BioOne COMPLETE

A Species-Level Phylogeny of Old World Fruit Bats with a New Higher-Level Classification of the Family Pteropodidae

Authors: Almeida, Francisca Cunha, Simmons, Nancy B., and Giannini, Norberto P.

AMERICAN MUSEUM NOVITATES

A Species-level Phylogeny of Old World Fruit Bats with a New Higher-level Classification of the Family Pteropodidae

FRANCISCA CUNHA ALMEIDA,[1,2] NANCY B. SIMMONS,[3] AND NORBERTO P. GIANNINI[3,4,5]

ABSTRACT

Old World fruit bats (Chiroptera: Yinpterochiroptera: Pteropodidae) are a diverse radiation endemic to the tropics of Africa, Asia, Australia, and nearby island archipelagos. Recent molecular analyses have provided considerable resolution of phylogenetic relationships within this group, but many points of uncertainty have remained including the position of several enigmatic taxa (e.g., *Notopteris*, *Eidolon*), relationships among species in more diverse subfamilies and genera (e.g., Pteropodinae, *Pteropus*, *Epomophorus*), and topology of the backbone of the tree. Here we provide a new, synthetic analysis including representatives of all 45 currently recognized genera and enhanced sampling in several speciose genera. Our matrix included four nuclear genes regions (vWF, RAG1, RAG2, and BRCA1) and four mitochondrial gene loci (Cytb, tRNA valine, 12S rRNA, and 16S rRNA) for a total of >8000 bp including new sequence data for 13 species. Maximum likelihood and Bayesian analyses resulted in trees supporting recognition of six main suprageneric clades similar in content to those identified in our previous studies. We did not recover strong support for relationships among the main clades along

[1] Instituto de Ecología, Genética y Evolución de Buenos Aires – CONICET, Buenos Aires, Argentina.

[2] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.

[3] Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York.

[4] Unidad Ejecutora Lillo, CONICET-FML, Argentina.

[5] Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina.

the backbone of the tree, but identified many well-supported clades within all of the major groups. Based on these results, we propose a new classification for Pteropodidae comprising eight subfamilies and 14 tribes, and including several new and/or replacement higher-level taxonomic names for which we provide morphological diagnoses.

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:95775197-7608-4C36-B768-C91154C6E093.

INTRODUCTION

Old World fruit bats, also known as megabats, comprise the Family Pteropodidae, the third largest bat family (Simmons and Cirranello, 2019). Pteropodidae includes 45 currently recognized genera and a minimum of 200 species, six of which are extinct beyond reasonable doubt (Giannini, 2019; Simmons and Cirranello, 2019). Megabats are found throughout Africa, the Asian tropics, Australia, and many islands of the Indian and Pacific oceans where they play important ecological roles in seed dispersal and pollination (Nowak, 1994). Although some pteropodids use echolocation (Yovel et al., 2011; Lee et al., 2016; Boonman et al., 2014), most rely on vision and olfaction to navigate and find plant food sources. Pteropodidae is also functionally diverse; for example, it exhibits the widest variation in body size seen in any family of bats, ranging from 14 g to more than 1000 g (Moyers-Arévalo et al., 2018). Relative gigantism observed in some pteropodid species has been associated with the evolutionary loss of echolocation abilities, which may have released selective constraints on body size (Moyers-Arévalo et al., 2018). The majority of pteropodids are frugivorous; however, some species feed exclusively or opportunistically on nectar, pollen, and/or floral parts, while others include leaves, bark, and possibly sap in their diets (Kunz and Pierson, 1994; Giannini, 2019). In the Old World tropics, some pteropodid species are thought to be reservoirs of zoonotic viruses, since evidence of infection from filoviruses (e.g., ebola), henipaviruses (e.g., hendra), and coronaviruses (e.g., SARS) has been detected in healthy animals (Leroy et al., 2005; Towner et al., 2007; Hayman et al., 2010; Halpin et al., 2011; Olival et al., 2013).

The monophyly of Pteropodidae is widely accepted and the group has been consistently recovered in numerous molecular phylogenetic studies independent of taxonomic sampling, analytic methods, and the genetic markers used (Teeling et al., 2002, 2005; Shi and Rabosky, 2015; Amador et al., 2018). Similarly, its sister position to the insectivorous echolocating superfamily Rhinolophoidea has been confirmed in numerous studies since Hutcheon et al. (1998) first suggested "microbat" paraphyly due to "megabats" recovered as sister to rhinolophoids (e.g., Teeling et al., 2002, 2005; Shi and Rabosky, 2015; Amador et al., 2018). By contrast, some relationships within Pteropodidae remain contentious, although interesting results have accumulated over the past 20 years as a series of molecular phylogenetic studies have approached the problem of internal relationships of Pteropodidae with ever-increasing sampling of its diversity (e.g., Hollar and Springer, 1997; Juste et al., 1999; Álvarez et al., 1999; Giannini and Simmons, 2003, Almeida et al., 2011, Shi and Rabosky, 2015; Amador et al., 2018). These studies have uncovered many disagreements between topologies derived from molecular analyses

and morphology-based classifications originally proposed by Andersen (1912) and significantly improved by Bergmans (1997; see also Giannini and Simmons, 2005). Some recent studies focused on particular groups and proposed relevant changes in the classification (Giannini et al., 2006, 2008, 2009; Nesi et al., 2013; Hassanin, 2014; Almeida et al., 2016). A new subfamily Eidolinae was erected to contain the rather enigmatic genus *Eidolon* (Almeida et al., 2016), and *Boneia* joined *Dobsonia*, *Aproteles*, and *Harpyionycteris* in a substantially expanded Harpyionycterinae (Giannini et al., 2006, 2009). Other studies made progress sorting out relationships within the more speciose subfamilies; e.g., Cynopterinae (Almeida et al., 2009) and Pteropodinae (Almeida et al., 2014). Finally, Rousettinae was redefined to accommodate the African endemic tribes Scotonycterini, Epomophorini, Stenonycterini, Myonycterini, and Plerotini, together with the widespread Rousettini (Almeida et al., 2016, Nesi et al., 2013).

Despite these recent advancements in phylogenetics and classification of Pteropodidae, some important relationships within the clade remain unresolved. This is the case with the problematic genus *Notopteris* Gray (1859), an endemic of Fiji, New Caledonia, and Vanuatu, which includes just two species that share unusual morphological characters, such as a long free tail (Andersen, 1912; Hill, 1983; Giannini and Simmons, 2005). *Notopteris* was included in the subfamily Pteropodinae by Bergmans (1997) but was recovered as sister to *Nyctimene* by Almeida et al. (2011) in an arrangement that nonetheless lacked statistical support. Although this result could reflect the large amount of missing data for this taxon in the matrix (only mitochondrial loci rRNA 12S and 16S), another possibility is that *Notopteris* might represent a relatively independent lineage without close affinities to any other pteropodid genus or subfamily (see Almeida et al., 2011).

Almeida et al. (2011) included 56 terminals representing 42 pteropodid genera. Their study, based on 8181 bp (including both nuclear and mitochondrial loci), recovered several clades with high statistical support, among them many of Bergmans' (1997) suprageneric groups. However, the analyses of Almeida et al. (2011) revealed an apparent polytomy at the base of the pteropodid tree. A careful inspection of the data showed that such a result could not be explained by bias or phylogenetic conflict between the eight loci represented in the matrix, and additional analyses suggested that some branches might indeed have zero length for the dataset used. As a conclusion, Almeida et al. (2011) hypothesized that crown pteropodids experienced an explosive radiation, which would account for the blurred phylogenetic signal at the base of their phylogeny. Several characteristics of the family are compatible with a scenario of explosive radiation, including high diversity in species richness and relative morphological disparity, the origin of key innovations related to the loss of echolocation, and acquisition of new feeding habits (Almeida et al., 2011). Demographic factors may also have played a role as many pteropodid species have insular distribution, especially the most speciose genus, *Pteropus*. While Almeida et al. (2011) included just a handful of *Pteropus* species, an important fraction of them were represented in another study that focused on pteropodines (Almeida et al., 2014). In that contribution, the authors reallocated many *Pteropus* species to mostly new species groups that differed considerably from previous arrangements that were all essentially traceable back to Andersen (1912).

Here we readdress the phylogenetics of Pteropodidae using a comprehensive species-level sampling, including representatives of all 45 currently recognized genera and sequence data from a total of 139 ingroup terminals. This taxonomic sample improves sequence sampling for several problematic taxa including *Notopteris* in addition to enhanced coverage for species in many other groups not included in previous simultaneous analyses. Our goal is to propose a new formal, fully revised and updated classification of the Pteropodidae that reflects the structure of monophyletic groups recovered, and also to resolve most of long-standing taxonomic issues (e.g., preoccupied names improperly used for over a century) in the Old World fruit bats.

MATERIAL AND METHODS

Taxonomic Sampling

Our matrix included a total of 145 species, 139 of which were pteropodids. The ingroup species represent all 45 currently recognized pteropodid genera. The majority of the ~47 pteropodid species missing from the matrix belong to the highly diverse genera *Nyctimene* (a genus including ≥16 species), *Dobsonia* (≥14 species), and *Pteropus* (≥65 species; Simmons and Cirranello, 2019), which were represented in our matrix by six, eight, and 51 species, respectively. Our approach in this study was to use total evidence, including all species with available sequences, no matter the number of loci or length of the sequences available. The six outgroup species belong to the superfamily Rhinolophoidea, a group that has been consistently shown to be sister to Pteropodidae (e.g., Teeling et al., 2002, Amador et al., 2018; Lei and Dong, 2016). A list of species included in this study is provided in the supplementary material (table S1, available online at doi.org/10.5531/sd.sp.39).

Molecular Matrix

Our matrix included a total of eight loci. Four of those were nuclear gene regions: exon 28 of the von Willebrand factor gene (vWF, 1230 bp), partial recombination activating gene 1 (RAG1, 1084 bp), partial recombination activating gene 2 (RAG2, 760 bp), and partial breast cancer 1 gene (BRCA1, about 1370 bp). The other four loci were genes of the mitochondrial genome: complete cytochrome *b* gene (Cytb, 1140 bp), partial rRNA 12S gene (1069 bp), the valine tRNA gene, and partial rRNA 16S gene (1330 bp), totaling about 2550 bp. We obtained many of these sequences in previous studies (Giannini et al., 2006, 2008, 2009; Almeida et al., 2009, 2011, 2014, 2016), while sequences for 13 species were newly acquired for the current study using protocols and primers as previously published. Other sequences, however, were obtained by other authors, and so we downloaded these from GenBank. Accession numbers of each sequence used in this study are listed in supplementary table S2.

Multiple sequence alignments were obtained for each locus individually with the software MAFFT version 7 (Katoh and Standley, 2013). Exception was made for the three RNA genes, which were treated as a single continuous sequence due to their molecular contiguity in the mitochondrial genome. This particular alignment was treated with Gblocks for

the removal of "gappy" regions that could have been misaligned (Castresana, 2000). Individual gene trees were then obtained and checked for unexpected results that could point to sample misidentification. The Almeida et al. (2011) study used the same set mitochondrial and nuclear loci sampled in a similar diversity of genera, and, through statistical tests, demonstrated that there is no incongruence of phylogenetic signal between this set of genes in this clade. We therefore proceeded with the concatenation of all six alignments into a single matrix with 7866 characters for the current study.

Phylogenetic Analysis

The best partition scheme for the data in our matrix was evaluated with the program PartitionFinder v. 1.1, which was prompted with the beginning and ending of each protein-coding gene separated into coding positions plus the fragment containing the mtRNA genes. The best scheme thus identified included nine partitions of the data, and these were later employed in both maximum likelihood and Bayesian inference tree searches. The former searches were done with RAxML v. 8 (Stamatakis, 2014), applying the GTRCAT substitution model to all partitions, which were treated separately for model-parameter estimation. The best tree was obtained from 100 independent runs. Statistical support for clades was assessed with 1000 nonparametric bootstrap replicas, with clade recovery percentages later plotted on the most likely tree. Bayesian inference searches were run on MrBayes (Ronquist and Huelsenbeck, 2003) employing for each partition the optimum substitution model according to PartitionFinder. Two MCMC were run for 15 million generations, with trees and parameters sampled every 5000 generations. Runs were checked for convergence using Tracer v. 1.6 (Rambaut et al., 2014), using as criteria effective sample sizes for each parameter larger than 200. The first 25% of trees of each run were discarded as burn-in; the remaining trees were then summarized into a majority rule consensus tree that was visualized with FigTree (Rambaut, 2009).

Additionally, we obtained an ultrametric dated tree using the Bayesian approach implemented in the program BEAST 1.8.4 (Drummond et al., 2012). This approach allows for dating a phylogenetic tree, but at the same time performs Bayesian tree searches that will be constrained for some clades depending on the age calibration used. In view of a dearth of good fossil records for Pteropodidae, we employed dates estimated by Amador et al. (2018) in a study based on more than 800 bat species of all families and 44 fossil-based calibration points. Following their results, we chose the divergence-date estimates obtained for six highly supported clades (so to have minimal effect on the topology) as age constraints to calibrate our pteropodid phylogeny. Age constraints were set with a normal distribution (including the confidence interval of the previous estimates) with the following taxa and parameters: split between Rhinolophidae and Hipposideridae (mean = 50, standard deviation = 5), crown Pteropodidae (25, 2), *Hipposideros* (24.5, 2), *Rousettus* (9, 4), Cynopterini (8, 5), and *Pteropus* (7, 2). The sequence data employed in our study were separated into the optimum partitioning scheme to which were applied the best substitution models according to PartitionFinder. We employed an uncorrelated relaxed clock (Drummond et al., 2006), birth-death process with incomplete sampling as tree prior, and soft bound age constraints with normal distri-

bution based on the dates' confidence intervals from Amador et al. (2018). The MCMC was done in two runs of 15 million generations, sampling every 5000, after which convergence was checked with Tracer. As expected, resulting divergence-date estimates for all clades within Pteropodidae were very similar to those obtained in Amador et al. (2018), generally within ±1 million years.

RESULTS AND DISCUSSION

Phylogeny and Evolution

ML and BI trees were very similar, differing topologically only in a few clades and in some clade support measures (fig. 1). All analyses recovered Pteropodidae as monophyletic and strongly supported (supplementary figs. S1 and S2). As we previously observed in a genus level study (Almeida et al., 2011), six main suprageneric clades were recovered mostly with high statistical support, whereas two genera (*Eidolon* and *Notopteris*) did not fall in any of these suprageneric clades. Also confirming our previous findings, relationships between the main clades received low support in general, with a few exceptions in the BI inference (fig. 1): macroglossines + Harpyionycterinae in one clade, and Nyctimeninae + Pteropodinae + *Notopteris* in another clade, which were recovered in more than 95% of the posterior samples of the BI trees. Cynopterinae appeared as sister to all other pteropodids, although statistically significant support was recovered only in the dated tree, making this position unreliable (fig. 1). Cynopterines contained its two tribes, Balionycterini and Cynopterini, as previously reported (see Almeida et al., 2009). The next split in the BI trees (from both the dated and the unconstrained analyses) separates Rousettinae, a fully supported grouping of seven successive tribes, from the remaining subfamilies. Rousettinae as currently understood (see Almeida et al., 2016) replaces a previous, more restricted biogeographic concept of an endemic African clade proposed by Hollar and Springer (1997); in its new definition it includes also some typically Asian forms (*Eonycteris* and basal *Rousettus*), an arrangement also recovered here. Tribes in Rousettinae were recovered as monophyletic with Scotonycterini successively sister to Eonycterini, Rousettini, Stenonycterini, Myonycterini, Plerotini, and Epomophorini (see also Nesi et al., 2013; Almeida et al., 2016). The monotypic subfamily Eidolinae appeared in different unsupported positions, depending on the analysis.

A suprageneric group appears in all trees, including two previously recognized subfamilies Macroglossinae (a preoccupied name corrected here to Macroglossusinae; see below, Taxonomic updates) and Harpyionycterinae; no morphological synapomorphies have been detected for this unranked clade, and statistical support for this grouping was present only in the Bayesian trees (BI, pp [posterior probability] = 0.96). The other suprageneric clade that was consistently recovered consists of a heterogeneous group inclusive of *Notopteris*, Nyctimeninae, and Pteropodinae (BI, pp = 0.98). Placement of *Notopteris* has been contentious, often classified either among typical nectar-feeding pteropodids (Andersen 1912), with flying foxes in the Pteropodinae (e.g., Bergmans 1997), or in a subfamily of its own, as adopted here (see below and also Giannini, 2019). The largest pteropodid group in terms of species diversity, Pteropodinae, contained three well-defined clades classified here as tribes (see below): monkey-faced bats and relatives, blossom bats

in the genera *Melonycteris* and *Nesonycteris*, and flying foxes. The latter included the genera *Styloctenium*, *Neopteryx*, *Acerodon*, and the speciose *Pteropus*.

The genus *Pteropus* was found to be monophyletic in our analyses except for the unsupported position of the form currently classified as *P. personatus*, whose position remains uncertain, appearing either linked with *Acerodon* (in the BI tree) or outside the *Acerodon* + *Pteropus* clade, and in both cases with little or no support. *Pteropus scapulatus* was sister of all typical *Pteropus* species (to the exclusion of problematic *personatus*) and represents an early invasion of the Australian continent, which, interestingly, had no consequences for the diversification of *Pteropus* as it remains the single species originating in this branch. By contrast, high speciation rates appear to have been the emerging process governing all subsequent diversification in this genus based on our results. In our analysis, four major clades of *Pteropus* species branched after *P. scapulatus* and included members of the *lombocencis* and *pelagicus* species groups (first clade, predominantly micronesian); *livingstonii* and *vampyrus* species groups (second clade, SE Asian and W Indian Ocean); *capistratus*, *vetulus*, and *samoensis* species groups (third clade, meganesian and Central Polynesian); and *poliocephalus*, *ocularis*, and *griseus* species groups (widespread in Australasia). Group membership in our study matches that of Almeida et al. (2014; see fig. 1), with addition here of *P. melanotus* to the *griseus* species group (as in previous study by Phalen et al., 2017). This arrangement is also compatible to that of Tsang (2015). Only one species group is missing in our analysis (the *melanopogon* species group, linked to *griseus* species group by Tsang, 2015), and the extinct *P. subniger* from the Mascarenes (incertae sedis; see Almeida et al., 2014).

The age of the Pteropodidae (~25 mybp; fig. 2) makes it one of the youngest bat families. This late Oligocene age was closely followed by independent origination of phytophagous bats (Stenodermatinae, Phylostomidae) in the New World (Rojas et al., 2016; Amador et al., 2018). Both events occurred during a phase of climate warming that saw global temperatures increase to end-Eocene levels, and likely affected positively plant diversity (Zachos et al., 2001). The specialization of phytophagous bats in both the Old (Pteropodidae) and New World (clades inside Phyllostomidae) suggests that they found a highly reliable source of energy and nutrients in plants, but in all cases, plant clades were older than bat clades, indicating that pteropodids and phyllostomids jumped into previously established plant-animal interaction processes, likely between arboreal mammals and these plants millions of years before (see Sánchez and Giannini, 2018; Fleming and Kress, 2011).

CLASSIFICATION AND TAXONOMIC UPDATES

The phylogenetic structure recovered in our study indicates that several taxonomic changes in the higher-level classification of pterodids are necessary, and our recommendations are shown in table 1 (complete down to species level in table S2, available online at: doi.org/10.5531/sd.sp.39). We recognize eight subfamilies and 14 tribes. This classification resembles that of Bergmans (1997), the last formal classification of the entire family Pteropodidae, but it also differs from it in some important aspects. We erect four new tribes, correct two preoccupied subfamily names, and propose the emended diagnosis of *Epomophorus* now inclusive of *Micropteropus* and of one spe-
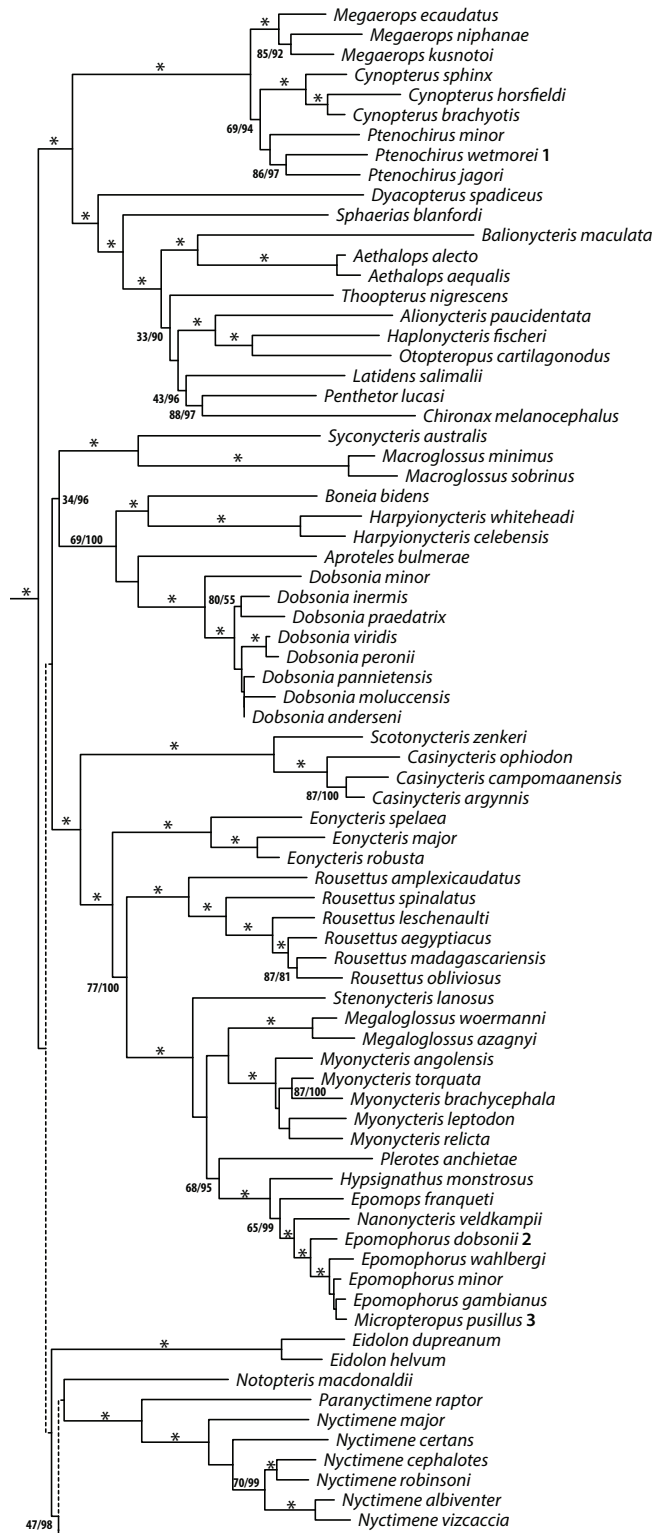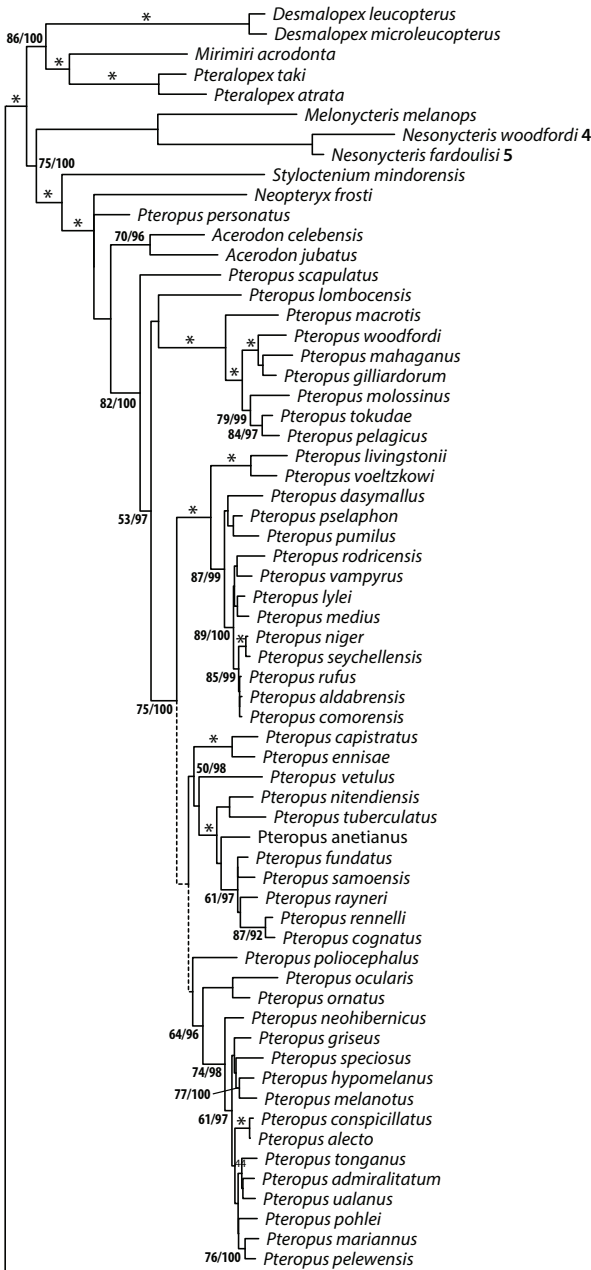
FIGURE 1. Maximum likelihood tree (see text for details) with statistical support values showed on nodes. Asterisks designate nodes with pp ≥ 0.95 (from Bayesian inference, shown as percentages) and bootstrap (maximum likelihood) ≥ 90. Nodes without values had pp ≤0.90 and bootstrap ≤70. Species names on tree reflect the nomenclatural changes proposed herein, with older names for the affected taxa as follows: 1 = *Megaerops wetmorei*, 2 = *Epomops dobsonii*, 3 = *Micropteropus pusillus*, 4 = *Melonycteris woodfordi*, 5 = *Melonycteris fardoulisi*.
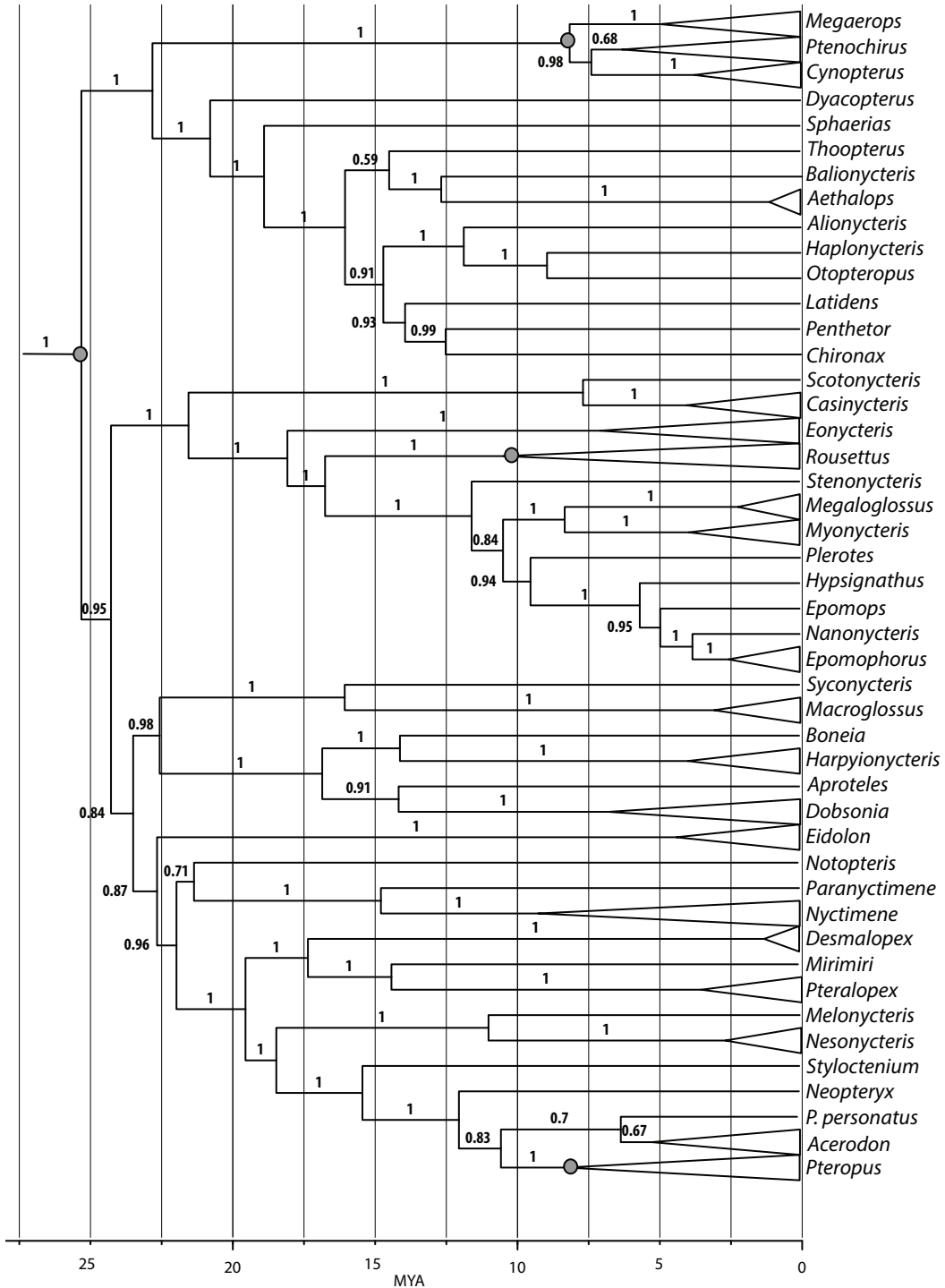
FIGURE 2. Dated tree with genera represented by more than one species in the analysis collapsed. Circles designate nodes that were used in the calibration of the molecular clock. Scale in million years ago.

TABLE 1. New classification of Pteropodidae based on the phylogenetic results presented herein.

Family Pteropodidae Gray, 1821.

Subfamily Cynopterinae Andersen, 1912
 Tribe Cynopterini
  Genera *Cynopterus, Ptenochirus, Megaerops*
 Tribe Balionycterini
  Genera *Dyacopterus, Balionycteris, Chironax, Thoopterus, Sphaerias,*
  Aethalops, Penthetor, Latidens, Alionycteris, Otopteropus, Haplonycteris

Subfamily Macroglossusinae new subfamily
 Genera *Macroglossus, Syconycteris*

Subfamily Harpyionyterinae Miller, 1907
 Tribe Harpyionycterini, new Tribe
  Genera *Hapyionycteris, Boneia*
 Tribe Dobsoniini Andersen, 1912
  Genera *Dobsonia, Aproteles*

Subfamily Rousettinae Andersen, 1912
 Tribe Rousettini Andersen, 1912
  Genus *Rousettus*
 Tribe Eonycterini Almeida et al., 2016
  Genus *Eonycteris*
 Tribe Epomophorini Gray, 1866
  Genera *Epomophorus, Hypsignathus, Epomops, Nanonycteris*
 Tribe Myonycterini Lawrence and Novick, 1963
  Genera *Myonycteris, Megaloglossus*
 Tribe Stenonycterini Nesi et al., 2013
  Genus *Stenonycteris*
 Tribe Scotonycterini, Bergmans, 1997
  Genera *Scotonycteris, Casinycteris*
 Tribe Plerotini, Bergmans, 1997
  Genus *Plerotes*

Subfamily Eidolinae Almeida et al., 2016
 Genus *Eidolon*

Subfamily Notopterisinae new subfamily
 Genus *Notopteris*

Subfamily Nyctimeninae Miller, 1907
 Genera *Nyctimene, Paranyctimene*

Subfamily Pteropodinae Gray, 1821
 Tribe Pteropodini Gray, 1821
  Genera *Pteropus, Acerodon, Styloctenium, Neopteryx*
 Tribe Melonycterini, new tribe
  Genera *Melonycteris, Nesonycteris*
 Tribe Pteralopini, new tribe
  Genera *Pteralopex, Desmalopex, Mirimiri*

cies formerly included in *Epomops*. Remaining issues in pteropodid classification chiefly revolve around uncertainties related to topology of the backbone of the pteropodid tree, poorly sampled species, and lack of morphological correlates of molecular groupings. *Pteropus* in particular, comprising, in our sample, some eight major subclades that include a total of 13 species groups (Almeida et al., 2014), still awaits formal classification in subgenera (see Almeida et al., 2014).

On the basis of our phylogeny, we formalize below taxonomic changes in the classification of Pteropodidae (summarized in table 1) that include new taxonomic units for which we provide descriptions, replacement of preoccupied names, and a formal reclassification of several species that are allocated to other genera; for some of these taxa, an emended diagnosis is provided as needed.

Notopterisinae, New Subfamily

TYPE GENUS: *Notopteris* Gray, 1859.

CONTENTS: Contains one genus, *Notopteris* Gray, 1859, and two species: *N. macdonaldi* Gray, 1859, and *N. neocaledonica* Trouessart, 1908.

SYNONYMS: Notopterini Koopman and Jones, 1970 (unavailable and preoccupied; see below).

DESCRIPTION AND DIAGNOSIS: A moderately sized pteropodid (FA 60–72 mm) with a long tail (subequal in length to the forearm) and wing membranes that meet at the middorsal line, giving a naked-backed appearance. Dental formula i2/2, c1/1, p2/2, m2/3 × 2 = 28, although upper i1 is often lost in adults; anterior lower premolar larger than any other lower premolar or molar; premaxillae well developed and coossified anteriorly, facial process of premaxilla approximately 2× wider dorsally than ventrally; infraorbital canal long; metacarpal formula III< IV≤V; terminal phalanx of digit III subequal to or longer than metacarpal of that digit; no claw on second digit of wing; tibia length approximately half that of forearm; tongue long, approximately 1.5× length of the mandible; no obvious sexual dimorphism.

COMMENTS: Koopman and Jones (1970) coined the name "Notopterini" for a tribe of pteropodids including *Notopteris* and *Melonycteris*, but they did not make this name available under the rules of the International Commission on Zoological Nomenclature (ICZN) because this taxon was not identified as new and the authors failed to provide a description or diagnosis indicating the characters purported to differentiate this taxon. As reviewed by Baker et al. (2016), the current Code (ICZN, 1999) is unambiguous about what is required for a family-group name (including subfamilies and tribes) to be available. In addition to requirements for publication, the name must be a noun in the nominative plural formed from the stem of an available generic name (articles 11.7.1 and 13.2) or the whole genus name (art. 29.1), which must be cited in the description (art. 16.2); and the name must end with an appropriate family-group name suffix (arts. 11.7.1.3 and 29.2). For all names published after 1930, the name must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (art. 13.1.1) or a bibliographic reference to such a statement (art. 13.1.2); it may include a diagnosis to differentiate it from related and similar groups (recommendation 13A). And, as with all taxonomic names, family-group names are required to conform to the principle of homonymy (arts. 52, 53.1, 55), which notes that when two or more taxa are distinguished from each other, they must not be denoted by the same name.

The rules for formation of family-group names are straightforward and involve application of appropriate suffixes (-idae for a family name, -inae for a subfamily name, and –ini to the name of a tribe) to the Greek or Latin stem of a genus name (ICZN, 1999: art. 29). In the case

of *Notopteris*, the Greek stem is composed of two parts: *noto-* (Greek for "back") and *pter-* (Greek for "wing") forming *notopter-* (back wing). The appropriately formed family group names for this taxon would thus be Notopteridae, Notopterinae, and Notopterini, the latter of which was used by Koopman and Jones (1970) for the pteropodid bat group including *Notopteris* and *Melonycteris* (the latter presumably including *Nesonycteris*). In grouping these taxa together those authors were apparently following Andersen (1912), who did not propose a formal name for this group but variously referred to it as the "Notopterine section" of the Macroglossinae (Andersen, 1912: lxii), or as the "Notopterides" (Andersen, 1912: lxv). Bergmans (1997) noted this history and attributed authorship of the Tribe Notopterini to Andersen (1912), but this was incorrect – authorship of the formal family-group name Notopterini as applied to bats dates to Koopman and Jones (1970), a fact noted by Koopman (1994).

Regardless of issues of availability and authorship, yet another problem exists with the use of Notopterini as a family-group name in Chiroptera: it is preoccupied by Notopteridae Bleeker, 1859, a family of osteoglossiform fishes commonly known as knifefishes. Notopteridae Bleeker, 1859, is based on *Notopterus* Lacépède, 1800, which has the same Greek stem as *Notopteris* Gray, 1859. To avoid homonymy, any family-group names based on the stem *notopter-* can be applied only to fishes including *Notopterus* based on the principle of priority (which applies to family-group names and covers homonyms as well as synonyms; ICZN, 1999: arts. 23.1, 23.4) because these names were used in fishes prior to their use in bats. Homonymy from similar but not identical generic names that share the same stem is recognized by the Code (arts. 29.3, 29.6, 55.3), and recommendation 29A explicitly offers a preferred means of addressing this problem: authors are advised to use the entire generic name as the stem in formulating a new family-group taxon. In the case of bats, *notopteris-* thus would be the appropriate stem for formation of new family-group names. We thus propose Notopterisinae as a new family-group name for the clade including the type genus *Notopteris*. The new subfamily Notopterisinae differs from prior concepts (e.g., Notopterini Koopman and Jones, 1970) additionally in being restricted to only the genus *Notopteris*.

Macroglossusinae, New Subfamily

Type genus: *Macroglossus* F. Cuvier, 1824.

Contents: Includes two genera, *Macroglossus* F. Cuvier, 1824, and *Syconycteris* Matschie, 1899, and five species classified into two genera: *M. sobrinus* Andersen, 1911, *M. minimus* (E. Geoffroy, 1810), *Syconycteris australis* (Peters, 1867), *S. hobbit* Ziegler, 1982, and *S. carolinae* Rozendaal, 1984.

Synonyms: Macroglossinae Harris, 1939 (preoccupied; see below).

Diagnosis: Small to small-medium (in adults, interspecific ranges of head-body length 49–97 mm, forearm 37–61 mm, body weight 13–47 g; Giannini et al., 2019), long-snouted nectarivorous pteropodids with tail, uropatagium, and calcar rudimentary (*Macroglossus*) or absent (*Syconycteris*), rostrum long, strongly deflected ventrally with respect to the basicranial axis; dentition generally weak; tongue greatly elongated with long, unfringed filiform papillae on tip.

Comments: As in the case of *Notopteris* developed above, the widely used subfamily name Macroglossinae is preoccupied as it designates sphingid lepidopterans of subfamily Macroglossinae Harris, 1839, tribe Macroglossini Harris, 1839, and subtribe Macroglossina Harris, 1839, referred to genus *Macroglossum* Scopoli, 1777. We applied the same concept as in *Notopteris* (see above), providing a replacement name by changing the name of this subfamily to Macroglossusinae, using the entire genus name *Macroglossus* as valid stem and adding the suffix -inae, again following recommendation 29A of the Code. The content is now restricted to genera *Macroglossus* and *Syconycteris* to the exclusion of other nectar-feeding pteropodids previously thought to be closely related: the "macroglossine section" of Andersen (1912) that formerly included *Eonycteris* (relocated to Rousettinae), *Melonycteris* and *Nesonycteris* (relocated to Pteropodinae), and *Notopteris* (placed on a family of its own; see above).

Melonycterini, New Tribe

Type genus: *Melonycteris* Dobson, 1877.

Contents: Includes two genera, *Melonycteris* Dobson, 1877, and *Nesonycteris* Thomas, 1887, and three species: *M. melanops* Dobson, 1877, *Nesonycteris fardoulisi* (Flannery, 1995), and *N. woodfordi* (Thomas, 1887).

Description and Diagnosis: Small to moderately sized pteropodids (FA 42 –63 mm) with vestigial anterior upper and lower premolars; dental formula i2/1–2, c1/1, p3/3, m2/3 × 2 = 32–34; middle lower premolar smaller than either molar; premaxillae well developed and in simple contact (or not in contact) anteriorly; facial process of premaxilla approximately 2–3× wider dorsally than ventrally; infraorbital canal long; metacarpal formula III< IV≤V; terminal phalanx of digit III subequal to or longer than metacarpal of that digit; claw present on digit II of wing in some species; tibia much less than half the length of the forearm; tail absent.

Comments: This tribe is equivalent to the genus *Melonycteris* as recognized by many authors (e.g., Flannery, 1995; Simmons and Cirranello, 2019). We treat *Nesonycteris* as a genus distinct from *Melonycteris*; see comments under *Nesonycteris* below.

Pteralopini, New Tribe

Type genus: *Pteralopex* Thomas, 1888.

Contents: Contains three genera, *Pteralopex* Thomas, 1888, *Mirimiri* Helgen, 2007, and *Desmalopex* Miller, 1907, and eight species: *Pteralopex anceps* K. Andersen, 1909, *P. atrata* Thomas, 1888, *P. flanneryi* Helgen, 2005, *P. pulchra* Flannery, 1991, and *P. taki* Parnaby, 2002; *Mirimiri acrodonta* (Hill and Beckon, 1978); and *Desmalopex leucopterus* (Temminck, 1853) and *D. microleucopterus* Esselstyn et al., 2008.

Description and diagnosis: Large to very large flying-fox-like pteropodids (FA 116–171 mm); dental formula i2/2, c1/1, p3/3, m2/3 × 2 = 34; upper molar teeth subquadrate to quadrate in occlusal view; premaxillae well developed and either in simple contact or co ossified anteriorly;

postorbital process very long, often contacts zygoma to completely enclose the orbit posteriorly; second phalanx of digit IV of wing longer than first phalanx; claw present on digit II of wing.

COMMENTS: The recent segregation of the Fijian monkey-faced bat in a genus of its own (*Mirimiri*) is strongly supported here by the very long branch separating the two *Pteralopex* species included in this study (*P. atrata* and *P. taki*) and *Mirimiri acrodonta*; mutual synapomorphies are listed in Helgen (2005). In addition, the relationship between *Desmalopex* (formerly in *Pteropus*) and monkey-faced bats (*Pteralopex* + *Mirimiri*) is also strongly supported (see also Almeida et al., 2014, 2018). Therefore, inclusion of the three genera in this new tribe is confirmed.

Harpyionycterini, New Tribe

TYPE GENUS: *Harpyionycteris* Thomas, 1896.

CONTENTS: Includes two genera, *Harpyionycteris* Thomas, 1896 and *Boneia* Jentink, 1879, and three species: *Harpyionycteris whiteheadi* Thomas, 1896, *H. celebensis* Miller and Hollister, 1921, and *Boneia bidens* Jentink, 1879.

DIAGNOSIS: No morphological diagnostic characters have been identified for this tribe. However, *Harpyionycteris* + *Boneia* compose a well-supported group (fig. 1).

COMMENTS: This new tribe is one of two tribes (see also below) recognized here within the subfamily Harpyionycterinae Miller, 1907, whose contents were established by Giannini et al. (2009) as including *Harpyionycteris*, *Boneia*, *Dobsonia*, and *Aproteles*. Previously, *Boneia* was treated as a subgenus of *Rousettus* (e.g., Bergmans, 1994, 1997; Bergmans and Rozendaal, 1988), or as a valid genus associated with *Rousettus* (e.g., Andersen, 1912; Koopman, 1993) on the basis of morphological similarity. However, *Boneia* has been consistently recovered in phylogenetic analyses as sister to *Harpyionycteris* (Giannini et al., 2009, Almeida et al., 2011, Amador et al., 2018), a result reproduced herein as well, which is the basis of recognizing this tribe within Harpyionycterinae. *Harpyionycteris* has long been considered an early offshoot of the pteropodid tree chiefly due to its unusually multicuspidate dentition resembling a (primitive mammalian) tribosphenic pattern (e.g., Slaughter, 1970). Significantly, Andersen (1912) nevertheless noted the close affinity with *Dobsonia*, which was first confirmed phylogenetically only recently (in Giannini et al., 2006). Therefore, the dentition and other characters such as the procumbent premaxilla, mandibular symphysis, and incisors of *Harpyionycteris* have been interpreted as uniquely derived traits of this genus (Giannini et al., 2006). Hassanin et al. (2016) used Boneini as a tribe-level name for a group whose membership corresponds to that of Harpyionycterinae Miller, 1907, as modified by Giannini et al. (2009), and Boneini is therefore considered a junior synonym.

Dobsoniini Andersen, 1912

TYPE GENUS: *Dobsonia* Palmer, 1898.

CONTENTS: Includes two genera, *Dobsonia* Palmer, 1898, and *Aproteles* Menzies, 1977, and 14 species: *Dobsonia anderseni* Thomas, 1914, *D. beauforti* Bergmans, 1975, *D. chapmani* Rabor, 1952, *D. crenulata* K. Andersen, 1909, *D. emersa* Bergmans and Sarbini, 1985, *D.*

exoleta K. Andersen, 1909, *D. inermis* K. Andersen, 1909, *D. minor* (Dobson, 1879), *D. moluccensis* (Quoy and Gaimard, 1830), *D. pannietensis* (De Vis, 1905), *D. peronii* (E. Geoffroy Saint-Hilaire, 1810), *D. praedatrix* K. Andersen, 1909, *D. viridis* (Heude, 1896); and *Aproteles bulmerae* Palmer, 1977.

DIAGNOSIS: Midsized to large pteropodids uniquely characterized by the combination of wings that originate from the spine, thus giving the appearance of bare-backed bats, and the dental formula I 0–1/0, C 1/1, P 2/3, M 2/3. Other bare-backed bats (*Rousettus spinalatus* and *Notopteris* spp.) always exhibit at least one lower incisor, but in addition these species greatly differ in numerous other cranial and dental features as they belong in different subfamilies.

COMMENTS: Bergmans (1997) attributed the authorship of this tribe to Andersen (1912). Besides the extensive description of *Dobsonia* in Andersen (1912), to our knowledge there is no proper diagnosis of this tribe as currently composed (*Dobsonia* plus the more recently described *Aproteles*), only the mention of its constituent genera by Bergmans (1997), and hence the diagnosis provided above. *Dobsonia* and *Aproteles* are quite alike and differ chiefly in dental formula, with *Aproteles* completely lacking incisors, both upper and lower, and *Dobsonia* species lacking the claw on index finger (present in *Aproteles*). *Aproteles* is monotypic and contains the critically endangered, New Guinea highlands endemic, *A. bulmerae*, while *Dobsonia* is more speciose and geographically widespread, albeit the distribution of the genus is centered also in New Guinea. First discovered as a subfossil dated 12000 years old, some evidence suggests that *Aproteles* has been in decline perhaps for millennia, probably due to hunting by humans both prehistorically (as first encountered as food remains in archaeological sites), and currently in its limited range (Flannery, 1995). Competition for caves with *Dobsonia* species may be an additional cause of decline (Bonaccorso, 1998); our tree shows that *Dobsonia* species are all considerably younger than its sister *Aproteles*, thus contributing some support to this hypothesis.

Epomophorus Bennett, 1835

TYPE SPECIES: *Pteropus gambianus* Ogilby, 1835.

CONTENTS: Includes 11 species: *Epomophorus angolensis* Gray, 1970, *E. anselli* Bergmans and van Strien, 2004, *E. crypturus* Peters, 1852, *E. dobsonii* Bocage, 1889, *E. gambianus* (Ogilby, 1835), *E. grandis* (Sanborn, 1950), *E. labiatus* (Temminck, 1837), *E. minor* Dobson, 1879, *E. wahlbergi* (Sundevall, 1846), *E. pusillus* Peters, 1867, and *E. intermedius* (Hayman, 1963).

SYNONYMS: *Micropteropus* Matschie, 1899.

EMENDED DIAGNOSIS: Typical epomophorine pteropodids with epaulettes in adult males and tufts of white hairs medially and laterally on the ears in both sexes; five to six thickened palatal ridges present; and postdental palate deeply concave.

COMMENTS: *Epomophorus minimus* Claessen and De Vree, 1991, is provisionally considered a junior synonym of *E. minor* Dobson, 1879, pending thorough revision of small-sized *Epomophorus* in the *minor-minimus-labiatus* complex, of which *E. anselli* may also be part.

Our revised definition of *Epomophorus* contains species historically assigned to this genus, along with species subsequently transferred to *Epomops* (i.e., *dobsonii*), species included in *Micropteropus* as subgenus of *Epomophorus* (i.e., *pusillus*), and species originally described in *Micropteropus* (i.e., *grandis*, *intermedius*). Therefore, in this treatment *Epomophorus* contains, in addition to its typical species, all three species previously assigned to *Micropteropus* (thus considered a junior synonym at the genus level), as well as the form *dobsonii* (formerly in *Epomops*). This broadly defined, inclusive *Epomophorus* is justified based on findings that the aforementioned species nest within the smallest clade containing the typical *Epomophorus* species in all recent phylogenies (Almeida et al., 2016; Amador et al., 2018; Nesi et al., 2011, 2013), including this study. This arrangement is supported by our reinterpretation of palatal-ridge patterns (discussed further below), which provides a clear synapomorphy for this redefined *Epomophorus*.

Epomophorus, as defined and diagnosed here, exhibits 5–6 thickened palatal ridges in all 11 species, with the following variation among species. The other three genera in tribe Epomophorini (*Hypsignathus*, *Epomops* and *Nanonycteris*) bear just three such thickened ridges. Typical *Epomophorus* (*E. gambianus*, *E. crypturus*, *E. wahlbergi*, *E. angolensis*, *E. labiatus*, *E. minor*, *E. minimus*, and *E. anselli*) all have the typical pattern of six thickened palatal ridges, with some interspecific variation that includes ridges with or without a median notch, and ridges whose location varies with respect to the dentition (e.g., one versus two postdental ridges; Bergmans, 1997). Species previously referred to *Micropteropus* (*pusillus*, *grandis*, and *intermedius*) all have six thickened palatal ridges, of which the first is large, undivided, and hastate, while the next five ridges are divided by a deep, continuous median groove; furthermore, ridges two through six are in close contact in *intermedius* and *pusillus* (see Bergmans, 1988, 1997). *Epomophorus dobsonii* has five ridges, but the second one is incipiently split; we observe that this may be the result either of fusion (of formerly separate ridges two and three) or of a division of the second ridge (Bergmans, 1997). In addition, *E. dobsonii* lacks the typical condition of the pterygoid bone seen in *Epomops* (the genus to which it was referred to for most of its taxonomic history), namely, a pterygoid bone not rolled up to form a deep cavity as is typically present in *Epomops buettikoferi* and *E. franqueti* (this trait was figured in Bergmans, 1989: figs. 6, 12). Instead, the pterygoid in *Epomophorous dobsonii* resembles that of other epomophorines including all *Epomophorus* (Bergmans, 1989: fig. 9). The condition of the postdental palate in *E. dobsonii* and all species previously referred to *Micropteropus* also matches typical *Epomophorus*, which have deeply concave postdental palate (see Bergmans, 1988, 1989, 1997; Giannini and Simmons, 2005), as opposed to palate only weakly concave in *Epomops* (Bergmans, 1989).

Nesonycteris Thomas, 1887

Type species: *Nesonycteris woodfordi* Thomas, 1887.

Contents: Includes two species: *Nesonycteris fardoulisi* (Flannery, 1993) and *N. woodfordi* Thomas, 1887.

Synonyms: None.

Diagnosis: *Nesonycteris* species lack a claw on the second digit (present in *Melonycteris*), lack the first lower incisor (present in *Melonycteris*), and present dorsal and ventral body fur similarly light orange brown (*Melonycteris* has a dark brown venter and orange dorsum).

Comments: *Nesonycteris* is often included in *Melonycteris* (e.g., Flannery, 1993; Simmons and Cirranello, 2019), but the phylogenetic results reported here recovered the two species of *Nesonycteris* forming a strongly supported clade that is sister to *Melonycteris* and separated by a very long branch dated with a point estimate of their split at 10 mybp. Moreover, *Melonycteris* and *Nesonycteris* each exhibit apomorphies (see Diagnosis above) that, together with our phylogenetic results, warrant recognition of two genera.

Megaerops Peters, 1865

Type species: *Pachysoma ecaudatus* Temminck, 1837.

Contents: Includes four species: *Megaerops ecaudatus* (Temminck, 1837), *M. kusnotoi* Hill and Boeadi, 1978, *M. niphanae* Yenbutra and Felten, 1983, and *M. albicollis* (Francis, 1989). It does not include the form *wetmorei*, transferred to *Ptenochirus* as *P. wetmorei*.

Synonyms: None; included as a subgenus of *Pachysoma* (= *Cynopterus*).

Emended diagnosis: Cynopterine genus with tail generally absent (extremely short, up to 4 mm only in some western Malaysian specimens of *M. albicollis*), rostrum short and deep, extremely deep in type species, with upper incisors unequal (I2 about one half of I1), upper canine relatively short and with mesial surface convex (without mesial groove), single lower incisor represented by i2 (see Giannini and Simmons, 2007), lower canine very short.

Comments: Simmons (2005) recognized four species of *Megaerops*: *M. ecaudatus*, *M. niphanae*, *M. kusnotoi*, and *M. wetmorei*, the latter with two distinct subspecies, the Philippine *M. w. wetmorei* and the Sundaic *M. w. albicollis* Francis, 1989. Recently, Giannini (2019) recognized *albicollis* as a separate, valid species of *Megaerops*, and transferred typical *wetmorei* to *Ptenochirus*, as *P. wetmorei*. Here we provide additional justification for these changes. On the basis of three specimens (two from Borneo and one from peninsular Malaysia), Francis (1989) described a distinct cynopterine taxon, *Megaerops wetmorei albicollis*, noting, however, that "differences [with respect to *M. w. wetmorei* from Mindanao] seem sufficient to warrant taxonomic recognition, but because of the geographic separation and the small number of specimens available, I consider it most appropriate to recognize them at the subspecific level" (Francis, 1989: 2878). We believe that Francis's intuition was correct about the species-level status of this new taxon. New specimens have expanded the previously known distribution to Sumatra and confirmed the distinctiveness of *albicollis* (see Maharadatunkamsi and Maryanto, 2002). Furthermore, Francis (1989) correctly specified a number of external and craniodental characters that distinguish *albicollis* from *wetmorei*. It turns out that these differences largely serve to distinguish *Megaerops* from *Ptenochirus* at the genus level, which is in line with the consistent recovery of *wetmorei* grouping in *Ptenochirus* and separate from *Megaerops* in phylogenetic analyses (e.g., Almeida et al., 2009; this study). These observations led Giannini (2019) to recognize *albicollis* as a valid species within *Megaerops* (as M. *albicollis*, new combina-

tion) with Sundaic distribution as typical of *Megaerops*, and to include *wetmorei* in the Philippine *Ptenochirus* (as monotypic *P. wetmorei*) with a distribution in Mindanao only. *Megaerops albicollis* has not been included in any phylogeny to date, but it is similar to other *Megaerops* in craniodental characters and in the uniform light-brown, creamy pelage, particularly apparent in *M. niphanae*, from which it can be distinguished by the distinctive, ample white ruff (the species epithet means "white collar"). By contrast, the pelage pattern of *Ptenochirus wetmorei* is typical of *Ptenochirus* species, i.e., dark gray head, dark muzzle, rusty ruff, and grayish-brown to rusty-brown body pelage. The tail is absent in *Megaerops* except in some specimens of *albicollis* (up to 4 mm; see Francis 1989, Giannini 2019). Craniodental characters of *M. albicollis* are typical of *Megaerops* and distinct from *Ptenochirus*, as follows: rostrum short, deep, and wide (vs. longer, shallower, and narrower in *Ptenochirus*); palate wide and semicircular (vs. narrow with slightly divergent tooth rows in *Ptenochirus*); dentition weak, with upper canine and premolars almost vertical, short (vs. dentition generally stronger, with noticeably longer, procumbent upper canines, and premolars with longer, shorter main cusp in *Ptenochirus*). These differences are schematically illustrated by Francis (1989: fig. 2).

Ptenochirus Peters, 1861

Type species: *Ptenochirus jagori* (Peters, 1861).

Contents: Includes three species: *Ptenochirus jagori* (Peters, 1861), *P. minor* (Yoshiyuki, 1979), and *P. wetmorei* (Taylor, 1934). *Ptenochirus* as thus recognized does not include *albicollis,* currently treated as *Megaerops albicollis* but originally described as *Megaerops wetmorei albicollis* Francis, 1999 (see details above).

Synonyms: None; described by Peters as a subgenus of *Pachysoma* (= *Cynopterus*).

Diagnosis: As in Andersen (1912), a cynopterine genus with upper incisors unequal (inner incisors considerably bulkier and longer than minute outer incisors), upper canine with deep anteromedial (i.e., mesial) groove (inconspicuous in *P. wetmorei*), single lower incisor representing i2 (see also Giannini and Simmons, 2007), tail always present (range across species 3–18 mm), head pelage significantly darker than body pelage, rusty brown ruff.

Comments: *Ptenochirus wetmorei* was originally described in *Megaerops* chiefly because it lacks a tail, which is characteristic of *Megaerops* among cynopterine genera (see Taylor, 1934). *Ptenochirus wetmorei* indeed appears intermediate between typical *Ptenochirus* and *Megaerops* in some morphological aspects (very short tail, upper canine with barely noticeable or lacking groove), but a closer relationship of this form to *Ptenochirus jagori* (and *P. minor*) than to *Megaerops* species was found in the first comprehensive study of cynopterine relationships by Almeida et al. (2009), a finding replicated in this study.

CONCLUSIONS

A dated phylogeny of the speciose bat family Pteropodidae is presented here sampling ~70% of currently recognized species and all 45 genera. We recovered support for eight major

clades, all now identified at subfamily level, although relationships among these taxa along the backbone of the tree remained mostly unresolved. Several subfamilies contain well-supported internal structure that is recognized in tribes both previously proposed and new taxa described herein. We applied taxonomic changes to the classification of Pteropodidae to reflect our phylogenetic results, including proposal of new tribes, correction of preoccupied names at subfamily level, redefinition with emended diagnosis of a key African genus, *Epomophorus,* recognition of *Nesonycteris* as a genus distinct from *Melonycteris*, and reorganization of species and subspecies previously included in *Megaerops wetmorei*. In sum this represents a new phylogeny-based classification of the Pteropodidae, and invites a reinterpretation of evolutionary history of this diverse clade. A preliminary view of this history based on our results suggests a South-East Asian origin for the family associated with a complete shift to phytophagy; an early, rapid dispersal of main-subclade ancestors to reach most continents and near-continent islands presently occupied by the descendant species; and a recent phase of oceanic dispersal and spectacular diversification in flying foxes (*Pteropus*), which successfully reached remote-island environments of the western Indian and northwestern Pacific oceans and central Polynesia.

ACKNOWLEDGMENTS

REFERENCES

Almeida, F.C., N.P. Giannini, R. DeSalle, and N.B. Simmons. 2009. The phylogenetic relationships of cynopterine fruit bats (Chiroptera: Pteropodidae: Cynopterinae). Molecular Phylogenetics and Evolution 53: 772–783.

Almeida, F.C., N.P. Giannini, R. DeSalle, and N.B. Simmons. 2011. Evolutionary relationships of the Old World fruit bats (Chiroptera, Pteropodidae): another star phylogeny? BMC Evolutionary Biology 11: 1–17.

Almeida, F.C., N.P. Giannini, N.B. Simmons, and K.M. Helgen. 2014. Each flying fox on its own branch: A phylogenetic tree for *Pteropus* and related genera (Chiroptera: Pteropodidae). Molecular Phylogenetics and Evolution 77: 83–95.

Almeida, F.C., N.P. Giannini, and N.B. Simmons. 2016. The evolutionary history of the African fruit bats (Chiroptera: Pteropodidae). Acta Chiropterologica 18: 73–108.

Álvarez ,Y., et al. 1999. Molecular phylogeny and morphological homoplasy in fruitbats. Molecular Biology and Evolution 16: 1061–1067.

Amador, L.I., R.L. Arévalo-Moyers, F.C. Almeida, S.A. Catalano, and N.P. Giannini. 2018. Bat systematics in the light of unconstrained analyses of a comprehensive molecular supermatrix. Journal of Mammalian Evolution 25: 37–70.

Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum, 2nd ed., vol. 1: Megachiroptera. Trustees British Museum, London, ci + 854 pp.

Baker, R.J., S. Solari, A. Cirranello, and N.B. Simmons. 2016. Higher level classification of phyllostomid bats with a summary of DNA synapomorphies. Acta Chiropteralogica 18: 1–38.

Bergmans, W. 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera) 1: general introduction; material and methods; results: the genus *Epomophorus* Bennett, 1836. Beaufortia 38: 75–146.

Bergmans, W. 1989. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera) 2: the genera *Micropteropus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899, and *Plerotes* Andersen, 1910. Beaufortia 39: 89–153.

Bergmans, W. 1994. Taxonomy and biogeography of African fruitbats (Mammalia, Megachiroptera) 4: the genus *Rousettus* Gray, 1821. Beaufortia 44: 79–126.

Bergmans, W. 1997. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera) 5: the genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899 and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. Beaufortia 47: 11–90.

Bergmans, W., and F. G. Rozendaal. 1988. Notes on collections of fruit bats from Sulawesi and some off-lying islands (Mammalia, Megachiroptera). Zoologische Verhandelingen 248: 1–74.

Bonaccorso, F.J. 1998. Bats of Papua New Guinea. Washington, DC: Conservation International.

Boonman, A., S. Bumrungsri, and Y. Yove. 2014. Nonecholocating fruit bats produce biosonar clicks with their wings. Current Biology 24: 2962–2967.

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552.

Drummond, A.J., S.Y. Ho, M.J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4: e88.

Drummond, A.J., M.A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29: 1969–1973.

Flannery, T.F. 1993. Revision of the genus *Melonycteris* (Pteropodidae: Mammalia). Records of the Australian Museum 45: 59–80.

Flannery, T.F. 1995. Mammals of New Guinea. Sydney: Reed.

Fleming, T.H., and W.J. Kress. 2011. A brief history of fruits and frugivores. Acta Oecologica 37: 521–530.

Francis, C.M. 1989. Notes on fruit bats (Chiroptera, Pteropodidae) from Malaysia and Brunei, with the description of a new subspecies of *Megaerops wetmorei* Taylor, 1934. Canadian journal of Zoology 67: 2878–2882.

Giannini, N.P. 2019. Pteropodidae. *In* D.E. Wilson and R. Mittermeier (editors), Handbook of the Mammals of the World. 9. Bats: 16–61. Barcelona: Lynx Edicions.

Giannini, N.P. and N.B. Simmons. 2003. A phylogeny of megachiropteran bats (Mammalia: Chiroptera: Pteropodidae) based on direct optimization analysis of one nuclear and four mitochondrial genes. Cladistics 19: 496–511.

Giannini, N.P. and N.B. Simmons. 2005. Conflict and congruence in a combined DNA-morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). Cladistics 21: 411–437.

Giannini, N.P., and N.B. Simmons. 2007. Element homology and the evolution of dental formulae in megachiropteran bats (Mammalia: Chiroptera: Pteropodidae). American Museum Novitates 3559: 1–27.

Giannini, N.P., F.C. Almeida, N.B. Simmons, and R. DeSalle. 2006. Phylogenetic relationships of the enigmatic harpy fruit bat, *Harpyionycteris* (Mammalia: Chiroptera: Pteropodidae). American Museum Novitates 3533: 1–12.

Giannini, N.P., F.C. Almeida, N.B. Simmons, and K.M. Helgen. 2008. The systematic position of *Pteropus leucopterus* and its bearing on the monophyly and relationships of *Pteropus* (Chiroptera: Pteropodidae). Acta Chiropterologica, 10: 11–20.

Giannini, N.P., F.C. Almeida, and N.B. Simmons. 2009. Phylogenetic relationships of harpyionycterine megabats (Chiroptera: Pteropodidae). In R.S. Voss and M.D. Carleton, Systematic mammalogy: contributions in honor of Guy G. Musser. Bulletin of the American Museum of Natural History 331: 183–205.

Halpin, K., A et al. 2011. Pteropid bats are confirmed as the reservoir hosts of henipaviruses: a comprehensive experimental study of virus transmission. American Journal of Tropical Medicine and Hygiene 85: 946-951.

Hassanin, A. 2014. Description of a new bat species of the tribe Scotonycterini (Chiroptera, Pteropodidae) from southwestern Cameroon. Comptes Rendus Biologies 337: 134–142.

Hassanin, A., et al. 2016. Comparative phylogeography of African fruit bats (Chiroptera, Pteropodidae) provide new insights into the outbreak of Ebola virus disease in West Africa, 2014–2016. Comptes Rendus Biologies 339: 517-528.

Hayman, D.T.S., et al. 2010. Long-term survival of an urban fruit bat seropositive for ebola and Lagos bat viruses. PLoS One 5: e11978.

Helgen, K.M. 2005. Systematics of the Pacific monkey-faced bats (Chiroptera: Pteropodidae), with a new species of *Pteralopex* and a new Fijian genus. Systematics and Biodiversity 3: 433–453.

Hill, J.E. 1983. Bats (Mammalian: Chiroptera) from Indo-Australia. Bulletin of the British Museum (Natural History). Zoology Series 45: 103-208.

Hollar, L.J., and M.S. Springer. 1997. Old World fruit bat phylogeny: evidence for convergent evolution and an endemic African clade. Proceedings of the National Academy of Science of the United States of America 94: 5716–5721.

International Commission on Zoological Nomenclature (ICZN). 1999. International code of zoological nomenclature, 4th ed. London: International Trust for Zoological Nomenclature.

Juste B., J., Y. Álvarez, E. Tabarés, A. Garrido-Pertierra, C. Ibáñez, and J.M. Bautista. 1999. Phylogeography of African fruit bats (Megachiroptera). Molecular Phylogenetics and Evolution 13: 596–604.

Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

Koopman, K.F. 1993. Order Chiroptera. In D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference. Washington: Smithsonian Institution Press.

Koopman, K.F. 1994. Chiroptera: systematics. Handbook of Zoology, vol. 8, Mammalia, part 60. New York: Walter de Gruyter.

Koopman, K.F., and J.K. Jones, Jr. 1970. Classification of bats. In B.H. Slaughter and D.W. Walton (editors), About bats: a chiropteran biology symposium: 22–28. Dallas: Southern Methodist University Press.

Kunz, T.H., and E.D. Pierson. 1994. Bats of the World: an introduction. *In* R.M Nowak (editor), Walker's bats of the world. Baltimore: John Hopkins University Press.

Lee, W J., B. Falk, C. Chiu, A. Krishnan, and C.F. Moss. 2016. Asymmetric multi-frequency biosonar beam pattern of tongue-clicking bat, *Rousettus aegyptiacus*. Journal of the Acoustical Society of America 139: 2115–2115.

Lei, M., and Dong, D. 2016. Phylogenomic analyses of bat subordinal relationships based on transcriptome data. Scientific Reports 6: 27726.

Leroy, E.M., et al. 2005. Fruit bats as reservoirs of ebola virus. Nature 438: 575–576.

Maharadatunkamsi, M., and Maryanto, I. 2002. Morphological variation of the three species fruit bat genus *Megaerops* from Indonesia with its new distribution record. Treubia 32: 63–85.

Moyers-Arévalo, R.L., L.I. Amador, F.C. Almeida, and N.P. Giannini. 2018. Evolution of body mass in bats: Insights from a large supermatrix phylogeny. Journal of Mammalian Evolution. [doi: 10.1007/s10914-018-9447-8]

Nesi, N., E. Nakouné, C. Cruaud, and A. Hassanin. 2011. DNA barcoding of African fruit bats (Mammalia , Pteropodidae): the mitochondrial genome does not provide a reliable discrimination between *Epomophorus gambianus* and *Micropteropus pusillus*. Comptes Rendus Biologies 334: 544–554.

Nesi, N., et al. 2013. Molecular systematics and phylogeography of the tribe Myonycterini (Mammalia, Pteropodidae) inferred from mitochondrial and nuclear markers. Molecular Phylogenetics and Evolution 66: 126–137.

Nowak, R.M.. 1994. Walker's bats of the world. Baltimore, MD: John Hopkins University Press.

Olival, K.J., et al. 2013. Ebola virus antibodies in fruit bats, Bangladesh. Emerging Infectious Diseases 19: 270–273.

Phalen, D.N., et al. 2017. Genetic diversity and phylogeny of the Christmas Island flying fox (*Pteropus melanotus natalis*). Journal of Mammalogy 98: 428–437.

Rambaut, A. 2009. FigTree. Online resource (http://tree.bio.ed.ac.uk/software/figtree/).

Rambaut, A., M.A. Suchard, D. Xie, and A.J. Drummond. 2014. Tracer v 1.6. Online resource (http://tree.bio.ed.ac.uk/software/tracer/).

Rojas, D., O.M. Warsi, and L.M. Dávalos. 2016. Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant neotropical diversity. Systematic Biology 65: 432–448.

Ronquist, F., and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Sánchez, M.S., and N.P. Giannini. 2018. Trophic structure of frugivorous bats in the Neotropics: emergent patterns in evolutionary history. Mammal Review 48: 90–107.

Simmons, N.B. 2005. Order Chiroptera. *In* Wilson D.E. and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference. Baltimore, MD: Johns Hopkins University Press.

Simmons, N.B. and A.L. Cirranello. 2019. Bat species of the world: a taxonomic and geographic database. Online resource (https://batnames.org), accessed November 1, 2019.

Shi, J.J., and D.L. Rabosky. 2015. Speciation dynamics during the global radiation of extant bats. Evolution 69: 1528–545.

Slaughter, B.H. 1970. Evolutionary trends of chiropteran dentitions. *In* B.H. Slaughter and D.W. Walton (editors), About bats: a chiropteran biology symposium: 83. Dallas: Southern Methodist University Press.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313.

Teeling, E.C., O. Madsen, R.A. Van Den Bussche, W.W. de Jong, M.J. Stanhope, and M. Springer. 2002. Microbat paraphyly and the convergent evolution of a key innovation in Old World rhinolophoid microbats. Proceeding of the National Academy of Science of the United States of America 99: 1431–1436.

Teeling, E.C., M.S. Springer, O. Madsen, P. Bates, S.J. O'brien, and W. Murphy. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307: 580–584.

Towner, J.S., et al. 2007. Marburg virus infection detected in a common African bat. PloS One 2: e764.

Tsang, S.M.S. 2015. Phylogeography of Southeast Asian flying foxes (Chiroptera: Pteropodidae: *Pteropus*). Ph.D. dissertation, City University of New York.

Yovel, Y., M. Geva-Sagiv, and N. Ulanovsky. 2011. Click-based echolocation in bats: not so primitive after all. Journal of Comparative Physiology A 197: 515–530.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. science 292: 686-693.