandwidth (kHz)	Peak frequency (kHz)
M. alvarezi	9	2.84 ± 0.88	89.66 ± 11.58	79.7 ± 5.8
M. philippinensis	1	2.14	102.02	82.07

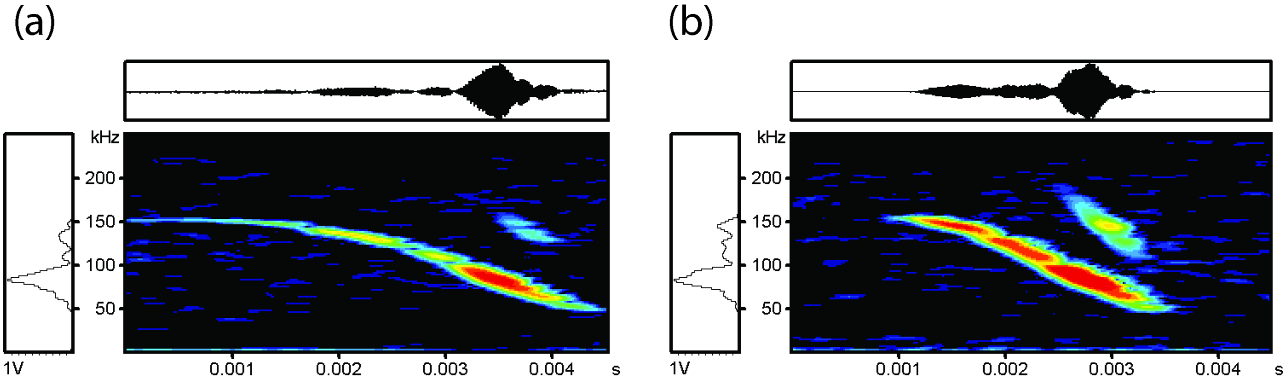

FIGURE 7. Power spectrum, waveform and spectrogram from representative echolocation calls from *Murina alvarezi* (FMNH 205830) (a) and *M. philippinensis* (FMNH 205835) (b).

Morphometric Analysis

Results of the PCA are presented in Fig. 6. The first 2 principal components explain 99% of the total variance with PC1, a size component, accounting for 97.4% of the variance, with high positive loadings for all characters. PC2 is a shape component (1.6%) with much of this variance attributed to two species, *M. hilonghilong* and *M. mindorensis*, both of which are large species represented by one male and one female. The larger species *M. hilonghilong*, has a narrower skull (POC, M^2M^2, and BBC) relative to its large size (CM_3L, 4DM, HCP and PAL), but both species are large relative to the other Philippine *Murina.* In all species but M. *luzonensis*, females are larger than males, and in all species males and females differ in shape. *Murina luzonensis* males and females are about equal in size but differ in shape. The *M. suilla* group of species vary in size from the smallest *M. suilla* from Java, Sabah and Sarawak to the largest of the group, *M. suilla* from Mindoro Island, the only island in the Philippines where *M. suilla* has been found (aside from the tentatively referred specimen from Palawan). Intermediate in size is the small *Murina philippinensis* within the *suilla* group, which is widespread in the Philippines.

Discussion

Biogeography

Our study focuses on the species limits of *Murina* within the Philippines. Although the Philippines comprise only a small portion of the total range of the genus, most of the archipelago is composed of islands shaped by dramatic tectonic events that began at least 40 MYA (Hall 1998, 2012) and by more recent Pleistocene climatic and sea-level fluctuations, and thus provides a theatre for investigating the timing of dispersal and the effects of geographic isolation on these bats. In particular, some of the modern islands were connected to one another during Pleistocene periods when sea level dropped about 120 m below the present level, but many of these large "ice age" islands remained separated from each other by deep oceanic channels (Fig. 1; Heaney 1986, 1991; Heaney *et al.* 2016b). Previous studies have shown that each of the larger isolated islands during the Late Pleistocene supported faunas of non-volant mammals that typically included 70 to 95% endemic species (Heaney 1986; Heaney *et al.* 2016 a, b), marking them as globally important centres of mammalian endemism.

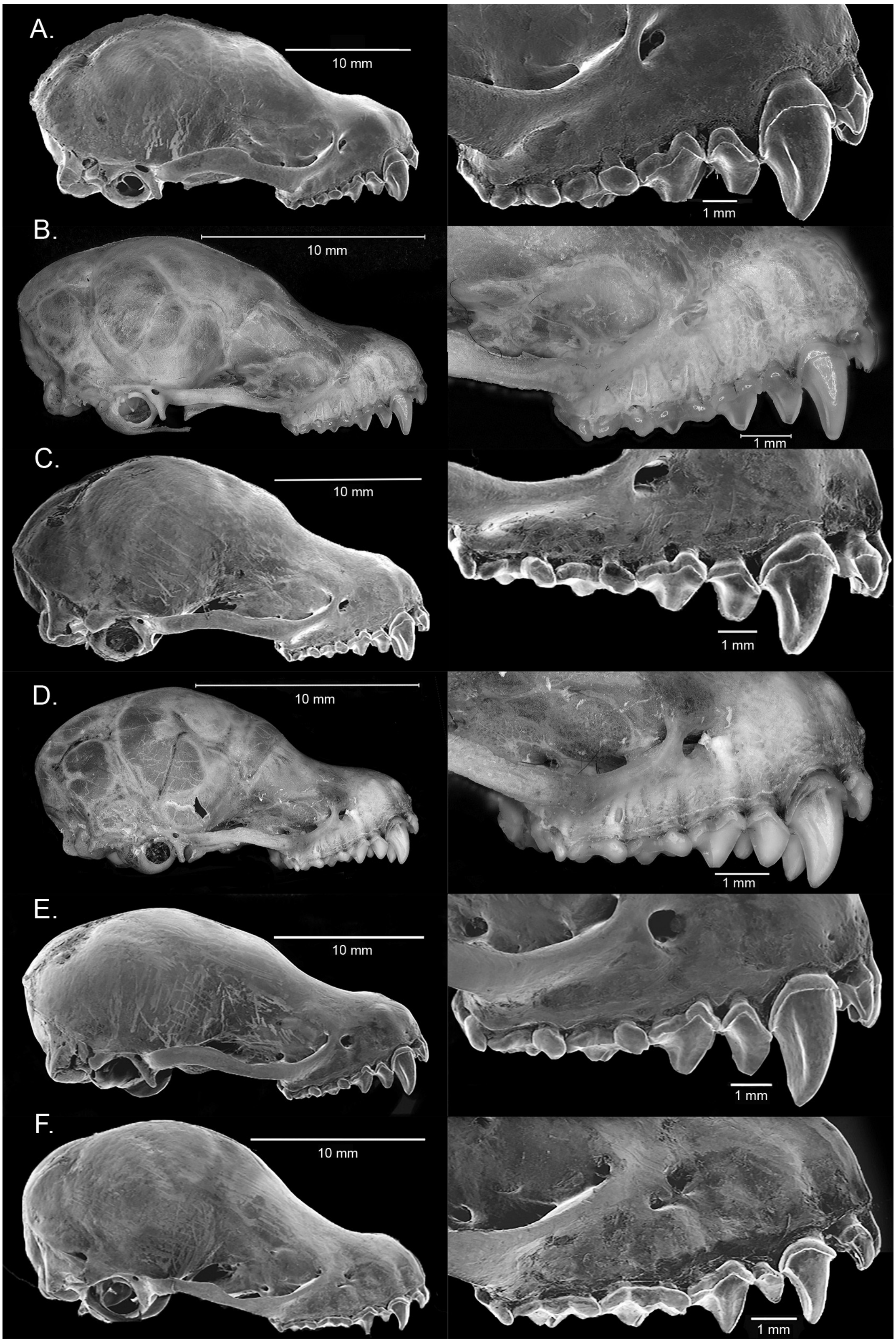

FIGURE 8. Skull profiles of right side of skull and upper right toothrow of holotypes of six new species of *Murina* from the Philippines. A *M. hilonghilong* **sp. nov.** (FMNH 190118); B *M. mindorensis* **sp. nov.** (FMNH 228475); C *M. baletei* **sp. nov.** (FMNH 205411); D *M. luzonensis* **sp. nov.** (FMNH 190764); E *M. alvarezi* **sp. nov.** (FMNH 205831); F *M. philippinensis* **sp. nov.** (FMNH 205834).

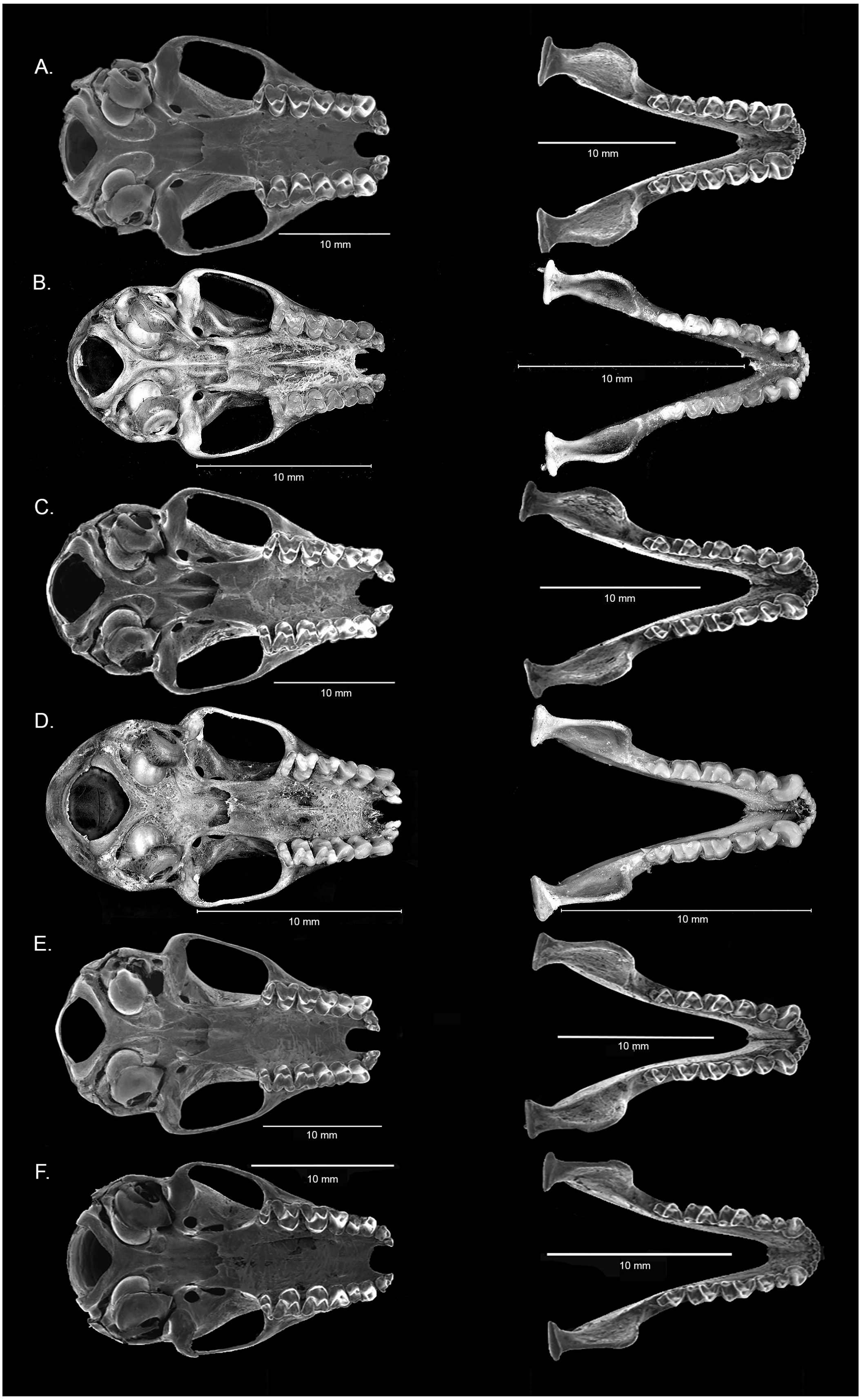

FIGURE 9. Ventral view of skull and dorsal view of mandible of holotypes of six new species of *Murina* from the Philippines. A *M. hilonghilong* **sp. nov.** (FMNH 190118); B *M. mindorensis* **sp. nov.** (FMNH 228475); C *M. baletei* **sp. nov.** (FMNH 205411); D *M. luzonensis* **sp. nov.** (FMNH 190764); E *M. alvarezi* **sp. nov.** (FMNH 205831); F *M. philippinensis* **sp. nov.** (FMNH 205834).

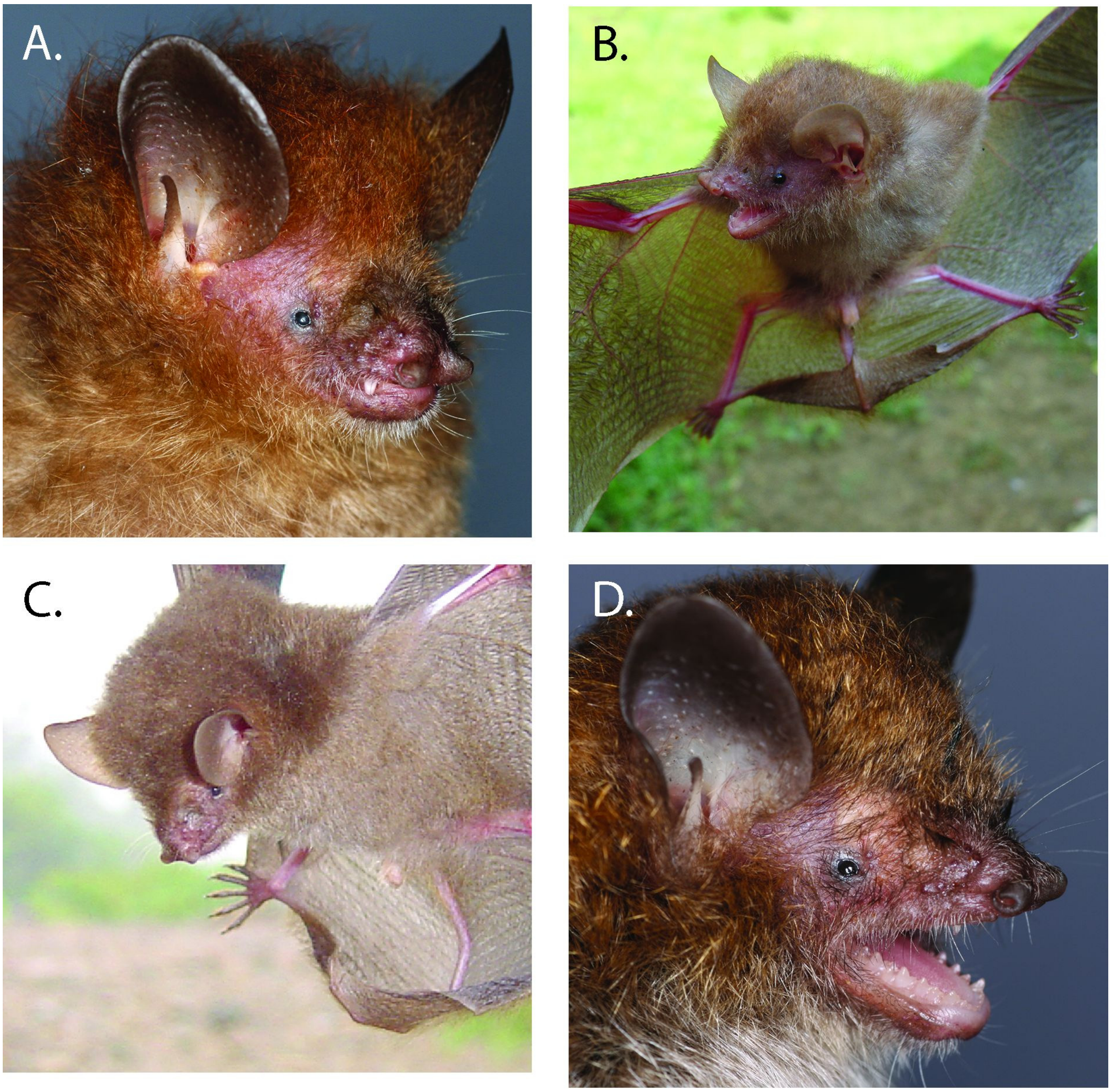

FIGURE 10. Representative photographs of *M. alvarezi* (A, paratype, FMNH 205827; photo: J. Sedlock), *M. baletei* (B, holotype, FMNH 205411; photo: D. Balete), *M. luzonensis* (C, holotype FMNH 190764; photo: D. Balete), *M. philippinensis* (D, holotype, FMNH 205834; photo: J. Sedlock).

In addition to these species-level patterns of endemism among small mammals, recent studies have demonstrated extensive phylogenetic diversification within the oceanic Philippines, with three endemic clades of murid rodents having produced 21 species of cloud rats (tribe Phloeomyini; Ochoa *et al.* 2021; Rowsey *et al.* 2018), about 45 species of earthworm mice (Chrotomys Division; Heaney *et al.* 2018; Rowsey *et al.* 2018; Rickart *et al.* 2019), and at least seven species of moss mice in the *Tarsomys* clade (Rowsey *et al.* 2022). Much of the speciation occurred within the larger isolated islands of Greater Luzon (e.g., Balete *et al.* 2012; Justiniano *et al.* 2015), Greater Mindanao (e.g., Balete *et al.* 2015; Rowsey *et al.* 2022), and some within the smaller island of Greater Mindoro (Heaney *et al.* 2018), but a strong role for intra-archipelago colonization and diversification has also been demonstrated (e.g., Steppan *et al.* 2003).

Among Philippine bats, only fruit bats of the family Pteropodidae have been the subjects of extensive studies of patterns of endemism, geographic variation, and species limits (Heaney & Rickart 1990; Heaney 1991; Peterson & Heaney 1993; Roberts 2006a, b; Heaney & Roberts 2009). These studies show evidence of extensive speciation having taken place within the Philippines, with one endemic clade including three species in *Ptenochirus*, and nine putative species in the endemic clade comprised of the genera *Alionycteris*, *Haplonycteris*, and *Otopteropus* (Almeida *et al.* 2011; Nesi *et al.* 2021), including seven cryptic species currently treated as *H. fischeri* (Roberts 2006b; Heaney & Roberts 2009). In both cases, two and sometimes three species within an endemic clade occur sympatrically, suggesting differentiation into distinct niches.

Pteropodids show patterns of areas of endemism similar to those of the non-volant mammals, albeit at a lower percentage of endemism. For example, two of 15 species (13%) on Greater Luzon are endemic; three of 17 on Greater Mindanao (18%); three of 14 on Greater Mindoro (21%); and four of 14 on Greater Negros-Panay (29%) (Heaney 1991; Esselstyn 2007; Heaney *et al.* 2010). In each case, we include in these counts seven cryptic endemic species currently treated as *Haplonycteris fischeri* (Roberts 2006b; Heaney & Roberts 2009).

These observations lead to three issues regarding the patterns of distribution for *Murina*, which is the first non-pteropodid, widespread bat in the Philippines to be studied in detail (but see also Sedlock *et al.* 2020). As noted above, our phylogenetic analysis produced robust support for the recognition of five distinct species within the *M. cyclotis* group (Fig. 2: *M. baletei*, *M. alvarezi, M. hilonghilong*, *M. luzonensis*, and *M. mindorensis*) but the more basal relationships are not well resolved. If future studies provide additional support for this grouping, this would indicate extensive endemic speciation in the Philippines and dispersal back to the Asian mainland (e.g., leading to *M. lorelieae*).

As shown in Fig.1, the distributions of the endemic species of *Murina* named here are consistent with those shown by non-volant mammals and fruit bats, although not perfectly so. *Murina mindorensis* occurs only on Mindoro, *M. baletei* and *M. luzonensis* occur in southern and northern Luzon respectively, within areas of endemism that are paralleled by non-volant native mammals (Heaney *et al.* 2016a, b), and *M. hilonghilong* is a Mindanao endemic that occurs only in a limited area (Fig. 1). *Murina alvarezi* occurs on several of the late Pleistocene islands, including Greater Mindanao, Greater Negros-Panay, and two small oceanic islands (Siquijor and Sibuyan) that lie near to the two larger islands just mentioned. This implies somewhat greater dispersal ability than nearly any of the non-volant native mammals (Heaney 1986; Heaney *et al.* 2016a, b). Overall, Philippine endemic *Murina* fit readily into patterns of endemism noted for many other groups of Philippine mammals.

Finally, we note that there is only limited sympatry apparent among Philippine *Murina*, except at the level of the two major species-groups. *Murina suilla* occurs sympatrically with *M. mindorensis* on Mindoro, and *M. philippinensis*, which is closely related to *M. suilla*, occurs widely within the oceanic Philippines where it overlaps in distribution with most, and perhaps all five endemic species related to *M. cyclotis*. Within the five species related to *M. cyclotis*, there is no evidence of sympatry except for *M. hilonghilong* and *M. alvarezi*. This suggests that the largely allopatric species of the *M. cyclotis* group either have yet to evolve sufficient ecological differences to allow co-occurrence or have remained isolated due to weak dispersal abilities, unlike the endemic pteropodids which show several instances of sympatry within endemic clades. In contrast, endemic clades of non-volant small mammals within the Philippines often form speciose syntopic communities (Heaney *et al.* 2016b; Rickart *et al.* 2016). Species within these non-volant small mammal communities possess distinctly different feeding niches (Petrosky *et al.* 2021), whereas species within the *M. cyclotis* group in the Philippines may have similar foraging behaviors as insect gleaners in cluttered forested environments. Compared to rodents, however, bats are still under-sampled so the extent of sympatry might be higher in *Murina* and the recent increase in clearing of lowland forests may have resulted in local extirpations of populations or broader extinctions of species.

We see evidence that bats of the genus *Murina* have responded to geographic and geological circumstances in ways different to both pteropodid fruit bats and to native non-volant mammals. Two lineages (one that includes *M. suilla*, *M. florium*, and *M. philippinensis*, and the other includes the *M. cyclotis* group, Fig. 2) likely colonized from the southeastern portion of the Asian continent or nearby continental shelf, and probably not from Taiwan or mainland China or from Sulawesi or Australia/New Guinea. However, in both lineages, species outside of the Philippines are embedded within the clades in ways that suggest that the Philippines may have served as the source of species now found on the Sunda Shelf (*M. suilla*), Flores, Sulawesi and New Guinea (*M. florium*), and southern China *(M. lorelieae*); these hypotheses deserve further testing. Future research should concentrate on examining more genomic data to test the recognition of these species and to better understand the biogeography of species of *Murina* in the Philippines relative to those species the Sunda Shelf, Wallacea and mainland Asia.The timing of arrival by the lineages that now occur in the Philippines can be estimated from calibrated phylogenies such as Fig. 4. It should be noted that the dates are based on poor fossil records and, at times, assumptions about average rates of mutation, and thus should be viewed as estimates, not precise values. Nevertheless, when interpreted cautiously, they may give us insights into the dynamics of diversification over long timespans. In this case, the common ancestor of the five Philippine species of the *M. cyclotis* group arrived by about 11.7 mya, and diversification began by about 11 mya. The ancestor of *M. philippinensis* may have arrived as early as 6.35 mya, and diversification of island populations began by 4.1 mya. Although estimated to have arrived 11 mya, diversification within the widespread species *M. alvarezi* began by 2.46 mya. In the paper by Wang *et al.* (2024), the authors identified a population decline in most species of Murininae during the Pleistocene, however, our molecular dated tree estimates that most speciation within the genus had already occurred by the Pliocene.

Our data, which indicate that *Murina* has been present within the Philippines for over 11 my, can be compared with estimates for the arrival to, and subsequent diversification within the Philippines by endemic lineages of *Kerivoula*, which like *Murina* is a small, forest-associated, insectivorous bat. It is estimated that *K. whiteheadi* arrived by about 7.06 mya, *K. hardwickii* by 7.20 mya, and *K. papillosa* by about 7.04 (Sedlock *et al.* 2020).

Fruit bats of the family Pteropodidae may also be compared, based on a calibrated phylogeny by Almeida *et al*. (2020). The common ancestor of the large endemic radiation of dwarf fruit bats that includes *Alionycteris*, *Haplonycteris*, and *Otopteropus* arrived as early as 14 mya, and diversification began by about 12 mya. A second endemic radiation, represented by three species in the endemic genus *Ptenochirus*, began diversifying by about 7.5 mya. Some lineages may have arrived earlier. For example, the Philippine endemic genus *Desmalopex* diverged from its relatives in New Guinea and islands to the east about 17 mya, but currently we have no way to know if it arrived in the Philippines at that time, or later. *Styloctenium* diverged from its relatives in the New Guinea area at about the same time (ca. 16 mya) and now has two closely related species that live on Sulawesi and Mindoro.

The timing of arrival of lineages of non-volant mammals in the oceanic Philippines was similar. The ancestor of Philippine endemic cloud rats (Tribe Phloeomyini) diverged from its relatives in continental SE Asia by about 15 mya and began diversifying ca. 11 mya (Rowsey *et al.* 2022). The endemic lineage of "earthworm mice" (*Chrotomys* Division, as defined by Musser & Carleton (2005) diverged from its relatives by 15 mya and began diversifying by 7 mya. The moss mice "*Tarsomys* clade" (as defined by Rowsey *et al.* 2022) arrived about 2.4 mya and began diversifying almost immediately. Shrews (*Crocidura*, Family Soricidae), though now represented by eight species in the oceanic Philippines, also arrived only recently, estimated at 2–5 mya (Esselstyn & Brown 2009; Esselstyn *et al.* 2011).

These data taken together imply that some extant lineages of endemic Philippine bats began arriving at least by 12 mya, and perhaps as early as 17 mya. Other arrivals of endemic, diversified lineages were more recent, often in the range of four to seven million years ago. Perhaps surprisingly, given their lesser dispersal abilities, non-volant mammals began arriving in the oceanic Philippines at least by 11 mya, and perhaps by 15 mya, with subsequent arrivals taking place rarely but persistently thereafter. Thus, by the middle to late Miocene, the oceanic portions of the Philippines had been reached by lineages still represented today by diverse assemblages of bats and non-volant mammals, with *Murina* among them. At the time, the Philippine archipelago was composed of smaller, more scattered islands, but some of them have likely remained continuously above water and have grown through volcanic and other tectonically related geological processes (Heaney *et al.* 2016b; Hall 2012, 2013). In this sense, the modern mammal fauna of the oceanic Philippine islands has been marked by long-term persistence and diversification, best measured on a timescale of millions of years.

Conservation Remarks

As foliage-roosting species *Murina* are known to be forest-dependent across Southeast Asia (Heaney *et al.* 2010; Francis 2019), and as a result, are vulnerable to forest loss. In the Philippines, all specimens in this study were captured within second-growth or primary forest, and most within protected areas. Despite this, deforestation within Key Biodiversity Areas (KBAs)—many of which comprise federally Protected Areas—is occurring across the Philippines (Apan *et al.* 2017; Daipan 2021), primarily due to *kaingin* (shifting agriculture) and mineral mining. For example, from 2000–2019, Mt. Hilong-hilong, the only site where *M. hilonghilong* was captured, lost 518 ha/year resulting in 4.14% forest cover loss over 9 years. Mount Kampalili-Puting Bato KBA, also in the eastern Mindanao biodiversity corridor and harboring *M. alvarezi*, experienced an 8.04% forest cover loss within the same timeframe (Daipan 2021). Mount Hilong-hilong is within the Caraga area, where forests on ultramafic soils are rich in nickel—a mineral growing in demand for its use in electric car and other batteries (Golroudbary *et al.* 2022; Sarmiento &

Demetillo 2017). Currently, there are 58 large-scale metallic mines (38 nickel) operating in the Philippines, and the majority of these are in eastern Mindanao—nickel in the northern Caraga area (Region XIII) and copper farther south (https://mgb.gov.ph). These mining operations involve direct deforestation and soil removal but are likely to contribute to indirect forest loss as well in areas adjacent to the mining operation (Giljum *et al.* 2022). The expansion of this type of mining and illegal forms of forest loss across the archipelago serve as a serious threat to the six species we described here, as well as all other forest-dependent species.

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Online supplementary information

The supplementary file is available online at figshare online data repository (DOI: 10.6084/m9.figshare.29247413).

Figure S1. Neighbour-joining tree of *Murina* from DBY gene. Bootstrap support is indicated at the nodes for 50% or greater.

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APPENDIX

APPENDIX 1. Specimens used in morphological analysis of Philippine *Murina*.

Males

Institution	Catalogue #	Genus	Species	Country	Island
FMNH	146890	*Murina*	*alvarezi*	Philippines	Romblon
FMNH	147078	*Murina*	*alvarezi*	Philippines	Mindanao
FMNH	190119	*Murina*	*alvarezi*	Philippines	Mindanao
FMNH	202815	*Murina*	*alvarezi*	Philippines	Bohol
FMNH	202816	*Murina*	*alvarezi*	Philippines	Bohol
FMNH	205827	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205828	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205830	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	209659	*Murina*	*alvarezi*	Philippines	Siquijor
FMNH	209660	*Murina*	*alvarezi*	Philippines	Siquijor
FMNH	166429	*Murina*	*baletei*	Philippines	Luzon
FMNH	205411	*Murina*	*baletei*	Philippines	Luzon
FMNH	573774	*Murina*	*baletei*	Philippines	Catanduanes
FMNH	190118	*Murina*	*hilonghilong*	Philippines	Mindanao
FMNH	190764	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	190765	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	228475	*Murina*	*mindorensis*	Philippines	Mindoro
FMNH	186818	*Murina*	*philippinensis*	Philippines	Mindanao
FMNH	195493	*Murina*	*philippinensis*	Philippines	Mindanao
FMNH	205834	*Murina*	*philippinensis*	Philippines	Cebu
RMNH	15229	*Murina*	*suilla*	Indonesia	Java
RMNH	15235	*Murina*	*suilla*	Indonesia	Java
RMNH	15237	*Murina*	*suilla*	Indonesia	Java
ROM	117940	*Murina*	*suilla*	Malaysia	Sabah
ROM	117950	*Murina*	*suilla*	Malaysia	Sabah
ROM	117956	*Murina*	*suilla*	Malaysia	Sabah

Females

Institution	Catalogue #	Genus	Species	Country	Island
FMNH	186817	*Murina*	*alvarezi*	Philippines	Mindanao
FMNH	205826	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205829	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205831	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205832	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	205833	*Murina*	*alvarezi*	Philippines	Cebu
FMNH	209658	*Murina*	*alvarezi*	Philippines	Siquijor
FMNH	166428	*Murina*	*baletei*	Philippines	Luzon
FMNH	177471	*Murina*	*baletei*	Philippines	Luzon
FMNH	177472	*Murina*	*baletei*	Philippines	Luzon
FMNH	205410	*Murina*	*baletei*	Philippines	Luzon

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APPENDIX 1. (Continued)

FMNH	218203	*Murina*	*baletei*	Philippines	Luzon
FMNH	573776	*Murina*	*baletei*	Philippines	Luzon
FMNH	191407	*Murina*	*hilonghilong*	Philippines	Mindanao
FMNH	169020	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	176550	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	180287	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	214117	*Murina*	*luzonensis*	Philippines	Luzon
FMNH	228476	*Murina*	*mindorensis*	Philippines	Mindoro
FMNH	205412	*Murina*	*philippinensis*	Philippines	Luzon
FMNH	205835	*Murina*	*philippinensis*	Philippines	Cebu
RMNH	15225	*Murina*	*suilla*	Indonesia	Java
RMNH	15233	*Murina*	*suilla*	Indonesia	Java
RMNH	15316	*Murina*	*suilla*	Indonesia	Java
RMNH	35772	*Murina*	*suilla*	Indonesia	Java
ROM	48164	*Murina*	*suilla*	Malaysia	Sarawak
ROM	117936	*Murina*	*suilla*	Malaysia	Sabah
ROM	117949	*Murina*	*suilla*	Malaysia	Sabah
FMNH	230253	*Murina*	*suilla*	Philippines	Mindoro
FMNH	230254	*Murina*	*suilla*	Philippines	Mindoro

APPENDIX 2. Specimens of *Murina*, *Harpiocephalus* and outgroups used in Cytb analysis.

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
OCUM	S6010		*Myotis*	*ikonnikovi*		AB106594.1
TTU	152080		*Kerivoula*	*hardwickii*		EU188768.1
ROM	106379	2	*Murina*	*feae*	Laos	PV659164
ROM	106380	3	*Murina*	*feae*	Laos	PV659165
ROM	106382	4	*Murina*	*fionae*	Laos	PV659166
ROM	106383	5	*Murina*	*fionae*	Laos	PV659167
ROM	106386	6	*Murina*	*feae*	Laos	PV659168
ROM	106411	7	*Murina*	*eleryi*	Laos	PV659169
ROM	106419	8	*Murina*	*huttoni*	Laos	PV659170
ROM	106420	9	*Murina*	*huttoni*	Laos	PV659171
ROM	106426	10	*Murina*	*huttoni*	Laos	PV659172
ROM	106431	11	*Murina*	*cyclotis*	Laos	PV659173
ROM	106445	12	*Murina*	*eleryi*	Laos	PV659174
ROM	106461	13	*Murina*	*cyclotis*	Laos	PV659175
ROM	106466	14	*Murina*	*annamitica*	Laos	PV659176
ROM	106477	16	*Murina*	*feae*	Laos	PV659177
ROM	106478	17	*Murina*	*eleryi*	Laos	PV659178
ROM	106492	18	*Murina*	*annamitica*	Laos	PV659179
ROM	107584	19	*Murina*	*cyclotis*	Vietnam	PV659180
ROM	107693	21	*Murina*	*cyclotis*	Vietnam	PV659181
ROM	107739	22	*Murina*	*harrisoni*	Vietnam	PV659182
ROM	107749	23	*Murina*	*harrisoni*	Vietnam	PV659183

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APPENDIX 2. (Continued)

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
ROM	107750	24	*Murina*	*harrisoni*	Vietnam	PV659184
ROM	110684	26	*Harpiocephalus*	*harpia*	Laos	PV659185
ROM	110708	28	*Murina*	*walstoni*	Laos	PV659186
ROM	110709	29	*Murina*	*walstoni*	Laos	PV659187
ROM	110715	30	*Murina*	*cyclotis*	Laos	PV659188
ROM	110719	32	*Murina*	*walstoni*	Laos	PV659189
ROM	110720	33	*Murina*	*cyclotis*	Laos	PV659190
ROM	110941	39	*Murina*	*walstoni*	Vietnam	PV659191
ROM	111286	41	*Murina*	*eleryi*	Vietnam	KT762295
ROM	111287	42	*Murina*	*cyclotis*	Vietnam	PV659192
ROM	111300	44	*Murina*	*eleryi*	Vietnam	KT762296
ROM	111301	45	*Murina*	*feae*	Vietnam	PV659193
ROM	111302	46	*Murina*	*feae*	Vietnam	PV659194
ROM	111307	47	*Murina*	*feae*	Vietnam	PV659195
ROM	111308	48	*Murina*	*eleryi*	Vietnam	PV659196
ROM	111359	49	*Murina*	*huttoni*	Vietnam	PV659197
ROM	111360	50	*Murina*	*eleryi*	Vietnam	PV659198
ROM	111361	51	*Murina*	*annamitica*	Vietnam	PV659199
ROM	111375	52	*Murina*	*cyclotis*	Vietnam	PV659200
ROM	111399	53	*Murina*	*eleryi*	Vietnam	PV659201
ROM	112344	54	*Harpiocephalus*	*harpia*	Vietnam	PV659202
ROM	112345	55	*Murina*	*cyclotis*	Vietnam	PV659203
ROM	112362	56	*Murina*	*cyclotis*	Vietnam	PV659204
ROM	112822	57	*Murina*	*hilgendorfi*	China	PV659205
ROM	112832	58	*Murina*	*hilgendorfi*	China	PV659206
ROM	113014	59	*Murina*	*aenea*	Malaysia	PV659207
ROM	113106	60	*Murina*	*aenea*	Malaysia	PV659208
ROM	114934	61	*Harpiocephalus*	*harpia*	China	PV659209
ROM	114938	62	*Murina*	*huttoni*	China	PV659210
ROM	114956	63	*Harpiocephalus*	*harpia*	China	PV659211
ROM	115043	64	*Murina*	*huttoni*	China	PV659212
ROM	117936	66	*Murina*	*suilla*	Sabah	PV659213
ROM	117940	68	*Murina*	*suilla*	Sabah	PV659214
SEN	83723	69	*Murina*	*suilla*	Sabah	PV659215
USNM	573774	72	*Murina*	*baletei*	Philippines	PV659216
USNM	573776	73	*Murina*	*baletei*	Philippines	PV659217
MSB	93159	74	*Murina*	*florium*	Sulawesi	PV659218
ROM	114969	75	*Murina*	*huttoni*	China	PV659219
ROM	116040	76	*Murina*	*cyclotis*	China	PV659220
ROM	116041	77	*Harpiocephalus*	*harpia*	China	PV659221
ROM	116047	78	*Murina*	*leucogaster*	China	PV659222
ROM	116049	79	*Murina*	*leucogaster*	China	PV659223
ROM	116053	80	*Murina*	*cyclotis*	China	PV659224

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APPENDIX 2. (Continued)

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
ROM	116059	81	*Murina*	*cyclotis*	China	PV659225
ROM	116064	82	*Murina*	*feae*	China	PV659226
ROM	116065	83	*Murina*	*cyclotis*	China	PV659227
ROM	116071	84	*Murina*	*eleryi*	China	PV659228
ROM	116099	85	*Murina*	*eleryi*	China	KT762301
ROM	116123	86	*Murina*	*feae*	China	PV659229
ROM	116124	87	*Murina*	*eleryi*	China	PV659230
ROM	116150	88	*Murina*	*leucogaster*	China	PV659231
ROM	116177	89	*Murina*	*leucogaster*	China	PV659232
ROM	116181	90	*Murina*	*chrysochaetes*	China	PV659233
ROM	116183	91	*Murina*	*feae*	China	PV659234
ROM	116364	93	*Murina*	*eleryi*	China	PV659235
ROM	116476	94	*Murina*	*cyclotis*	China	PV659236
ROM	116482	95	*Murina*	*cyclotis*	China	PV659237
ROM	116463	96	*Murina*	*harrisoni*	China	PV659238
ROM	116468	97	*Murina*	*harrisoni*	China	PV659239
ZMMU	S-173235	100	*Murina*	*hilgendorfi*	Russia	PV659240
ZMMU	S-173249	101	*Murina*	*ussuriensis*	Russia	PV659241
ZMMU	S-175150	102	*Murina*	*sp g*	Vietnam	PV659242
ROM	116171	107	*Murina*	*lorelieae*	China	PV659243
HNHM	2004.19.15	108	*Harpiola*	*isodon*	Taiwan	PV659244
HNHM	2004.19.13	109	*Harpiola*	*isodon*	Taiwan	GQ168914
ZMMU	S-180001	110	*Harpiola*	*isodon*	Vietnam	PV659245
ROM	110439	111	*Murina*	*cf cyclotis*	Thailand	PV659246
ROM	118507	112	*Murina*	*eleryi*	China	PV659247
ROM	118531	113	*Murina*	*shuipuensis*	China	PV659248
FMNH	186818	114	*Murina*	*philippinensis*	Philippines	PV659249
FMNH	190764	115	*Murina*	*luzonensis*	Philippines	PV659250
FMNH	190765	116	*Murina*	*luzonensis*	Philippines	PV659251
FMNH	190766	117	*Murina*	*luzonensis*	Philippines	PV659252
FMNH	195493	118	*Murina*	*philippinensis*	Philippines	PV659253
FMNH	146890	119	*Murina*	*alvarezi*	Philippines	PV659254
FMNH	147078	120	*Murina*	*alvarezi*	Philippines	PV659255
FMNH	166428	121	*Murina*	*baletei*	Philippines	PV659256
FMNH	166429	122	*Murina*	*baletei*	Philippines	PV659257
FMNH	169020	123	*Murina*	*luzonensis*	Philippines	PV659258
FMNH	177471	124	*Murina*	*baletei*	Philippines	MG194466
FMNH	180287	126	*Murina*	*luzonensis*	Philippines	PV659259
FMNH	186817	127	*Murina*	*alvarezi*	Philippines	PV659260
FMNH	190763	128	*Harpiocephalus*	*harpia*	Philippines	PV659261
FMNH	76069	129	*Murina*	*pluvialis*	India	PV659262
FMNH	76084	130	*Murina*	*cyclotis*	India	PV659263
HZM	136316	131	*Murina*	*harrisoni*	Cambodia	PV659264

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APPENDIX 2. (Continued)

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
HZM	238178	132	*Murina*	*harrisoni*	Vietnam	PV659265
ZMMU	S-182119	133	*Murina*	*harpioloides*	Vietnam	PV659266
FMNH	190109	135	*Harpiocephalus*	*harpia*	Philippines	PV659267
FMNH	191407	136	*Murina*	*hilonghilong*	Philippines	PV659268
FMNH	193499	137	*Harpiocephalus*	*harpia*	Philippines	PV659269
FMNH	194724	138	*Harpiocephalus*	*harpia*	Philippines	PV659270
FMNH	194725	139	*Harpiocephalus*	*harpia*	Philippines	PV659271
FMNH	190118	140	*Murina*	*hilonghilong*	Philippines	PV659272
FMNH	190119	141	*Murina*	*alvarezi*	Philippines	PV659273
FMNH	202815	142	*Murina*	*alvarezi*	Philippines	PV659274
FMNH	202816	143	*Murina*	*alvarezi*	Philippines	PV659275
ZMMU	S-182084	144	*Murina*	*hilgendorfi*	Russia	PV659276
ZMMU	S-173232	147	*Murina*	*hilgendorfi*	Russia	PV659277
ZMMU	S-184750	148	*Murina*	*ussuriensis*	Russia	PV659278
ZMMU	S-175207	149	*Murina*	*ussuriensis*	Russia	PV659279
ZMMU	S-184673	150	*Murina*	*annamitica*	Vietnam	PV659280
ZMMU	S-184674	151	*Murina*	*cyclotis*	Vietnam	PV659281
ZMMU	S-184675	152	*Murina*	*cyclotis*	Vietnam	PV659282
FMNH	205410	153	*Murina*	*baletei*	Philippines	PV659283
FMNH	205411	154	*Murina*	*baletei*	Philippines	PV659284
FMNH	205826	155	*Murina*	*alvarezi*	Philippines	PV659285
FMNH	205827	156	*Murina*	*alvarezi*	Philippines	PV659286
FMNH	205828	157	*Murina*	*alvarezi*	Philippines	PV659287
FMNH	205829	158	*Murina*	*alvarezi*	Philippines	PV659288
FMNH	205830	159	*Murina*	*alvarezi*	Philippines	PV659289
FMNH	205831	160	*Murina*	*alvarezi*	Philippines	PV659290
FMNH	205832	161	*Murina*	*alvarezi*	Philippines	PV659291
FMNH	205833	162	*Murina*	*alvarezi*	Philippines	PV659292
FMNH	205412	163	*Murina*	*philippinensis*	Philippines	PV659293
FMNH	205834	164	*Murina*	*philippinensis*	Philippines	PV659294
FMNH	205835	165	*Murina*	*philippinensis*	Philippines	PV659295
ROM	120474	166	*Murina*	*eleryi*	Vietnam	PV659296
ROM	118236	167	*Harpiocephalus*	*harpia*	Laos	AJ841971
ROM	118347	168	*Murina*	*cyclotis*	Laos	AJ841973
FMNH	209658	171	*Murina*	*alvarezi*	Philippines	PV659297
FMNH	209659	172	*Murina*	*alvarezi*	Philippines	PV659298
FMNH	209660	173	*Murina*	*alvarezi*	Philippines	PV659299
FMNH	206220	174	*Murina*	*philippinensis*	Philippines	PV659300
ZMMU	S-186686	175	*Harpiola*	*isodon*	Vietnam	PV659301
ZMMU	S-186699	176	*Murina*	*chrysochaetes*	Vietnam	PV659302
ZMMU	S-186687	180	*Harpiola*	*isodon*	Vietnam	PV659303
FMNH	214117	181	*Murina*	*luzonensis*	Philippines	PV659304
FMNH	218203	182	*Murina*	*baletei*	Philippines	PV659305

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APPENDIX 2. (Continued)

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
FMNH	221990	183	*Harpiocephalus*	*harpia*	Philippines	PV659306
FMNH	222887	184	*Harpiocephalus*	*harpia*	Philippines	PV659307
FMNH	228475	185	*Murina*	*mindorensis*	Philippines	PV659308
FMNH	228476	186	*Murina*	*mindorensis*	Philippines	PV659309
FMNH	230252	187	*Harpiocephalus*	*harpia*	Philippines	PV659310
FMNH	230253	188	*Murina*	*suilla*	Philippines	PV659311
FMNH	230254	189	*Murina*	*suilla*	Philippines	PV659312
		500	*Murina*	*hilgendorfi*	Unknown	AB085733
		503	*Harpiocephalus*	*harpia*	Taiwan	GQ168918
		504	*Harpiocephalus*	*harpia*	Vietnam	GQ168923
		506	*Harpiola*	*isodon*	Taiwan	GQ168920
MNHN		507	*Murina*	*pluvialis*	India	JQ044689
MNHN		508	*Murina*	*cyclotis*	Laos	JQ044692
MNHN		509	*Murina*	*feae*	India	JQ044694
		510	*Murina*	*bicolor*	Taiwan	JQ044696
		516	*Murina*	*fanjingshanensis*	China	KT180333
		517	*Murina*	*aenea*	Malaysia	GQ168906
		518	*Murina*	*aenea*	Malaysia	GQ168907
		519	*Murina*	*bicolor*	Taiwan	GQ168919
		520	*Murina*	*bicolor*	Taiwan	GQ168921
EBDD	25753	521	*Murina*	*annamitica*	Laos	AJ841972
		522	*Murina*	*harrisoni*	Laos	AJ841974
MNHN		523	*Murina*	*cyclotis*	Cambodia	GQ168916
MNHN		524	*Murina*	*cyclotis*	Vietnam	GQ168917
		525	*Murina*	*eleryi*	China	GQ168908
		526	*Murina*	*florium*	Papua, NG	GQ168902
		527	*Murina*	*gracilis*	Taiwan	GQ168900
		528	*Murina*	*gracilis*	Taiwan	GQ168903
MNHN		529	*Murina*	*hilgendorfi*	South Korea	GQ168909
		530	*Murina*	*fanjingshanensis*	China	GQ168910
		531	*Murina*	*fanjingshanensis*	China	GQ168912
MNHN		532	*Murina*	*peninsularis*	Cambodia	GQ168911
		533	*Murina*	*puta*	Taiwan	GQ168901
		534	*Murina*	*fanjingshanensis*	China	DQ435071
		535	*Murina*	*sp*	China	EF570883
		536	*Murina*	*suilla*	Java	GQ168905
MNHN		537	*Murina*	*harrisoni*	Vietnam	GQ168913
		538	*Murina*	*harrisoni*	Vietnam	GQ168922
		539	*Murina*	*feae*	Vietnam	GQ168904
MNHN		540	*Murina*	*feae*	Cambodia	GQ168915
		542	*Murina*	*jaintiana*	India	JQ044690.1
		543	*Murina*	*rongjiangensis*	China	MF359930.1
		567	*Murina*	*sp*	Tibet	MZ540017

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APPENDIX 2. (Continued)

Institution	Accession Number	Sample ID	Genus	Species	Country	Genbank Cytb
		568	*Murina*	*sp*	Tibet	MZ540018
		569	*Harpiocephalus*	*harpia*	China	MN885881
		570	*Harpiocephalus*	*harpia*	Vietnam	MH137366
		571	*Murina*	*cyclotis*	Vietnam	MH137367
		572	*Murina*	*fanjingshanensis*	China	MF543062
		573	*Murina*	*hilgendorfi*	China	KX467598
HNHM	2007.28.2	574	*Murina*	*eleryi*	Vietnam	KT762294
ROM	111399	575	*Murina*	*eleryi*	Vietnam	KT762299
ROM	116182	576	*Murina*	*eleryi*	China	KT762303
ROM	116190	577	*Murina*	*eleryi*	China	KT762304
ROM	116199	578	*Murina*	*eleryi*	China	KT762305
ROM	116200	579	*Murina*	*eleryi*	China	KT762306
		674	*Murina*	*gracilis*	Taiwan	KJ198139
		675	*Murina*	*gracilis*	Taiwan	KJ198140
		676	*Murina*	*gracilis*	Taiwan	KJ198141
NTUM		804	*Murina*	*recondita*	Taiwan	KJ198269
NTUM		805	*Murina*	*recondita*	Taiwan	KJ198270
		806	*Murina*	*puta*	Taiwan	KJ198271
		1017	*Murina*	*puta*	Taiwan	KJ198482

APPENDIX 3. Specimens of *Murina*, *Harpiocephalus* and outgroups used in DBY analysis.

Institution	Accession #	Sample ID	Genus	Species	Country	Genbank DBY
FMNH	190763	128	*Harpiocephalus*	*harpia*	Philippines	PV659313
FMNH	190109	135	*Harpiocephalus*	*harpia*	Philippines	PV659314
FMNH	222887	184	*Harpiocephalus*	*harpia*	Philippines	PV659315
ROM	110667	25	*Harpiocephalus*	*harpia*	Laos	PV659316
ROM	116041	77	*Harpiocephalus*	*harpia*	China	PV659317
ZMMU	S-180001	110	*Harpiola*	*isodon*	Vietnam	PV659318
HNHM	2004.19.13	134	*Harpiola*	*isodon*	Taiwan	PV659319
ROM	106466	14	*Murina*	*annamitica*	Laos	PV659320
ROM	111361	51	*Murina*	*annamitica*	Vietnam	PV659321
FMNH	205411	154	*Murina*	*baletei*	Philippines	PV659322
FMNH	166429	122	*Murina*	*baletei*	Philippines	PV659323
USNM	573774	72	*Murina*	*baletei*	Philippines	PV659324
ROM	116181	90	*Murina*	*chrysochaetes*	China	PV659325
ROM	106431	11	*Murina*	*cyclotis*	Laos	PV659326
ROM	107584	19	*Murina*	*cyclotis*	Vietnam	PV659327
ROM	110720	33	*Murina*	*cyclotis*	Laos	PV659328
ROM	111375	52	*Murina*	*cyclotis*	Vietnam	PV659329
ROM	116053	80	*Murina*	*cyclotis*	China	PV659330
ROM	111286	41	*Murina*	*eleryi*	China	PV659331
ROM	106411	7	*Murina*	*eleryi*	China	PV659332
ROM	116071	84	*Murina*	*eleryi*	China	PV659333

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APPENDIX 3. (Continued)

Institution	Accession #	Sample ID	Genus	Species	Country	Genbank DBY
ROM	106477	16	*Murina*	*feae*	Laos	PV659334
ROM	106475	15	*Murina*	*feae*	Laos	PV659335
ROM	106379	2	*Murina*	*feae*	Laos	PV659336
ROM	111285	40	*Murina*	*feae*	Vietnam	PV659337
ROM	111301	45	*Murina*	*feae*	Vietnam	PV659338
ROM	106383	5	*Murina*	*fionae*	Laos	PV659339
MSB	93159	74	*Murina*	*florium*	Sulawesi	PV659340
ZMMU	S-182119	133	*Murina*	*harpioloides*	Vietnam	PV659341
ROM	107739	22	*Murina*	*harrisoni*	China	PV659342
ROM	116468	97	*Murina*	*harrisoni*	China	PV659343
FMNH	209659	172	*Murina*	*alvarezi*	Philippines	PV659344
FMNH	205827	156	*Murina*	*alvarezi*	Philippines	PV659345
FMNH	202815	142	*Murina*	*alvarezi*	Philippines	PV659346
FMNH	146890	119	*Murina*	*alvarezi*	Philippines	PV659347
ZMMU	173235	100	*Murina*	*hilgendorfi*	Russia	PV659348
FMNH	190118	140	*Murina*	*hilonghilong*	Philippines	PV659349
ROM	114938	62	*Murina*	*huttoni*	China	PV659350
ROM	114969	75	*Murina*	*huttoni*	China	PV659351
ROM	106419	8	*Murina*	*huttoni*	Laos	PV659352
ROM	116049	79	*Murina*	*leucogaster*	China	PV659353
ROM	116171	107	*Murina*	*lorelieae*	China	PV659354
FMNH	190764	115	*Murina*	*luzonensis*	Philippines	PV659355
FMNH	190766	117	*Murina*	*luzonensis*	Philippines	PV659356
FMNH	186818	114	*Murina*	*philippinensis*	Philippines	PV659357
FMNH	205834	164	*Murina*	*philippinensis*	Philippines	PV659358
ROM	118531	113	*Murina*	*shuipuensis*	China	PV659359
ZMMU	S-175150	102	*Murina*	*spG*	Vietnam	PV659360
FMNH	228475	185	*Murina*	*mindorensis*	Philippines	PV659361
ROM	117940	68	*Murina*	*suilla*	Sabah	PV659362
ZMMU	S-173249	101	*Murina*	*ussuriensis*	Russia	PV659363
ROM	110708	28	*Murina*	*walstoni*	Laos	PV659364
ROM	110719	32	*Murina*	*walstoni*	Laos	PV659365
ROM	110829	106	*Kerivoula*	*hardwickii*	Vietnam	PV659366
ROM	112857	104	*Myotis*	*ikonnikovi*	China	PV659367