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The systematic position of *Pteropus leucopterus* and its bearing on the monophyly and relationships of *Pteropus* (Chiroptera: Pteropodidae)

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Pteropus is the most speciose genus in Pteropodidae, currently comprising 65 species in 18 species groups. Here we examine whether *Pteropus* as currently understood is monophyletic. We sequenced three nuclear genes (RAG-1, RAG-2 and vWF) totalling c. 3.0 kbp from 18 species of *Pteropus* representing 12 species groups, plus *Acerodon celebensis* and megachiropteran outgroups representing all other subfamilies and tribes. Separate and combined parsimony and maximum likelihood analyses recovered a clade containing *Acerodon* as sister to all *Pteropus* species to the exclusion of the Philippine endemic taxon '*P. leucopterus*', rendering *Pteropus* paraphyletic. We propose the revalidation of *Desmalopex* Miller, 1907, an available generic name for leucopterus, adopting the name combination *Desmalopex leucopterus* (Temminck, 1853). We discuss implications of this result and anticipate further modifications of the classification of *Pteropus*.

Key words: Philippines, *Desmalopex leucopterus*, *Pteropus*, Megachiroptera, phylogeny

FINTRODUCTION

The chiropteran family Pteropodidae comprises 42 currently recognized genera and 186 species, of which as many as 65 species are classified in the genus *Pteropus* Brisson, 1762 (Simmons, 2005). Distributed from islands off the east coast of Africa to Polynesia in the Western Pacific, the majority of *Pteropus* species are Indian Ocean and Pacific island endemics. Andersen (1912) established the membership of the genus and clearly distinguished *Pteropus* species from other closely allied genera known at the time — *Acerodon* Jourdan, 1837, *Pteralopex* Thomas, 1888, and *Styloctenium* Matschie, 1899. Although subsequent authors have generally followed Andersen's (1912) generic arrangement of *Pteropus*, previous authors sometimes allocated a few species to separate genera, particularly Miller (1907), who erected the genus *Desmalopex* to accommodate a single distinctive species, *Pteropus leucopterus* Temminck, 1853, endemic to the Philippines [see description in Miller (1907) and Andersen (1909, 1912)]. Miller (1907: 60) highlighted affinities between *Desmalopex* and *Pteropus* but listed a number of characters that alternatively "distinctly suggest *Pteralopex*." Andersen (1909, 1912: 294) included *leucopterus* in *Pteropus* and associated this form with members of the *pselaphon* species group, which in his view "shows decidedly leanings towards the highly specialized genus *Pteralopex*."

Thus while both Miller (1907) and Anderson (1912) recognized the distinctive morphological attributes of *leucopterus*, their taxonomic arrangements differed markedly. Their mutually exclusive systematic hypotheses (*leucopterus* placed in a monotypic genus versus *leucopterus* included within *Pteropus*) have remained essentially untested since the beginning of the twentieth century. This fact has gone largely unrecognized because *leucopterus* has been included in *Pteropus* without comment by all recent authors (e.g., Corbet and Hill, 1992;

Koopman, 1993, 1994; Heaney *et al*., 1998; Simmons, 2005). Here we begin analyzing the complex problem of the composition and relationships of *Pteropus* by focusing on the relationship of *Pteropus leucopterus* to other members of this genus from different species groups, as well as to other pteropodine megabats. Based on parsimony and maximum likelihood analyses of DNA sequences from three nuclear coding genes, we provide evidence bearing on the phylogenetic position of *leucopterus* and on pteropodid systematics in general.

Materials and Methods

Taxa

For the purposes of this study we chose Pteropodini sensu Bergmans (1997) as the ingroup. We included as outgroups representatives of each main megachiropteran clade following Giannini and Simmons (2005) and Giannini *et al*. (2006). We choose the same taxa as in Giannini *et al*. (2006), specifically: *Nyctimene albiventer* and *N. vizcaccia* (Nyctimeninae), *Cynopterus sphinx* and *Ptenochirus jagori* (Cynopterinae), *Eonycteris spelaea*, *Rousettus amplexicaudatus,* and *R. aegyptiacus* (Rousettinae), *Myonycteris torquata* and *Megaloglossus woermanni* (Epomophorinae, Myonycterini), *Epomops franqueti* and *Epomophorus wahlbergi* (Epomophorinae, Epomophorini), *Harpyionycteris whiteheadi*, *Dobsonia inermis,* and *Dobsonia magna* (Harpyionycterinae), *Macroglossus minimus* (Macroglossinae), *Melonycteris (Nesonycteris) fardoulisi* [incertae sedis, variably associated with macroglossines (e.g., Andersen, 1912; Giannini and Simmons, 2005), pteropodines (e.g., Kirsch *et al*., 1995; Bergmans, 1997), and other groups], and *Eidolon helvum* [incertae sedis, allied to Rousettinae (Andersen, 1912; Bergmans, 1997) and Pteropodini (Giannini and Simmons, 2005)]. We included two microchiropteran bats [*Rhinopoma hardwickii* (Rhinopomatidae) and *Artibeus jamaicensis* (Phyllostomidae)] to provide an unambiguous root to our tree.

Ingroup taxa included typical pteropodine megabats available to us, including *Acerodon celebensis* and 18 species of *Pteropus* from 12 species groups (sensu Andersen, 1912): *Pteropus alecto* (*alecto* species group), *P. conspicillatus* (*conspicillatus* group), *P. pelewensis*, *P. tonganus* (*mariannus* group), *P. molossinus* (*molossinus* group), *P. neohibernicus* (*neohibernicus* group), *P. capistratus* (*temminckii* group), *P. poliocephalus* (*poliocephalus* group), *P. leucopterus* (*pselaphon* group), *P. anetianus*, *P. samoensis* (*samoensis* group), *P. scapulatus*, *P. woodfordi* (*scapulatus* group), *P. admiralitatum*, *P. pumilus*, *P. hypomelanus* (*subniger* group), *P. giganteus*, *P. lylei*, and *P. vampyrus* (*vampyrus* group).

Museum specimens referenced herein are deposited in the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); the Delaware Museum of Natural History, Wilmington (DMNH); the Field Museum of Natural History, Chicago (FMNH); the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH); the Senckenberg Museum, Frankfurt (SMF); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Morphological terminology and usage follow Andersen (1912) and Giannini *et al*. (2006*b*).

Sequences and Phylogenetic Analysis

We used sequences of exon 28 of the von Willebrand Factor gene (vWF, 1231 bp) from Giannini *et al*. (2006), and generated new vWF sequences for *Pteropus* species for this study. We also generated sequences of two other nuclear coding genes, the Recombination Activating Gene 1 (RAG-1, 1084 bp), and the Recombination Activating Gene 2 (RAG-2, 760 bp), for the total taxonomic sampling. Total DNA was obtained from preserved tissue samples (see voucher list in Appendix) with the DNeasy tissue kit (QIAGEN). PCR amplification was carried out using previously published primers [RAG-1 and RAG-2 (Teeling *et al*., 2000); vWF (Porter *et al*., 1996)]. To obtain both forward and reverse sequences for each gene region, internal primers were used for sequencing in addition to the PCR primers (sequences available upon request). All sequences were obtained with an automated ABI 3730XL sequencer. Sequence editing and prealignment were done with the Sequencher 4.2 software (Gene Codes). GenBank accession numbers and voucher information for megabats included in this study are provided in Appendix 1. In addition, we used published sequences for microbat outgroup taxa. GenBank accession numbers for *A. jamaicensis* are AY834655 (RAG-1), AY834663 (RAG-2), and AY834737 (vWF); for *R. hardwickii*, accession numbers are AF447518 (RAG-1), AF447535 (RAG-2), and AF447551 (vWF).

Sequences of our three genes were submitted to parsimony analysis, separately and in combination. Here we report results of our combined analysis based on a tree-search strategy that consisted of 1,000 replicates of random addition sequences of taxa, each followed by tree bisection reconnection branch swapping (TBR). An additional round of TBR was done on optimal trees obtained. Clade support was assessed using Bremer or decay values (Bremer, 1994) and jackknife character resampling (Goloboff *et al*., 2003*a*). We calculated Bremer values via incremental sampling of suboptimal trees (see Giannini and Bertelli, 2004). Briefly, we saved up to 1,000 suboptimal trees one step longer than the previous optimum in successive stages. That is, we first searched for suboptimal trees 1 step longer than the optimal tree length, next saving suboptimals up to 2, 3, 4, 5, 6, 7, 8, 9, and 10 steps longer than the optimal trees (9,968 trees up to 10 steps longer than the optimals were found). Second, jackknife frequencies were estimated from 5,000 replications using unbiased symmetric resampling (Goloboff *et al*., 2003*a*). These analyses were executed in TNT (Goloboff *et al*., 2003*b*, In press).

In addition, maximum likelihood (ML) analyses were performed for individual genes and the combined set using the GTR + Γ model. Parameters were estimated from the data for each gene separately, which were treated as partitions in the combined analysis. Starting trees were obtained by maximum parsimony and 100 runs were done on each initial tree to obtaining ML trees. Statistical support was obtained with 100 bootstrap replications. All the ML analyses were run with the program RAxML (Stamatakis, 2006).

Results

In the combined dataset, 751 sites were variable (RAG1 = 236, RAG2 = 163, vWF = 354) and 395 were parsimony informative (RAG1 = 116, RAG2 = 92, vWF = 187). Most of the substitutions were transitions (ti/tv: RAG2 = 10.3, RAG1 = 4.5,

vWF = 3.9), but neither transitions nor transversions were saturated in the sample (Fig. 1).

Our combined parsimony analysis of all three genes resulted in 92 trees of 1,327 steps (strict consensus in Fig. 2). An additional TBR round on those trees did not increase the set of optimal trees. Pteropodidae was recovered as monophyletic. *Nyctimene* was placed as sister to all other megachiropterans, but the backbone of the lower section of the tree was poorly supported. By contrast, clades representing a number of subfamilies and other recognized systematic groups were highly supported. Clades recovered included Cynopterinae; a highly-supported group of rousettines and epomophorines; Epomophorinae; a weak association of *Macroglossus* with a highly supported Harpyionycterinae clade; and a well-supported pteropodine clade (marked A in Fig. 2) inclusive of the genera *Melonycteris*, *Acerodon*, and *Pteropus*.

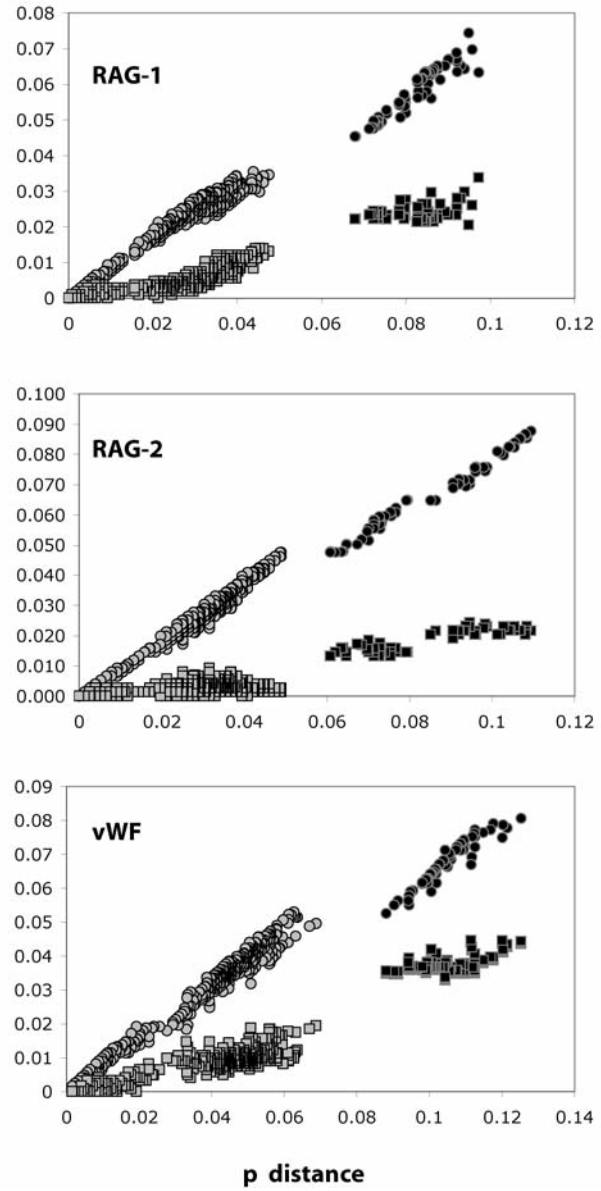

FIG. 1. Saturation plots of transitions and transversions for each gene analyzed. Proportions of each substitution type were plotted against uncorrected p distances. Circles represent transitions and squares represent transversions. Symbols representing the ingroup are shown in light grey and symbols representing the outgroup are shown in black

Within the pteropodine clade, *Melonycteris fardoulisi* and *Pteropus leucopterus* formed a trichotomy with a highly supported *Acerodon* + *Pteropus* group (clade B in Fig. 2). All the species of *Pteropus*, to the exclusion of *leucopterus*, were recovered as monophyletic with high support (clade C in Fig. 2). Resolution within *Pteropus* was poor. Only three clades were supported with resampling frequencies > 50%. These were *Pteropus anetianus* + *P. samoensis* (i.e., the *samoensis* species group); *Pteropus woodfordi* + *P. molossinus*, which renders the *scapulatus* species group (here represented by *P. scapulatus* and *P. woodfordi*) paraphyletic; and two clades with members from mixed species groups. Partial analyses using individual gene partitions (not shown) were less resolved; clades recovered in those analyses are marked with symbols in Fig. 1. In no case did *P. leucopterus* group with other *Pteropus* species.

The combined ML tree is shown in Fig. 3. This tree agrees with the combined parsimony tree (Fig. 2) in all supported groups specifically relevant to this study (marked A, B, and C). Groups A and B were recovered in separate ML analyses of each of the three genes, whereas group C was recovered in separate analyses of RAG-1 and vWF. Also, clades recovered within *Pteropus* were compatible across analyses (cf. Figs. 2 and 3).

SYSTEMATICS

Desmalopex Miller, 1907 is a valid pteropodid genus presently considered a junior synonym of *Pteropus* Brisson, 1762. In our combined analyses, as well as in individual-gene analyses, *leucopterus* never joined other species of *Pteropus*, demonstrating the paraphyly of *Pteropus* under its current generic definition (Andersen, 1912; Simmons, 2005). However, all other species of *Pteropus* were recovered as a natural group identified by shared changes in all three genes independently and in combination, clearly suggesting that *Pteropus* (at least as represented by our sampling) is indeed monophyletic to the exclusion of *leucopterus* (clade

C in Figs. 2 and 3) and is sister to the genus *Acerodon* (clade B in Figs. 2 and 3). '*Pteropus*' *leucopterus* is also easily diagnosed morphologically, unique amongst megachiropterans in exhibiting a mosaic of features recalling both *Pteralopex* and *Pteropus* (cf. Andersen, 1909). As a consequence, we remove *leucopterus* from *Pteropus* and resurrect *Desmalopex* Miller, 1907, originally erected to include this sole species, and adopt the combination *Desmalopex leucopterus* (Temminck, 1853). We briefly diagnose and discuss the content and distribution of *Desmalopex* below.

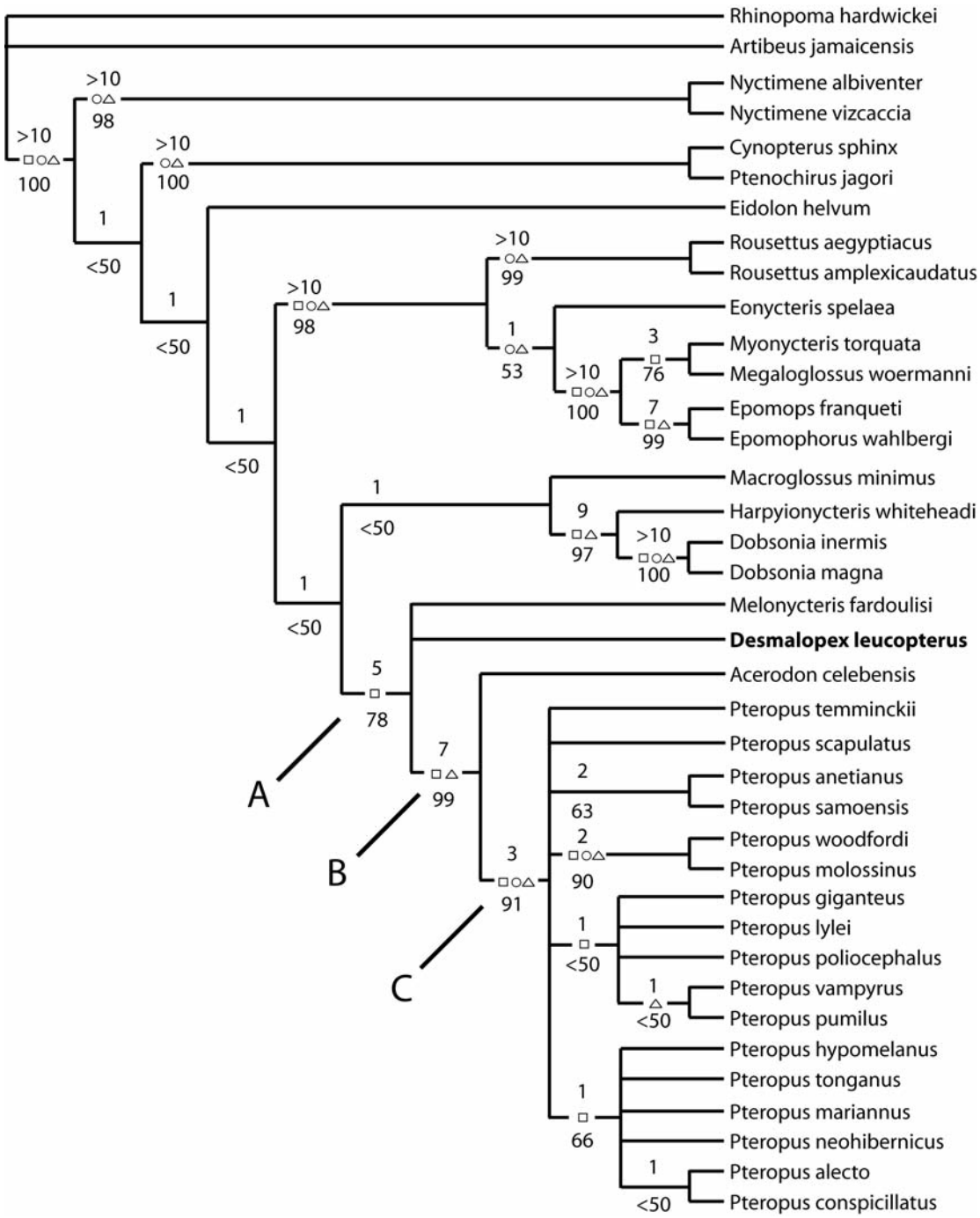

FIG. 2. Strict consensus tree resulting from a parsimony analysis of three nuclear coding genes combined (RAG-1, RAG-2, and vWF). Support values are given above (Bremer) and below (Jackknife) branches. Nodes supported by individual-gene analyses are marked with the following symbols: RAG-1 (□), RAG-2 (○), and vWF (△)

GENUS *DESMALOPEX* MILLER, 1907

Diagnosis

Desmalopex uniquely combines distinctive features of both *Pteropus* and *Pteralopex* sensu lato (i.e., incorporating both *Pteralopex* and *Mirimiri*). *Desmalopex* is a pteropodid genus uniquely characterized by its relatively large body size (forearm length ca. 100–150); relatively much shortened external ears; pale-dark mottled wing membranes (see below); unusually large and moderately spaced upper incisors, subequal in size, forming an arcuate row; large i2 (wide with one salient lateral cusp) but highly reduced i1, such that i2 is about five times larger than i1; relatively short canines, without a large secondary posterior cusp on C; relatively large first premolar that is permanent in both jaws; relatively small cheekteeth; P4 that is larger than M1, which is subsquare rather than rectangular; orbits deflected distinctly upward relative to the cranial axis; postorbital processes that are ossified to the zygomatic arches in mature individuals, a complete alar canal (an unusual feature in megachiropterans, seen elsewhere only in *Mirimiri* and some *Pteralopex*; cf. Giannini *et al*. 2006: 113); basicranial configuration in which the petrosal is somewhat sunk laterally, the posttympanic and paracondylar processes are unusually large, and the postglenoid foramen is displaced laterally; and relatively gracile mandible featuring a low-slung sloping symphysis and a short and slender coronoid process. We plan to explore in greater detail these and other morphological attributes (and their phylogenetic significance) in subsequent contributions.

Content and Distribution

Desmalopex is endemic to the oceanic Philippines. The type and only described species of

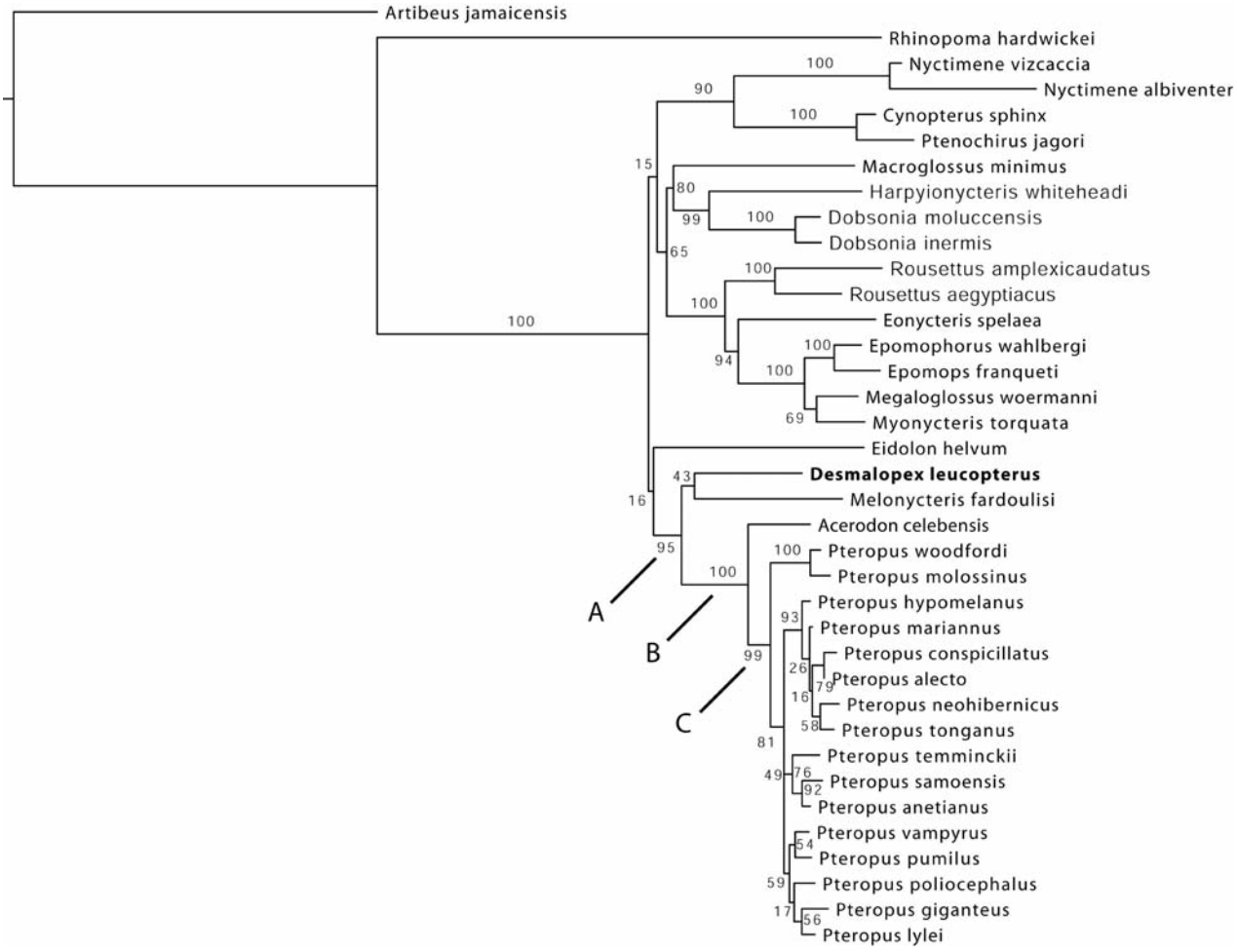

FIG. 3. ML tree of the combined set based on gene partitions modeled using GTR + Γ (likelihood score -11,490.72). Values near nodes represent bootstrap estimates of clade support based on 100 replications. *Pteropus scapulatus* was excluded from this analysis due to the influence of its missing data on branch lengths

Desmalopex is *Desmalopex leucopterus* (Temminck, 1853), known only from forested habitats (up to at least 2,300 m) on Luzon and the adjacent land-bridge island of Catanduanes (specimens at AMNH, BMNH, FMNH, RMNH, SMF, and USNM). Synonyms are *Pteropus chinenis* Gray, 1870 (misprovenanced from China; see Andersen, 1912) and an incorrect subsequent spelling of *leucopterus* under the name combination '*Spectrum leucopterum*' by Gray (1870). Currently undescribed species referable to *Desmalopex* have been recorded from the Philippine islands of Mindoro (in the Mindoro Faunal Region; see Heaney *et al*., 1998) and Dinagat (in the Mindanao Faunal Region; K. Helgen, personal observation — specimens at DMNH).

Discussion

Affinities of *Desmalopex* remain somewhat uncertain and invite speculation and further research. *Desmalopex* belongs in Pteropodinae sensu Bergmans (1997), but exactly where in this group is not yet clear. Within the subfamily Pteropodinae, Bergmans (1997) recognized three tribes: Pteropodini (including *Pteropus, Acerodon*, *Neopteryx*, *Styloctenium*, *Pteralopex*, and the more recently recognized genus *Mirimiri*; Helgen, 2005), a restricted Macroglossini (incorporating only *Macroglossus* and *Syconycteris*), and Notopterini (*Melonycteris* and *Notopteris*). The problematic African genus *Eidolon* was suggested as another candidate member of the Pteropodinae based on morphological evidence and a combined analysis including mitochondrial genes (Giannini and Simmons, 2005), but our current analyses using only nuclear genes either rejected this grouping (Fig. 2) or did not provide clear support for it (Fig. 3). Also from the current analysis [and some of our previous results; e.g., Giannini and Simmons (2003, 2005); Giannini *et al*. (2006)], it seems clear that *Macroglossus* [and thus its apparently closely-related sister lineage, *Syconycteris*; Andersen (1912), Kirsch *et al*. (1995)] does not belong in Pteropodinae. However, we recovered *Melonycteris* in clade A (Figs. 2 and 3), an arrangement recalling the DNA-DNA hybridization results of Kirsch *et al*. (1995), suggesting that the Notopterini may be part of Pteropodinae. Based on RAG-1 changes, *Desmalopex* joined *Melonycteris* and typical Pteropodini in a trichotomy (Fig. 2), suggesting that, pending further resolution, *Desmalopex* may belong in a separate tribe within the subfamily. The single-gene parsimony analyses did not favor any particular association of *Desmalopex* in this trichotomy. However, the combined ML analysis suggested, albeit weakly, that *Melonycteris* may join a clade including *Desmalopex* (Fig. 3).

Andersen (1912) included *leucopterus* in *Pteropus* within the *pselaphon* species group, which is characterized by many dental traits including heavy teeth, strong ledges (cingula), and relative enlargement of specific incisors (i1) and premolars (p1). To Andersen (1912: 294) 'the *pselaphon* group shows decidedly leanings towards the highly specialized genus *Pteralopex*'. We have not had access to tissue samples of *Pteralopex*, but we hypothesize that, as suggested by Miller (1907), *Desmalopex* may be part of a lineage including *Pteralopex* (and its more recently described sister genus, *Mirimiri*) and perhaps other pteropodine genera. To the craniodental characters, we add several external characters that may support such association. Some photographs of *Desmalopex* that we have seen seem to show that it has an eye with a red-orange iris, an interesting trait shared also with *Pteralopex* and *Mirimiri,* but also with some *Pteropus* species, in which genus the iris is more usually brown (Flannery, 1995; Helgen, 2005). The external ears of *Desmalopex*, like those of *Pteralopex* and *Mirimiri,* are relatively small in comparison to most species of *Pteropus* (Corbet and Hill, 1992; Helgen, 2005). *Desmalopex* also exhibits an uneven distribution of pigment in the patagia ['melanin spotting' of Giannini and Simmons (2005): character 33]. This character state is shared with *Pteralopex*, *Styloctenium*, some *Pteropus* species (e.g., *P. capistratus*), and is carried to an extreme in *Neopteryx* (see Hayman, 1946; Bergmans and Rozendaal, 1988). Perhaps significantly, melanin spotting is also present in *Melonycteris* and *Nesonycteris*, though it also occurs in at least one phylogenetically unrelated lineage, the Nyctimeninae, and as an individual feature in other pteropodid genera.

Regarding relationships within *Pteropus*, the nuclear genes that we sampled lack variation sufficient to provide resolution, suggesting that fast-evolving genes (e.g., mitochondrial markers) should be added to the analysis. However, we anticipate that species groups, as traditionally recognized since Andersen (1912), will require some major rearrangements. While our analyses either recover or did not strongly contradict some polytypic species groups (the *samoensis*, *tonganus*, *vampyrus* groups), monophyly of at least two such species groups were rejected. First, *P. woodfordi* (*scapulatus* species group) appeared as sister to *P. molossinus* (*molossinus* species

group) rather than *P. scapulatus*. Second, *P. pumilus* did not group with the other member of the *subniger* species group included in our study (*P. hypomelanus*). The significance of these results will be more fully explored elsewhere in a review of interspecific relationships among the remainder of species classified within *Pteropus*.

Unfortunately, we have not had access to tissues or sequences from *Pteropus insularis*, *P. pselaphon, P. pilosus,* or *P. tuberculatus,* all of which Andersen (1912) allied with *Desmalopex leucopterus* within his '*Pteropus pselaphon* group.' Further study is needed to firmly establish the phylogenetic placement of these species. However, we note that none of these species of *Pteropus* possess some of the more distinctive phenetic anatomical attributes of *P. leucopterus,* such as its mottled wings, relatively small and subsquare M1, extraordinary discrepancy in size between i2 and i1, co-ossification of the postorbital processes and the jugal spine of the zygomatic arches, and zygomata that are parallel-sided rather than bowed in dorsal view (each of these traits are instead shared with *Pteralopex*.)

Recognition of *Desmalopex* as a valid genus brings the number of recognized pteropodine genera (sensu Giannini and Simmons 2005: 24) to seven (Helgen, 2005; Simmons, 2005) or eight [including *Eidolon*; Giannini and Simmons (2005)]. With the exception of *Eidolon,* all of these lineages comprise relatively very large-bodied bats with distributions centered on the Indo-Australian region. One is widespread throughout Australasia and the Pacific and Indian Ocean regions (*Pteropus*), one is shared between Wallacea and the oceanic Philippines (*Styloctenium*), one occurs primarily throughout Wallacea and the oceanic Philippines but also extends marginally to the Sunda Shelf region on Palawan and adjacent islands (*Acerodon*), one is restricted to Sulawesi (*Neopteryx*), one is restricted to the oceanic Philippines (*Desmalopex*), one is restricted to the Solomon Archipelago (*Pteralopex*), and one is restricted to Fiji (*Mirimiri*) (Helgen, 2005; Simmons, 2005; Esselstyn, 2007).

As noted above, our results confirm that one lineage formerly classified among 'macroglossines' (Andersen, 1912; Giannini and Simmons, 2005; Giannini *et al*., 2006), represented by *Melonycteris* (endemic to the Bismarck Archipelago) and *Nesonycteris* (endemic to the Solomon Archipelago), variably recognized as separate genera or congeneric subgenera (Pulvers and Colgan, 2007), is also referable to the Pteropodinae (Bergmans, 1997). The West Pacific genus *Notopteris* (occurring in Vanuatu, New Caledonia, Fiji, and the subfossil record of Tonga), unsampled in our study, is potentially another member of this clade (Kirsch *et al*., 1995). Concentration of endemic pteropodine lineages throughout insular archipelagos from Sulawesi and the Philippines to the Solomons and Fiji indicates a probable origin for the group within the Indo-Pacific region's extensive island arc systems.

Finally, our parsimony analyses and our previous studies (Giannini and Simmons, 2005; Giannini *et al*., 2006) suggest that members of Pteropodinae are nested within Pteropodidae. By contrast, our combined ML analysis and a previous study that included a comparable sample of *Pteropus* species (Colgan and Da Costa, 2002: 19 species) place pteropodines in a more basal position amongst megachiropterans. However, the weakly supported backbone of both MP and ML trees (Figs. 2 and 3) indicate only uncertainty about the placement of pteropodines with this limited taxonomic sample.

Conclusions

We have provided evidence that *leucopterus* does not belong within the taxonomic boundaries of a monophyletic genus *Pteropus*, and resurrect *Desmalopex* Miller, 1907 as a valid generic name to accommodate this species. Morphological evidence points to an association of *Desmalopex* with *Pteralopex* and *Mirimiri*, and perhaps to pteropodine genera other than *Acerodon* and *Pteropus*. With the exclusion of *leucopterus*, monophyly of the genus *Pteropus* (as represented by a sample of 18 species from 12 species groups) is supported by shared changes in three nuclear coding genes. At least two of the currently recognized species groups of *Pteropus* may not be monophyletic.

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Appendix

Voucher information and GenBank accesion numbers of megabat specimens used in the present study, in alphabetical order by species. Imprecise localities are quoted. Abbreviations of Institutions: AM M, Australian Museum, Sydney; AMCC, Ambrose Monell Cryo Collection (AMNH); AMNH, American Museum of Natural History, New York; CMNH Carnegie Museum of Natural History, Pittsburgh; EBU Evolutionary Biology Unit, Australian Museum, Sydney; FMNH, Field Museum of Natural History, Chicago; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; ROM Royal Ontario Museum, Toronto; USNM Smithsonian Institution, National Museum of Natural History, Washington D.C. Other abbreviations refer to collector's catalog

Species	Voucher	Tissue ID	Accession numbers			Locality
			RAG-1	RAG-2	vWF	
AceFrodon celebensis	AMNH 272877	AMCC 124966	UE617946	UE617896	UE617928	'Indonesia, Sulawesi'
Cynopterus sphinx	AMNH 274354	AMCC 101688	UE617947	UE617897	DQ445697	Vietnam, Ha Giang Province, Vi Xuyen District, Cao Bo Commune, Mt Tay Con Linh II
Desmalopex leucopterus	FMNH EAR 1697	FMNH EAR 1697	UE617966	UE617915	UE617929	Philippines, Catanduanes
D. leucopterus	FMNH EAR 1698	FMNH EAR 1698				Philippines, Catanduanes
Dobsonia inermis	AMNH PRS 2771	AMCC 124428	UE617948	UE617898	DQ445686	Solomon Islands, Western Prov., New Georgia Group, Vonavona Lagoon
D. magna	AM M 20735	EBU 25757	UE617949	UE617899	UE617930	Papua New Guinea, Sideia Mission, Milne Bay Province
D. magna	MVZ 138495	MVZ 138495				Papua New Guinea, Baiyer River, Trauna Valley, Western Highlands Province
Eidolon helvum	CMNH 102020	SP 5079	UE617950	UE617900	UE617931	Kenya, Mbale, Kakamega District, Western province
E. helvum	CMNH 102021	SP 5080				Kenya, Mbale, Kakamega District, Western province
Eonycteris spelaea	MVZ 176480	MVZ 176480			DQ445685	China, Yunnan Province
E. spelaea	MVZ 176487	MVZ 176487	UE617951	UE617901	DQ445684	China, Yunnan Province
Epomophorus wahlbergi	AMNH 117336	JCK 4820	UE617953	UE617903	DQ445691	Mozambique, Zambezia, Mt. Namuli
Epomops franqueti	AMNH 238356	AMCC 109070	UE617952	UE617902	DQ445692	Central African Republic, Sangha, Dzanga-Sangha
Harpyionycteris whiteheadi	FMNH 146646	LRH 4811	UE617954	UE617904	DQ445690	Philippines, Mindanao, Bukidnon Prov., Mount Kitanglad Range
H. whiteheadi	FMNH 146650	LRH 4866			DQ445689	Philippines, Mindanao, Bukidnon Prov., Mount Kitanglad Range
Macroglossus minimus	CEF 800	AMCC 124283	UE617955	UE617905	DQ445693	Solomon Islands, Western Province, New Georgia Group, Vella Lavella Island
Megaloglossus woermanni	AMNH 268358	AMCC 109064	UE617956	UE617906	DQ445702	Central African Republic, Sangha, Dzanga-Sangha
Melonycteris fardoulisi	AMNH PRS 2653	AMCC 124279	UE617957	UE617907	DQ445699	Solomon Islands, Western Prov., New Georgia Group, Vella Lavella Island
Myonycteris torquata	AMNH 268362	AMCC 109058	UE617958	UE617908	DQ445700	Central African Republic, Sangha, Dzanga-Sangha
Nyctimene albiventer	No voucher	No voucher	AY249870	AF447531	AF447549	
N. vizcaccia	AMNH PRS 2636	AMCC 124208	UE617959	UE617909	DQ445698	Solomon Islands, Western Prov., New Georgia Group, Vella Lavella Island
Ptenochirus jagori	FMNH 175395	LRH 6700	UE617960	UE617910	DQ445696	Philippines, Luzon, Kalinga Prov., Balbalan Munic., Balbalasang
Pteropus alecto	AM M 32564	EBU 9873	UE617961	UE617911	UE617932	Australia, Lismore District, New South Wales
P. anetianus	AMNH 272874	AMCC 124963	UE617962	UE617912	UE617933	Vanuatu
P. capistratus	USNM LHE 1009	USNM LHE 1009				'Papua New Guinea'
P. capistratus	USNM 580018	USNM 580018	UE617975	UE617923	UE617943	'Papua New Guinea'
P. conspicillatus	MVZ 138494	MVZ 138494				Papua New Guinea, Madang, Madang province
P. conspicillatus	MVZ 140201	MVZ 140201	UE617963		UE617934	Papua New Guinea, Baitabag Plantation, Madang, Madang province
P. giganteus	CMNH 92205	NK 10524	EU617964	EU617913	EU617935	India, Araku, Andhra Pradesh

APPENDIX. CONTINUED

Species	Voucher	Tissue ID	Accession numbers			Locality
			RAG-1	RAG-2	vWF	
Pteropus giganteus	CMNH 92208	NK 10523				India, Araku, Andhra Pradesh
P. hypomelanus	Uncataloged	P 4447	UE617965	UE617914	DQ445687	Captivity Lubee Foundation
P. lylei	ROM 110943	F 44269	UE617967	UE617916	UE617916	Vietnam, Soc Trang
P. lylei	ROM 110944	F 44270				Vietnam, Soc Trang
P. molossinus	USNM 566567	USNM 566567	UE617969	UE617918	UE617938	'Caroline Islands'
P. molossinus	USNM 566568	USNM 566568				'Caroline Islands'
P. neohibernicus	AMNH 272872	AMCC 124961	EU617970	EU617919	EU617939	'Papua New Guinea'
P. pelewensis	USNM 566587	USNM 566587	XXXX	XXXX	XXXX	Palau
P. pelewensis	USNM 566588	USNM 566588	XXXX	XXXX	XXXX	Palau
P. poliocephalus	M 35496	EBU 13768	EU617971	EU617920	EU61740	Australia, Mortdale, New South Wales
P. pumilus	FMNH LRH 4261	FMNH LRH 4261	EU617972	EU617921	EU617941	'Philippines'
P. pumilus	FMNH SMG 2872	FMNH SMG 2872				'Philippines'
P. samoensis	AMNH 272876	AMCC 124965	EU617973	EU617922	EU617942	'American Samoa'
P. scapulatus	AM M 32440	EBU 9341	EU617794			Australia, Werrington Downs, Penrith, New South Wales
P. tonganus	AMNH 272873	AMCC 124962	EU617976	EU617924	DQ445695	Tonga
P. vampyrus	AMNH 272871	AMCC 124960				Unregistered
P. vampyrus	ROM 110948	F 44274	EU617977	EU617925	EU617944	Vietnam, Soc Trang
P. woodfordi	AMNH 272875	AMCC 124964	EU617978	EU617926	EU617945	'Solomon Islands'
Rousettus aegyptiacus	AMNH 117386	JCK 4960	EU617979	EU617927	DQ445688	Mozambique, Zambezia, Mt. Namuli
R. aegyptiacus	AMNH 117335	JCK 4821			DQ445694	Mozambique, Zambezia, Mt. Namuli
R. amplexicaudatus	No voucher	No voucher	AF447512	AF447529	AY057836	