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A NEW SPECIES OF *DESMALOPEX* (PTEROPODIDAE) FROM THE PHILIPPINES, WITH A PHYLOGENETIC ANALYSIS OF THE PTEROPODINI

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We describe a new species of flying fox of the genus *Desmalopex* from Mindoro Island, Philippines. Discrete and mensural morphological characters distinguish the new species from other flying foxes in Southeast Asia. The new species shares several probable morphological synapomorphies with *Desmalopex leucopterus*, including features of the pelage, patagia, dentition, and cranium, suggesting that the 2 species are closely related. We present phylogenetic analyses of mitochondrial DNA sequences, which support the taxonomic status of the new species and the recently revalidated genus *Desmalopex*. Together, *D. leucopterus* and the new species form a well-supported clade that may be sister to *Pteropus* + *Acerodon*, or perhaps more distantly related to these genera. Discovery of the new species highlights the need for continued biodiversity inventories in the Philippines, where new taxa are being discovered at a remarkable rate.

Key words: biodiversity, flying fox, fruit bat, Megachiroptera, Mindoro, taxonomy

The Philippine mammal fauna, despite being considered one of the world's highest priorities for conservation, remains poorly known in many respects (Heaney 2004; Heaney et al. 1998; Heaney and Regalado 1998). For example, new species are being discovered and described at a remarkable rate (e.g., Balete et al. 2006, 2007; Esselstyn 2007; Heaney and Tabaranza 2006; Helgen et al. 2007; Rickart et al. 2005). Many taxa are known from only a few specimens and basic aspects of their biology including distribution, abundance, and habitat preferences often are unknown (Esselstyn et al. 2004; Heaney et al. 1998). One such poorly known species, a flying fox from Mindoro Island, was 1st reported in 1998 when a synoptic account of the species' probable habitat use and conservation status was published under the name "*Pteropus* sp. A" (Heaney et al. 1998). At the time, only 1 specimen had been deposited in any natural history collection. Fortunately, during 2006, 12 additional specimens were obtained, making possible a thorough evaluation of the affinities of this putative novel species. Specimens of "*Pteropus* sp. A" (Heaney et al. 1998) closely resemble those of *Desmalopex leucopterus* (Temminck, 1853) in most features of discrete morphology; however, specimens of "*Pteropus* sp. A" are substantially smaller.

Miller (1907) removed *leucopterus* from *Pteropus* and designated it as the type and only representative of a novel genus (*Desmalopex*), based on several characters that suggested an affinity to *Pteralopex* Thomas and *Acerodon* Jourdan. Miller (1907) noted several characters of *Desmalopex* to support this designation, including the large size of the upper incisors, i2 larger than i1, P1 well developed (not deciduous), and orbits slightly upturned. Miller (1907) stated that *Pteralopex* was extreme in many of these respects, and that *Desmalopex* and *Acerodon* appeared to represent intermediates between *Pteropus* and *Pteralopex*.

Andersen (1909), having access to considerably more specimens of *Pteropus*, considered this designation unwarranted, stating that *D. leucopterus* shows no characters not exhibited by members of the *Pteropus pselaphon* group. Andersen's (1909) designation of *Desmalopex* as a junior synonym of *Pteropus* has been followed by most authors (e.g., Simmons 2005) until very recently.

Giannini et al. (in press) recently confirmed the validity of *Desmalopex* using phylogenetic analyses of nuclear DNA sequences from 3 genes. All of their analyses placed *D. leucopterus* outside *Pteropus* (sensu stricto). In their

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combined analysis, *D. leucopterus* formed a trichotomy with a monophyletic *Pteropus* + *Acerodon* and *Melonycteris*. Based on these results, Giannini et al. (in press) formally revalidated *Desmalopex*.

Herein, we formally describe "*Pteropus* sp. A" (Heaney et al. 1998) as representing a new species closely related to *D. leucopterus*, present a phylogenetic analysis of mitochondrial DNA sequences from several flying foxes from the region, and comment on the validity of the long-synonymized *Desmalopex*.

Materials and Methods

Morphological analyses.—Specimens examined in this study (Appendix I) are housed at the University of Kansas Natural History Museum (KU), Field Museum of Natural History (FMNH), Cincinnati Museum Center (CMC), United States National Museum of Natural History (USNM), Delaware Museum of Natural History (DMNH), and Philippine National Museum (PNM). All fieldwork procedures followed the animal care and use guidelines of the American Society of Mammalogists (Gannon et al. 2007).

External measurements were taken to the nearest millimeter on freshly euthanized specimens by JAE or HJDG, from the notes of field collectors, or from fluid-preserved specimens (forearm only). The following cranial and dental variables were measured to the nearest 0.1 mm by JAE or LRH with digital calipers: condylobasal length (CBL: posterior margin of occipital condyle to anterior margin of I1 at alveolus), zygomatic breadth (ZB), interorbital constriction (IOC: taken anterior to the postorbital process), mastoid breadth (MB), length of the maxillary toothrow (LMTR), and P3–M2. All toothrow measurements are alveolar.

We compared specimens of the new species to its putative sister taxon (*D. leucopterus*), sympatric members of the closely related genera *Acerodon* and *Pteropus* (*A. jubatus*, *A. leucotis*, *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*) and to 1 representative of the genus *Pteralopex* (*P. flanneryi*—Helgen 2005), which shares some morphological similarities with *Desmalopex*, especially in the dentition. We excluded *Neopteryx* Hayman and *Styloctenium* Matschie from these comparisons on the basis of their distinctive dental formulae, pigmented dentition, and facial markings (Andersen 1912; Esselstyn 2007; Miller 1907).

Molecular genetics.—We used a noncommercial guanidine thiocyanate method to extract DNA from liver and muscle tissues. Approximately 1 mm^3 of tissue was digested in 300 μl of cell lysis buffer (1 M NaCl, 0.1M Tris-Cl pH 8.0, 0.025 M ethylenediaminetetraacetic acid pH 8.0, and 0.5% sodium dodecyl sulfate) and 4–8 μl of Proteinase K at 55°C for 6–24 h. After digestion was complete, protein was precipitated out of solution by the addition of 4 M guanidine thiocyanate and 0.1 M Tris-Cl (pH 7.5) followed by vigorous mixing for 10–15 s and centrifuging (5 min at 13,000 rpm). Protein precipitate was discarded and DNA then precipitated from the supernatant by the addition of 300 μl of cold (−20°C) 100% isopropanol. The samples were gently mixed and centrifuged, as above. Isopropanol was discarded and the DNA pellet was washed in 70% ethyl alcohol. Ethanol was discarded and the samples were dried at room temperature for 10–24 h. Finally, DNA was resuspended in 0.01 M Tris-Cl (pH 8.0) and stored at −20°C.

A polymerase chain reaction was used to amplify the mitochondrial genes 12S and cytochrome *b*. To amplify 12S, we used the external primers 378F and 382R, plus the internal primers 12SARev and 317F (Ruedas and Morales 2005). Some samples were amplified using only the external primers, whereas others were amplified with 378F paired with 12SARev and 317F paired with 382R. We used these 4 primers and 3 new ones for sequencing (12SIntR: 5′ ACC GCC AAG TCC TTT GAG TT 3′; 12SIntF: 5′ GCC TAT ATA CCG CCA TCT TCA GC 3′; and 12SNstR: 5′ TRT GGA ATC TTC TGG GTG 3′). To amplify and sequence the 5′ end of cytochrome *b*, we used primers L14724 and H15275 (Sudman et al. 1994). We used Gotaq Green Master Mix (Promega Corp., Madison, Wisconsin) according to the manufacturer's instructions in a 25-μl reaction that included 100–2,000 ng of template DNA and 0.5–1.5 μl of 10 μM solutions of complementary primers. Thermal cycles consisted of an initial denaturation stage of 1 min at 94°C, followed by 30 cycles of denaturing at 94°C for 30 s, annealing at 54–55°C for 30 s, and extension at 72°C for 40 or 90 s (depending on the length of the fragment to be amplified). Polymerase chain reaction was completed with a final extension cycle at 72°C for 7 min. Amplification was verified by electrophoresis of 5 μl of polymerase chain reaction product on a 1% agarose gel stained with ethidium bromide. Products were photographed under ultraviolet light. Successfully amplified fragments were cleaned by adding 1 μl of a 20% dilution of Exo-Sap It (USB Corp., Cleveland, Ohio) and incubating at 37°C for 31 min, followed by 80°C for 15 min. Cleaned polymerase chain reaction products were cycle sequenced in a 10-μl reaction for both strands with a Big Dye Terminator 3.1 kit (Perkin-Elmer, Boston, Massachusetts) following the manufacturer's instructions. Thermal cycles were as follows: 95°C for 2 min, followed by 25 cycles of 95°C for 15 s, 50°C for 15 s (50–56°C for primers 12SARev and 382R), and 60°C for 4 min. Cycle sequencing products were cleaned using Sephadex Medium (GE Healthcare, Uppsala, Sweden) according to the manufacturer's instructions. Automated sequencing was completed on an ABI 3130*xl* (Applied Biosystems, Foster City, California).

We sought to include multiple species of *Pteropus*, at least 1 species each of *Acerodon* and *Pteralopex*, and both species of *Desmalopex* in order to test the validity of the putative new species as well as the relationship between *Desmalopex* and other genera of flying foxes. We obtained previously published sequences for relevant taxa from GenBank (Appendix II); because we had access to tissue samples from most of the relevant Philippine taxa, we did not use any GenBank sequences for ingroup taxa that originated from Philippine specimens. We deposited all new sequences generated by this study in the same database (Appendix II).

Phylogenetic analyses.—Sequences were edited and complementary strands aligned using Sequencher 4.5 (Genecodes, Ann Arbor, Michigan). Homologous sequences were aligned

using the default settings in MUSCLE 3.6 (Edgar 2004) and examined manually in Se-Al 2.0a11 (Rambaut 1996). Final alignments consisted of cytochrome-*b* sequences of 310–523 nucleotides and 12S sequences of 677–1,139 nucleotides. Variation in sequence length was due primarily to variation in the length of available sequences in GenBank, but also to our failure to amplify the 5′ end of 12S in 3 specimens of *Pteropus*. Gaps and missing data were treated as missing data in all phylogenetic analyses.

We used Akaike information criterion as implemented in MODELTEST 3.7 to select models of sequence evolution (Posada and Buckley 2004; Posada and Crandall 1998). We estimated phylogenetic relationships using maximum-likelihood and Bayesian approaches. Likelihood analyses were conducted using GARLI v0.951 (Zwickl 2006). We ran separate likelihood analyses on cytochrome *b* and 12S (both under GTR + I + G models of sequence evolution), as well as a combined Bayesian analysis. Topology searches in GARLI were conducted using 10 runs of 10,000 generations for each analysis. All model parameters were estimated during the topology search. Support for resulting clades was estimated by performing 100 bootstrap pseudoreplicates on each data set. The combined analysis was conducted in MrBayes 3.1 (Huelsenbeck and Ronquist 2001) with sequences partitioned by gene. The GTR + I + G model was applied to each gene and parameter estimates were allowed to vary independently for each partition. Our Bayesian analysis incorporated 4 runs with 4 chains each and was run for 3×10^6 generations. Trees were sampled every 1,000 generations and the first 1,000 samples were discarded as burn-in. Gaps were treated as missing characters in all analyses. We rooted our trees with *Cynopterus*, and included other non-pteropodine fruit bats (*Rousettus*, *Eonycteris*, and *Dobsonia*) because of their position relative to *Pteropus* in the phylogenetic hypotheses of Giannini et al. (in press) and Giannini and Simmons (2003, 2005). For the combined analysis, we concatenated cytochrome-*b* and 12S sequences from different species or specimens within *Dobsonia*, *Rousettus*, and *Cynopterus* (Appendix II).

Results

Morphological description.—On the basis of the morphological and genetic features summarized in the following sections, we document ''*Pteropus* sp. A'' (Heaney et al. 1998) as a distinct, undescribed species. The new species closely resembles *D. leucopterus* in most of the features of discrete morphology that we examined. However, it is substantially smaller than *D. leucopterus*, and differs in many subtle respects. Several probable synapomorphies described below imply a close relationship between these 2 species.

Desmalopex microleucopterus, new species

Holotype.—Adult male (PNM 5202; original field number J. A. Esselstyn 524; Figs. 1 and 2) captured 21 February 2006, originally fixed in 10% buffered formalin and subsequently stored in 70% ethyl alcohol. The skull has been removed and cleaned. An aliquot of liver was taken from the freshly euthanized animal and preserved in 95% ethyl alcohol, before being stored at −70°C.

Type locality.—Mount Siburan, Batong Buhay, Sablayan, Occidental Mindoro, Mindoro Island, Philippines, approximately 100 m above sea level (12.8348°N, 120.9302°E).

Paratypes.—Twelve additional specimens are known. Eleven of these were taken at the type locality (KU 164496, 164497, 164500; FMNH 190693, 190694, 190696, 190698–190701; PNM 5203); the 12th was taken in Mindoro Oriental, on Mt. Halcon at 725 m (FMNH 142577). FMNH 190696 consists of a skin and skeleton. All other paratypes are fluid specimens. The skulls have been removed and cleaned from all 3 KU paratypes, PNM 5203, and FMNH 190699 and 190700. All KU and PNM paratypes are adults, as are FMNH 142577, 190696, 190699, and 190700. FMNH 190693, 190694, 190698, and 190701 are subadults.

Distribution.—*Desmalopex microleucopterus* is probably endemic to Mindoro Island. It is known from 2 localities on the island, and may occur in additional areas that retain secondary or primary lowland forest. The 2 areas from which it has been recorded are approximately 100–450 and 725 m above sea level (see ''*Ecology*,'' below). The species is likely found in suitable habitats at intervening elevations.

Etymology.—The specific epithet refers to the small size of the new species relative to *D. leucopterus*, and its discrete morphological similarity and close relationship to *D. leucopterus*. We follow Heaney et al. (1998) and recommend Mindoro pallid flying fox as the English common name.

Diagnosis.—*Desmalopex microleucopterus* is a small, pale brown flying fox with mottled wings (Fig. 3). The species closely resembles *D. leucopterus* in most external, cranial, and dental characters, but is markedly smaller (Table 1; Fig. 1).

The pelage of *D. microleucopterus* is rather uniform in color, being slightly darker at the base of the hairs than near the tips and somewhat darker overall than is that of *D. leucopterus*. The distinction between the pale tips of hairs and darker bases is less apparent in the new species than in *D. leucopterus*, the hairs of which are cream at their tips on the dorsum. The legs of both species are moderately haired on their dorsal surfaces, but naked on the ventral side. There is dense, adpressed hair on the dorsal surface of the proximal two-thirds of the forearm. The pelage of both species is woolly throughout, but thicker and longer on the dorsum (most hairs > 10 mm in suprascapular region in *D. microleucopterus*) than on the venter (4- to 5-mm-long underfur with guard hairs reaching 11 mm in *D. microleucopterus*). The patagia of *D. microleucopterus* are medium brown and mottled with pale spots; those of *D. leucopterus* are similar, but somewhat paler. The brown areas of the patagia are more heavily pigmented, and thus less translucent, in *D. microleucopterus* than in *D. leucopterus*. The ears of *D. microleucopterus* are typically cream at the base and darken gradually to brown-gray at the margin. However, KU 164497 has ears that are predominately cream, with brown mottling, and a typically dark margin. The ears of *D. leucopterus* are similar in color to the common pattern in *D. microleucopterus*.

The dental formula for the 2 species is i 2/2, c 1/1, p 3/3, m 2/3, total 34. We follow Andersen (1912) and Giannini and Simmons

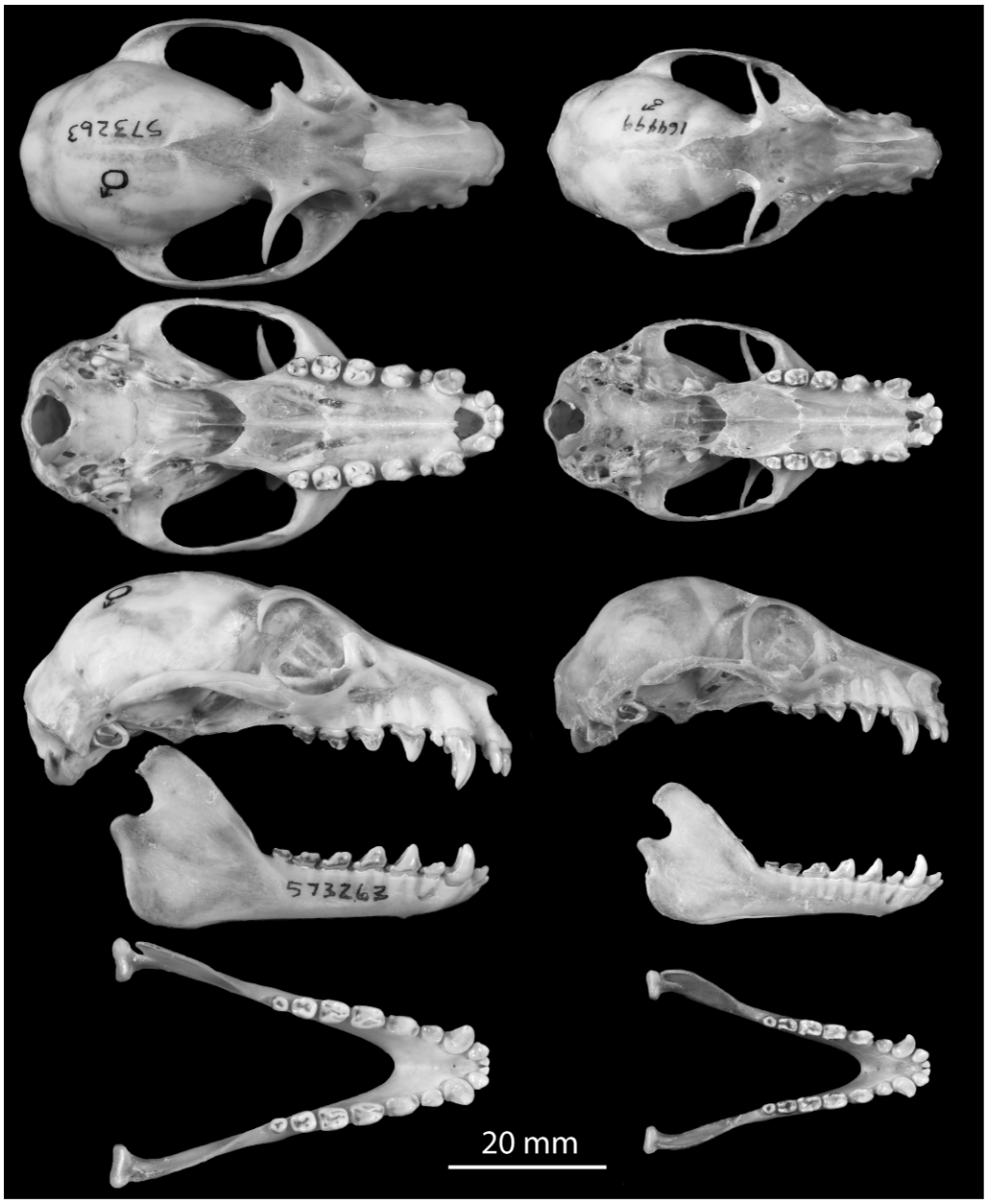

Fig. 1.—Photographs of the crania and mandibles of *Desmalopex leucopterus* (USNM 573263; left) and the holotype of *D. microleucopterus* (PNM 5202; right). From top to bottom: dorsal, ventral, and lateral views of crania and lateral and dorsal views of the mandibles.

(2007) in assuming that the upper teeth represent I1, I2, C1, P1, P3, P4, M1, and M2 and the lower i1, i2, c1, p1, p3, p4, m1, m2, and m3. In addition to the substantial difference in size between the 2 species (this and several characters listed below are visible in Figs. 1 and 2), the following diagnostic characters are offered, with contrasting features of *D. leucopterus* noted in parentheses: dentition relatively small (relatively large: the difference is most pronounced in P1; Fig. 1); a rudimentary, anterolingual cingulum on p3 (anterolingual cingulum well developed, forming a small shelf); p3 with a subtle to moderately well-developed lingual cusp inferior to the labial cusp (no secondary cusp in USNM 573263 and 574789 or DMNH 4500 and 4501, but a very small cusp in FMNH 140635 and USNM 356608); p4 with labial and lingual cusps subequal (labial more prominently superior to lingual); cusps on m1–3 somewhat less prominent (more prominent); cusps on P3–M2 less prominent (more prominent); toothrows more convergent anteriorly (toothrows relatively parallel); upper incisors form an arched row (row of incisors straighter); region of orbitosphenoid between optic canal and sphenoidal fissure narrow and thin (wide and thick); ossification between ectotympanic and basicranial region heavier (less ossified); ectopterygoid process prominent (small); hamulus pterygoideus more elevated (low and inconspicuous); degree of basicranial inflection somewhat less (greater degree of inflection; Fig. 1); mandibular notch more deeply incised (shallower incision; Fig. 1); and posterior margin of ramus between mandibular condyle and angular process more deeply incised (posterior margin entire; Fig. 1).

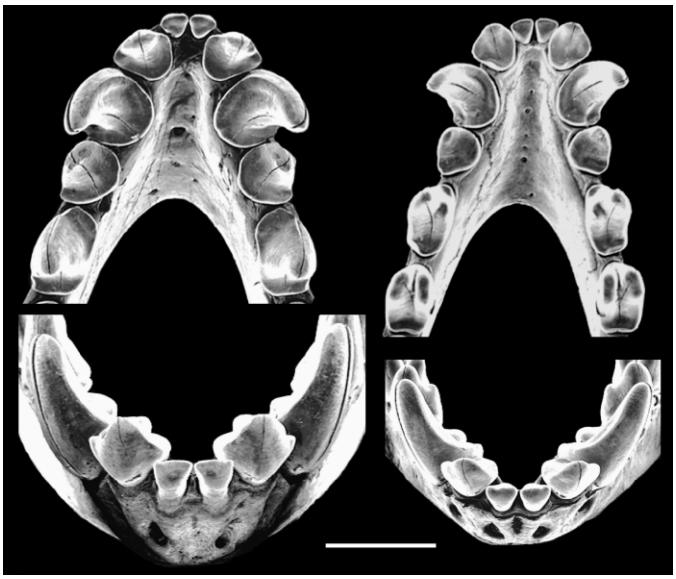

Fig. 2.—Scanning electron micrographs showing the lower incisors, canines, and anterior premolars of *Desmalopex leucopterus* (FMNH 140635; left) and the holotype of *D. microleucopterus* (PNM 5202; right). The upper images provide a dorsal view; the lower view is anterior. The scale bar represents 15 mm in FMNH 140635 and 10 mm in PNM 5202.

Fig. 3.—Photographs of *Desmalopex microleucopterus* (left) and *D. leucopterus* (right). Photograph of *D. microleucopterus* was taken by MGS. The specimen of *D. leucopterus* was captured on Catanduanes Island in 1991 and held in captivity at the Center for Tropical Conservation Studies, Silliman University. The photograph was taken by LRH in 1992. Images not to same scale.

Description.—Desmalopex microleucopterus is a small, pale brown flying fox with mottled wings (Fig. 3). The species shows little to no sexual dimorphism in size or color. *D. microleucopterus* is much smaller than *D. leucopterus*; there is no overlap in the ranges of cranial and external measurements (Table 1). These 2 species are paler than species of *Pteropus* known from the region, save *P. pumilus*. The wing membranes of *D. microleucopterus* attach to the sides of the back; on the foot, they attach between the 1st and 2nd digits. The feet are dark brown with sparse hair. On the face, the vibrissae are sparse; those of the muzzle are short (5–8 mm) relative to those found over the eyes ($\leq$15 mm). Relatively dense, short vibrissae (5–8 mm) are present on the chin. The rhinarium is similar in color to the hair of the face and the nostrils are anterolaterally oriented, but not elongate.

Pteropus pumilus is similar in size to *D. microleucopterus*, but its patagia are entirely pale and translucent, lacking the prominent melanin spotting noted in *D. leucopterus* and *D. microleucopterus*; its legs are less hirsute; and the supra-scapular region, head, and neck are much paler than the rest of the body, whereas specimens of both species of *Desmalopex* are rather uniform in color.

Cranially, *D. microleucopterus* and *D. leucopterus* differ from *P. dasymallus*, *P. hypomelanus*, *P. pumilus*, *A. jubatus*, *A. leucotis*, and *P. flanneryi* in the following ways: i2 larger than i1 (Fig. 2; this feature is more prominent in *P. flanneryi*, less prominent in *A. jubatus* and *A. leucotis*; i1 and i2 subequal in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); i2 bifid with medial cusp superior to lateral cusp (Fig. 2; in *P. flanneryi*, ridges that descend from height of incisor slightly serrated; i2 indistinctly bifid in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*, more prominently so in *A. jubatus* but cusps approximately equal in height); i2 possesses a broad, posterior surface that descends from the cutting edge to the posterior margin of the tooth in the new species, *D. leucopterus* (Fig. 2), and *P. flanneryi* (in all other specimens examined, i2 lacks this broad, posterior surface); c1 with prominent, basal shelf on posterior and lingual sides of the tooth (Fig. 2; in *P. flanneryi* the shelf is similar; in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus* the shelf is less prominent, but in the same position; in *A. jubatus* the shelf is less prominent, and entirely posterior, with the lingual side superior to the labial); p1 relatively robust (Fig. 2; similar in relative size to that of *P. flanneryi*; relatively smaller in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); p3 with a subtle secondary cusp, lingual to the superior, labial cusp in the new species and *Pteropus*, but lacking in 2 of 3 specimens of *D. leucopterus* (Fig. 2; secondary cusp more prominent in *A. jubatus*, *A. leucotis*, and *P. flanneryi*); upper incisors relatively large (similar in *P. flanneryi*; substantially less robust in *A. leucotis*, *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); upper incisors with posterior cingula forming a shelf (shelf less substantial in *P. dasymallus*; lacking in *A. leucotis*, *P. hypomelanus*, and *P. pumilus*; in *P. flanneryi*, shelf more prominent, with a secondary cusp on the medial, posterior margin of I2); P1 relatively robust in *D. leucopterus*, somewhat less in *D. microleucopterus* (similar in *P. flanneryi*; varies from a spicule to absent in *A. jubatus*, *A. leucotis*, *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); M2 quadrate in occlusal outline and moderately cuspidate (cusp prominence and shape similar in *A. jubatus*, more prominent in *P. flanneryi*; M2 round in cross section with relatively flat occlusal surface in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); rostrum broad (similar in *A. jubatus* and *A. leucotis*; broader in *P. flanneryi*; more gracile in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*); degree of basicranial inflection great (similar in *P. flanneryi*; less pronounced in all other species examined); and postorbital process prominent, either attaching to, or approaching the zygomatic arch (postorbital process more prominent in *P. flanneryi*; stout, but not approaching zygomatic

Table 1.—External, cranial, and dental measurements of adult specimens of *Desmalopex microleucopterus* and *D. leucopterus* taken in millimeters. Mass is given in grams. Abbreviated variables are defined in the text. Upper values are means, middle values are ranges, and lower values are sample size.

Taxon	CBL	ZB	IOC	MB	LMTR	P3–M2	Total length	Hind foot	Forearm	Mass
D. microleucopterus	46.64	26.30	7.90	16.39	17.33	12.73	143.3	31.1	99.8	143.3
	45.8–48.4	25.3–27.3	7.5–8.2	15.8–16.9	16.4–17.8	12.2–13.1	133–155	29–34	97–103	129–156
	9	9	9	9	9	9	6	7	9	7
D. leucopterus	58.70	34.28	9.37	20.50	22.16	16.32	204.6	46.4	139.0	306.85
	57.8–60.8	33.2–35.4	8.8–10.3	19.8–21.5	21.2–22.7	15.9–16.7	185–215	44.5–49	135–145	250–375
	5	5	6	5	5	5	5	5	3	5

arch in *A. jubatus* and *A. leucotis*; and less prominent in *P. dasymallus*, *P. hypomelanus*, and *P. pumilus*).

Ecology.—We studied the ecology of *D. microleucopterus* in the vicinity of Mt. Siburan, Occidental Mindoro in 2002 and 2006, within the jurisdiction of the Sablayan Prison and Penal Farm at approximately 12.80°N, 120.92°E.

On 2 days in June 2002, HJDG and MGS sampled fruit bats using four 12-m mist nets in an area of about 2 ha on Mt. Siburan. The area averaged 360 m elevation on a mix of gentle and steep slopes where slash-and-burn farming was practiced by indigenous people and prisoners and their families. Rice paddies covered most areas along streams, and bamboo thickets were common in agricultural areas. Remnants of lowland forest, dominated by trees of the family Dipterocarpaceae, retained some large trees (height up to 20 m and diameter at breast height of 900–1,200 mm), especially on steep hillsides, but the forest had been heavily degraded by logging. We captured 51 fruit bats belonging to 5 species: *Cynopterus brachyotis* ($n = 2$), *D. microleucopterus* ($n = 4$), *Eonycteris spelaea* ($n = 1$), *Ptenochirus jagori* ($n = 42$), and *P. pumilus* ($n = 2$).

During February 2006, JAE sampled the edge of selectively logged lowland forest and an adjacent agricultural area with a few guava trees. The area was approximately 100 m above sea level. In 32 net-nights (12 m of net for 1 night = 1 net-night), 70 pteropodids representing 9 species were captured: *C. brachyotis* ($n = 13$), *D. microleucopterus* ($n = 5$), *E. spelaea* ($n = 4$), *Haplonycteris fischeri* ($n = 3$), *Macroglossus minimus* ($n = 2$), *P. jagori* ($n = 28$), *P. pumilus* ($n = 3$), *Rousettus amplexicaudatus* ($n = 8$), and *Styloctenium mindorensis* ($n = 4$—Esselstyn 2007).

In June–July 2006, HJDG sampled on another part of Mt. Siburan at elevations from 100 to 450 m in an area with a similar mixture of slash-and-burn farms and secondary forest that included dipterocarps, *Macaranga*, figs (*Ficus*), Moracea, Myrtaceae, and *Dillenia*, as well as domestic and wild banana (*Musa*). *D. microleucopterus* was captured at 8 out of 16 netting sites, including the lowest and highest sites and in all habitat types sampled; most specimens were captured in disturbed forest or shrubby areas, not in primary forest or open agricultural sites. In a total of 215 net-nights (6 m of net for 1 night = 1 net-night), 206 individuals of 8 species of pteropodids were captured: *C. brachyotis* ($n = 55$), *D. microleucopterus* ($n = 16$), *E. spelaea* ($n = 12$), *M. minimus* ($n = 6$), *P. jagori* ($n = 102$), *P. pumilus* ($n = 12$), *R. amplexicaudatus* ($n = 1$), and *S. mindorensis* ($n = 2$). Examination of fecal material produced by *D. microleucopterus* showed the presence of seeds of *Ficus* (Moraceae), a species of Melastomataceae, and *Musa balbisiana* (Musaceae).

Examination of these data shows that *D. microleucopterus* is a member of a fruit bat community that is characteristic of disturbed lowland forest in other parts of the Philippines (e.g., Heaney et al. 1989, 1999; Heideman and Heaney 1989; Rickart et al. 1993), in which *P. jagori* is abundant and *P. pumilus* is present, and species that are common in open areas away from forest (*C. brachyotis*, *E. spelaea*, *M. minimus*, and *R. amplexicaudatus*) are uncommon to moderately abundant.

Little forest remains at low elevation on Mindoro (Custodio et al. 1996; Environmental Science for Social Change 1999; Kummer 1992), thus *D. microleucopterus* may be threatened by habitat loss. Flying foxes are hunted in the Philippines and this also may be a factor affecting the conservation status of *D. microleucopterus*. The roosting habits of this species are not known.

Phylogeny estimation.—Our phylogenetic analyses further support the designation of *D. microleucopterus* as a new species and the generic status of *Desmalopex*. Uncorrected genetic divergence between *D. microleucopterus* and its sister taxon, *D. leucopterus*, is estimated at 2.5% and 1.5% in cytochrome-*b* and 12S sequences, respectively. These levels of divergence are not great; however, together with the topology of the preferred tree, they do suggest that the 2 species represent independently evolving, monophyletic lineage segments.

All of our analyses recovered *Desmalopex* as a distinct clade not associated with *Pteropus* (Figs. 4 and 5). Our analysis of 12S sequences placed *Desmalopex* in a basal polytomy with *Cynopterus*, *Dobsonia*, and *Pteropus* + *Acerodon* + *Pteralopex* + *Rousettus* (Fig. 4A). The cytochrome-*b* data set resulted in a best tree that placed *Desmalopex* as the sister to *Acerodon* + *Pteropus* (Fig. 4B). In this tree, *Acerodon* nested within *Pteropus*, but the monophyly of this group was not well supported. Many of the deeper nodes in the 12S and cytochrome-*b* phylogenies are unresolved or receive low support. Despite the lack of resolution in these portions of the phylogenies, *Desmalopex* forms a monophyletic clade with 100% bootstrap support in both analyses. Our partitioned Bayesian analysis improved the resolution and support for some of the deeper nodes in the tree, particularly for the *Pteropus* + *Acerodon* clade (Fig. 5). In this analysis, *D. leucopterus* and *D. microleucopterus* were placed in a

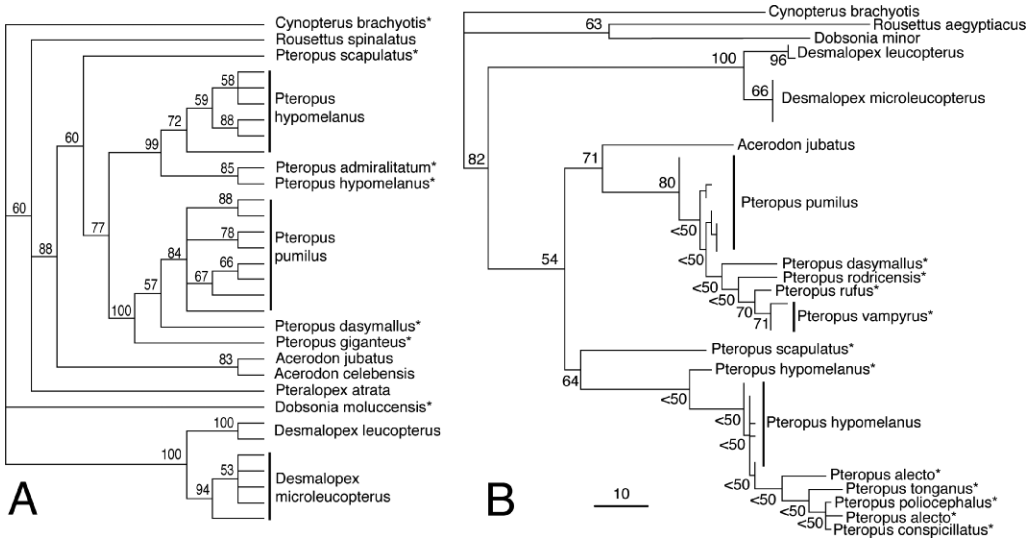

FIG. 4.—Results of maximum-likelihood analyses of mitochondrial DNA sequences: A) a majority-rule consensus tree resulting from analysis of 12S sequences; B) a maximum-likelihood phylogram resulting from analysis of cytochrome-*b* sequences. Numbers at the nodes represent bootstrap support values. Terminal labels marked with an asterisk represent unvouchered sequences we obtained from GenBank.

basal trichotomy with *Pteropus* + *Acerodon* and *Pteralopex*. *Desmalopex* was again well supported with 100% posterior probability (Fig. 5).

Our phylogenetic analyses imply that *Pteropus alecto*, *P. hypomelanus*, *P. pumilus*, and *P. scapulatus* are each paraphyletic or polyphyletic (Figs. 4 and 5). Although this may be due to missing characters in our combined data set, we suspect at least some cases are due to misidentifications of unvouchered specimens. Because most of the sequences we obtained from GenBank lack voucher information, we are unable to verify the sources of these sequences (Appendix II).

DISCUSSION

Biogeography and conservation.—A previous study of the biogeography of Philippine fruit bats listed Mindoro as having 10 known species, none of which are endemic, but considered the Mindoro fauna to be too poorly known to include in analyses (Heaney 1991). With the recent discovery of *D. microleucopterus* and *S. mindorensis* (Esselstyn 2007), 17% (2 of 12 species) of the island's pteropodid fauna is endemic, giving it a higher percentage of endemic species than any other Philippine island included in Heaney's (1991:153, table 3) comparisons. The correlation between species and island area provided by Heaney (1991: fig. 3) predicts that 13 species would be present on Mindoro. We note that 2 widespread species, *P. hypomelanus* and *Eonycteris robusta*, have not yet been reported from Mindoro; if they are found, Mindoro would have one of the richest pteropodid faunas, relative to island area, of any island in Indo-Australia. Mindoro should, accordingly, be recognized as an important subcenter of pteropodid diversity. However, the absence of records of widespread forms and the recent discovery of *D. microleucopterus* and *S. mindorensis* suggest that Mindoro's mammal fauna remains incompletely known and emphasizes the need for comprehensive surveys.

The documentation of 2 new pteropodids from Mindoro plus the recent recognition of an endemic species of *Dyacopterus* (Helgen et al. 2007) raises total Philippine pteropodid diversity to 26 species (including 1 putative species of *Haplonycteris* that has not been formally described), with 17 (65%) endemic to the archipelago (Heaney et al. 1998). These are among the highest levels of species richness and endemism for the family in any part of its range. If we assume that Andersen's (1912) *pselaphon* group (excluding *leucopterus*) belongs within *Pteropus*, then *Desmalopex* joins *Alionycteris*, *Haplonycteris*, *Otopteropus*, and *Ptenochirus* as genera endemic to the Philippines, and *Desmalopex* joins the list of 3 or 4 pteropodid clades in which speciation has taken place within the Philippines, raising to at least 8 (31%) the number of species that probably have arisen through speciation within the archipelago (Heaney 1991; Heaney and Rickart 1990). Clearly, the Philippines is a center of both diversity and diversification, with Mindoro playing a significant role in the pattern.

Much of this remarkable diversity is in need of conservation efforts, primarily through the protection of remaining forest habitats and the rehabilitation of others. Overhunting is an important issue for some species of pteropodids, especially large taxa that roost in colonies (Heaney et al. 1997; Mildenstein et al. 2005; Stier and Mildenstein 2005; Utzurrum 1992). Species that are dependant on relatively undisturbed forest and roost in large colonies are especially vulnerable.

Phylogenetic relationships.—Phylogenetic relationships among pteropodine genera are largely unknown, due in part to difficulties in obtaining tissue samples of several rarely collected taxa. Although no phylogenetic analyses have achieved comprehensive taxonomic sampling, some consistent patterns have emerged. For example, our phylogenetic estimates provide independent confirmation of the conclusion

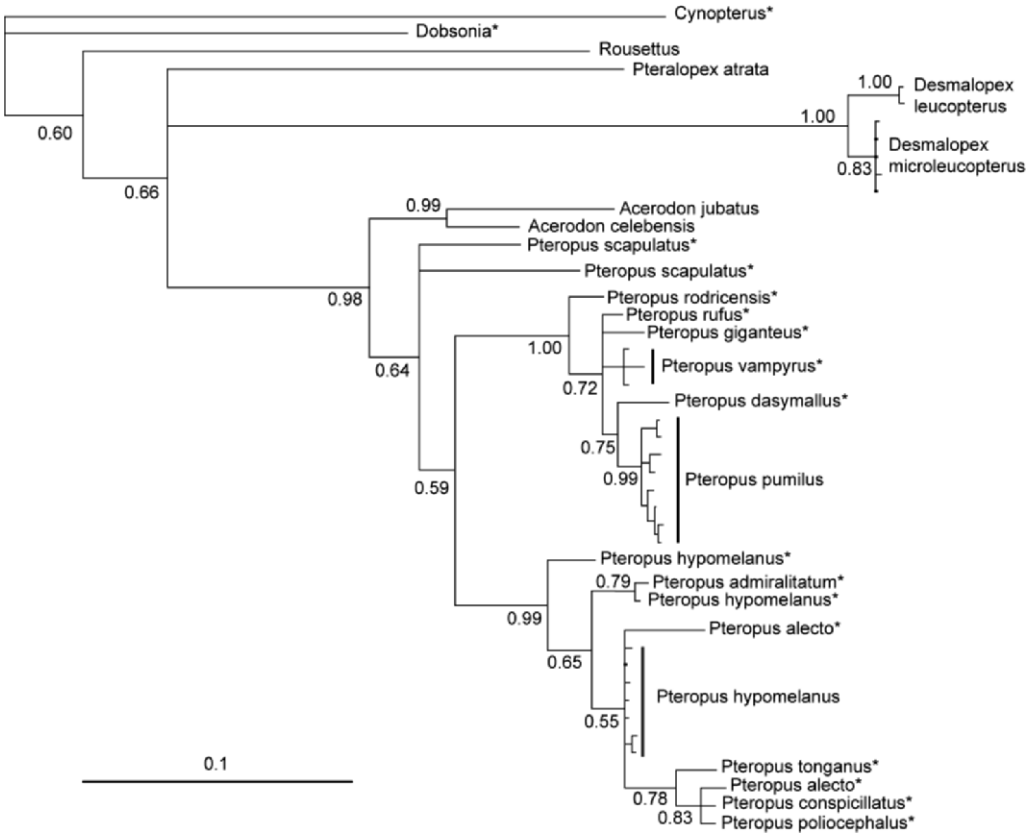

FIG. 5.—Majority-rule consensus tree resulting from a partitioned Bayesian analysis of cytochrome-*b* and 12S sequences. Numbers at the nodes represent posterior probabilities. Posterior probabilities from nodes below the species level have been removed for clarity of presentation. Terminal labels marked with an asterisk represent unvouchered sequences we obtained from GenBank.

of Giannini et al. (in press) that *Desmalopex* does not belong in *Pteropus*. Giannini et al. (in press) found *D. leucopterus* in a trichotomy with *Melonycteris* and *Acerodon* + *Pteropus*. Our analyses of mitochondrial DNA sequences placed *D. microleucopterus* and *D. leucopterus* as closely related sister-species forming a highly supported clade in the basal portions of the pteropodine phylogeny (Figs. 4 and 5).

BUOD

Isang bagong uriin ng paniki sa angkan ng *Desmalopex* ang inilalarawan galing sa pulo ng Mindoro, Pilipinas. Ang natatangi at ang panukat na morpolohiyang katangian nito ang siyang naging batayan upang ito ay ibukod sa ibang bagong uriin na malalaking paniki sa timog-silangang Asya. Ang bagong uriin na paniking ito ay mayroong mga katangian na kahalintulad sa *Desmalopex leucopterus*, kabilang na dito ang mga balahibo, patagia o ang balat na naturingang pakpak, ngipin at bungo, na nagmumungkahing ang dalawang paniking ito ay malapit na magka-uri. Ipinapakita namin ang phylogenetic na pagsusuri ng magkakasunod-sunod na mitochondrial DNA (mtDNA) na siyang nagpapatunay ng taxonomic status ng bagong uriin ng paniking ito at nagbibigay suporta sa kailan lamang na itinaas na angkang *Desmalopex*. Ang magkasamang *D. leucopterus* at ng bagong uriin ng paniking ito ay bumubuo ng isang ganap na suportadong grupo na isa lamang ang pinagmulang ninuno, na maaring kapatid na uri o malayong kamag-anak ng pinagsamang angkang *Pteropus* at *Acerodon*. Ang pagtuklas ng isang bagong uriin ng hayop sa Pilipinas ay nagbibigay diin upang ipagpatuloy ang mga pag-aaral ng mga natatanging buhay-ilang nito, kung saan kapuna-puna ang tulin ng pagtuklas ng mga bagong grupo ng buhay.

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APPENDIX I

The following specimens were included in our morphological comparisons. Collection locality and museum catalog numbers are given for each specimen. Museum acronyms are defined in the ''Materials and Methods.''

Acerodon jubatus ($n = 4$).—Philippines, Negros Island, Negros Oriental, Amio, Pamo-At (FMNH 65463); Philippines, Manila (KU 2092, 2093); Philippines, Mindanao Island, Sarangani (CMC 3116).

Acerodon leucotis ($n = 2$).—Philippines, Palawan, Busuanga Island, Busuanga, Singay (FMNH 63738); Palawan, Tara Island (CMC 2822).

Desmalopex leucopterus ($n = 7$).—Philippines, Catanduanes Island, Gigmoto, 1 km S, 600 m (FMNH 140635); Gigmoto, 1 km N, 8.5 km W, Buadan River, 200 m (USNM 573263); Philippines, Luzon Island, Cagayan, Baggao, Barrio Via, Sitio Hot Springs, W Foothills Sierra Madre Mts., 110 m (USNM 574789); Luzon Island, Quezon, Real, Kinanliman (USNM 356608); Luzon Island, Cavite, Mt. Palay Palay, Ternate (PNM 5181); Surigao del Norte, Dinagat Island, Loreto, Cambinliw (DMNH 4500, 4501).

Desmalopex microleucopterus ($n = 13$).—Philippines, Mindoro Island, Mindoro Oriental, Mt. Halcon, 725 m (FMNH 142577); Mindoro Island, Occidental Mindoro, Sablayan, Mt. Siburan, Batong Buhay, 12.8348°N, 120.9302°E, approximately 100 m (PNM 5202, 5203; KU 164496, 164497, 164500); Batong Buhay, Palbong (FMNH 190693, 190694, 190696, 190698–190701).

Pteralopex flanneryi ($n = 1$).—Solomon Islands, Isabel Island, Tunnibuli (FMNH 31561).

Pteropus dasymallus ($n = 2$).—Japan, Ryukyu Islands, Yayeyama Group, Ishigake Island, Kabi, 800 m (FMNH 47264); Philippines, Cagayan, Babuyan Islands, Babuyan Claro Island, Ayumit (PNM 5148).

Pteropus hypomelanus ($n = 7$).—Philippines, Cagayan, Babuyan Islands, Calayan Island, Calayan, Magsidel, Macarra, 19.294°N, 121.409°E, near sea level (KU 164094–164098); Calayan Island (KU 164099, 164100); Philippines, Palawan, Cuyo Island, Cuyo, Centro (FMNH 63745).

Pteropus pumilus ($n = 11$).—Philippines, Mindoro Island, Occidental Mindoro, Paluan, Harrison, Ulasan, 13.4466°N, 120.4259°E, 170 m (KU 165250–165255); Occidental Mindoro, Sablayan, Mt. Siburan, Batong Buhay, 12.8348°N, 120.9302°E, approximately 100 m (KU 164501–164503); Philippines, Negros Island, Negros Oriental, Mt. Talinis, 750 m (FMNH 142830); Mt. Talinis, 1,250 m (FMNH 142831).

APPENDIX II

Summary of taxa, specimen vouchers, and GenBank accession numbers for sequence data used in phylogenetic analyses. Information is provided for each species in the following order: country or island from which sample originated, museum acronym and catalog number of voucher specimens, and GenBank accession numbers (cytochrome *b*/12S). Specimens from the following institutions are included: University of Kansas Natural History Museum (KU); Field Museum of Natural History (FMNH); University of California at Berkeley,

Museum of Vertebrate Zoology (MVZ); Cincinnati Museum Center (CMC); United States National Museum (USNM); Utah Museum of Natural History (UMNH); Australian Museum (AM); American Museum of Natural History (AMNH); and Philippine National Museum (PNM). Tissue samples for specimens reported here with USNM and UMNH catalog numbers are archived at FMNH. Many of the sequences we obtained from GenBank lack voucher numbers, collection locality information, or both. We have verified the identification of specimens at KU, FMNH, and CMC only. Superscript numerals following GenBank accession numbers refer to the publication that originally reported the sequence.

Acerodon celebensis.—Indonesia: AM 27199 (none/U93071)[3].

Acerodon jubatus.—Philippines: CMC 3116 (EU330962/EU339322)[1].

Cynopterus brachyotis.—Philippines: USNM 573490 (AY922615/none)[10]. Malaysia: no voucher (none/EF139867)[6].

Desmalopex leucopterus.—Philippines: USNM 573263 (EU330964/EU339324)[1]; USNM 573264 (EU330965/EU339325)[1].

Desmalopex microleucopterus.—Philippines: PNM 5202 (EU330979/EU339338)[1]; PNM 5203 (EU330978/EU339337)[1]; KU 164496 (EU330976/EU339335)[1]; KU 164497 (EU330977/EU339336)[1]; KU 164500 (EU330982/EU339339)[1].

Dobsonia minor.—Papua New Guinea: MVZ 140208 (DQ445705/none)[2].

Dobsonia moluccensis.—Unknown: no voucher (none/U93065)[3].

Pteralopex atrata.—Guadalcanal: AM 19219, 19220 (none/U93069)[3].

Pteropus admiralitatum.—Unknown: no voucher (none/U93072)[3].

Pteropus alecto.—Australia: no voucher (AF144065/none)[5]. Unknown: no Voucher (DQ019615/None)[12].

Pteropus conspicillatus.—Unknown: no voucher (DQ019616/none)[12].

Pteropus dasymallus.—Okinawa: no voucher (NC_002612/NC_002612)[9].

Pteropus giganteus.—Unknown: no voucher (none/AY012138)[8].

Pteropus hypomelanus.—Philippines: FMNH 135671 (EU330968/EU339328)[1]; FMNH 135672 (EU330969/EU339329)[1]; FMNH 142475 (EU330972/EU339332)[1]; FMNH 150861 (EU330973/none)[1]; KU 164094 (EU330983/EU339342)[1]; KU 164095 (EU330984/EU339343)[1]; USNM 458447 (EU330963/EU339323)[1]. Malaysia: no voucher (DQ097823/none)[6]; no voucher (EF105539/none)[6]; no voucher (EF105540/none)[6]. Unknown: no voucher (none/U93073)[3].

Pteropus poliocephalus.—Unknown: no voucher (DQ019614/none)[12].

Pteropus pumilus.—Philippines: FMNH 135673 (EU330970/EU339330)[1]; FMNH 135674 (EU330971/EU339331)[1]; KU 164501 (EU330980/EU339340)[1]; KU 164502 (EU330981/EU339341)[1]; KU 165253 (EU330974/EU339333)[1]; KU 165254 (EU330975/EU339334)[1]; UMNH 28664 (EU330967/EU339327)[1]; USNM 573466 (EU330966/EU339326)[1].

Pteropus rodricensis.—Unknown: no voucher (AF044655/none)[4].

Pteropus rufus.—Madagascar: no voucher (AB085732/none)[11].

Pteropus scapulatus.—Unknown: no voucher (AF321050/AF321050)[7]. Unknown: no voucher (DQ019613/none)[12].

Pteropus tonganus.—Unknown: no voucher (AF044656/none)[4].

Pteropus vampyrus.—Malaysia: no voucher (DQ097824/none)[6]; no voucher (DQ097828/none)[6]; no voucher (DQ097829/none)[6].

Rousettus aegyptiacus.—Mozambique: AMNH 117335 (DQ445714/none)[2].

Rousettus spinalatus.—Malaysia: no voucher (EF139884/none)[6].

[1] This study.
[2] Giannini et al. (2006).
[3] Hollar and Springer (1997).
[4] Juste et al. (1999).
[5] Kennedy et al. (1999).
[6] Kho Han Guan and Abdullah (in litt.).
[7] Lin & Penny (2001).
[8] Murphy et al. (2001).
[9] Nikaido et al. (2000).
[10] Roberts (2006).
[11] Sakai et al. (2003).
[12] van den Hurk et al. (2007).