Morphological Diagnoses of Higher-Level Phyllostomid Taxa (Chiroptera: Phyllostomidae)

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Phyllostomidae (New World leaf-nosed bats), the second most speciose chiropteran family, is one of the best-known and well-studied chiropteran groups. Due to the ecological and morphological diversity of this family, comparative studies of phyllostomids abound in the literature, and numerous systematic and phylogenetic analyses have been published. Unfortunately, many of these studies have reached different conclusions concerning phyllostomid relationships, and have proposed different classification schemes. This has led to confusion, and highlighted the need for a well-supported and stable classification of the family, particularly at the level of subfamilies and tribes, areas of the greatest controversy. The goal of this paper is to provide morphological diagnoses of higher-level taxa (subtribes, tribes, and subfamilies). Herein we provide morphological diagnoses for 11 subfamilies (Macrotinae, Micronycterinae, Desmodontinae, Lonchorhininae, Phyllostominae, Glyphonycterinae, Glossophaginae, Lonchophyllinae, Carollinae, Rhinophyllinae, and Stenodermatinae), 12 tribes (Desmodontini, Diphyllini, Macrophyllini, Phyllostomini, Vampyrini, Choeronycterini, Glossophagini, Brachyphyllini, Lonchophyllini, Hsunycterini, Sturnirini, and Stenodermatini), and nine subtribes (Anourina, Choeronycterina, Brachyphyllina, Phyllonycterina, Vampyressina, Enchisthenina, Ectophyllina, Artibeina, and Stenodermatina).

Key words: morphology, taxonomy, Phyllostomidae

INTRODUCTION

Classification and taxonomy are often regarded as boring exercises in bookkeeping, but scientific names provide a critical framework for storage and communication of scientific knowledge. Herein, we define taxonomy as the description, naming, and classification of organisms. At alpha taxonomic levels (i.e., the level of the species), the importance of taxonomy is clear — it is difficult to imagine setting conservation priorities or conducting most field research without first identifying study organisms to species. However, at higher taxonomic levels, this clarity of purpose may not be as obvious. To quote Felsenstein (2004: 145):

"A phylogenetic systematist and an evolutionary systematist may make very different classifications, while inferring much the same phylogeny. If it is the phylogeny that gets used by other biologists, their differences about how to classify may not be that important. I have consequently announced that I have founded the fourth great school of classification, the It-Doesn't-Matter-Very-Much school."

Although we respect Felsenstein's (2004) view that it is the phylogeny that matters, referencing nodes on a phylogeny by numbers or letters — or reproducing large phylogenies simply to be able to talk about them — is cumbersome and can hinder effective scientific communication. To us, higher level taxonomy is important because it provides names, increasingly applied to clades that have been supported by data and tested through systematic research. This shorthand approach to discussion of phylogenetic groups is both satisfying and necessary. Names of phylogenetic groups are used in studies concerned with evolution (e.g., adaptive radiation, or biogeography), ecology (e.g., behavioral ecology), and conservation biology (e.g., hotspot location, identification of unique lineages). We believe that having a well-supported and stable classification for any group reduces confusion among non-experts, enabling productive discussion,

debate, and research. An instructive case is that of phyllostomid bats.

Biologists have been captivated by phyllostomid bats for well over a century. Not only is the family speciose, currently with 212 species in nearly 60 genera (N. B. Simmons and A. Cirranello, unpublished data), this group is arguably the most ecologically diverse family of extant mammals. Phyllostomid species span nearly the entire dietary diversity known for terrestrial mammals, with omnivorous, insectivorous, carnivorous, nectarivorous, frugivorous and even sanguivorous species (Gardner, 1977; Ferrarezzi and Gimenez, 1996). Phyllostomids are extremely morphologically diverse, and exhibit a large range of variation in body sizes, wing shapes, and flight behavior (Norberg and Rayner, 1987). Phyllostomids utilize more roost types than any other bat lineage, variously roosting in caves, tree cavities, hollow logs, furled leaves, inside termite nests and armadillo burrows, under bark chips, and in tents they construct out of leaves in highly stereotyped ways (Simmons and Voss, 1998; Simmons et al., 2002; Kunz and Lumsden, 2003). Not surprisingly, in the quest to understand and catalog such diversity, comparative studies abound in the literature, and numerous systematic and phylogenetic analyses have been published (see review in Wetterer et al., 2000). Unfortunately, many of these phylogenetic studies have reached different conclusions concerning phyllostomid relationships, and have proposed different classification schemes. This has led to confusion in the scientific community, particularly among ecologists who need to communicate easily about various phyllostomid groups. The goal of this paper is to provide morphological diagnoses of higher-level taxa (subtribes, tribes, and subfamilies) described by a companion paper (Baker et al., 2016), and discuss the morphological data supporting the arrangement of taxa proposed therein.

Numerous studies of phyllostomid bat phylogeny have been published over the past fifty years (for a review of the older literature, see Wetterer et al., 2000). The most taxonomically comprehensive studies based on direct analyses of data sets (i.e., not supertree analyses) are those of Wetterer et al. (2000), Baker et al. (2003), Rojas et al. (2011), Dumont et al. (2012), and Dávalos et al. (2012, 2014). Wetterer et al. (2000) used a largely morphological data set including characters from numerous anatomical systems. Parsimony analyses of these data found that taxa that shared feeding behaviors formed clades (Fig. 1); for example, all of

the nectar-feeding phyllostomid species formed a single clade, as did frugivores and insectivores — an arrangement generally in agreement with many traditional classifications (e.g., Miller, 1907; Simpson, 1945; Koopman 1993, 1994). On the basis of their phylogeny, Wetterer et al. (2000) proposed a revised classification of phyllostomids that remains widely followed (Table 1; e.g., Simmons, 2005) despite being contradicted by more recent studies (see below). Wetterer et al. (2000) defined taxa phylogenetically and while their classification retained many traditional groupings and names, it also introduced unranked names (e.g., Hirsutaglossa, Nullicauda) and redefined some genera.

In marked contrast to the results of Wetterer et al. (2000), most molecular studies have recovered trees in which members of feeding guilds do not necessarily group together, suggesting that major classification changes are necessary. In an analysis based on a 2.6 kb fragment of mtDNA (including 12SrRNA +RNA^{val}, 16SrRNA) and the nuclear RAG2 gene, Baker et al. (2003 — Fig. 2) found that nectar-feeding evolved more than once, and that insectivorous clades were distributed in several parts of the tree. Baker et al. (2003) tested the trees resulting from their study and the Wetterer et al. (2000) hypothesis and, not surprisingly, found them to be significantly different. To better reflect the phylogenetic relationships of phyllostomids, Baker et al. (2003) revised the classification of the group to recognize only monophyletic lineages detected in their study (Table 1). The classification thus proposed included several new family-group names and restricted or expanded previously established family-level names (e.g., Vampyressatini, Owen, 1987), as well as introducing new unranked taxa (e.g., Karyovarians, Dulcivarians).

Analyses based on larger gene samples have produced additional support for many of the clades detected by Baker et al. (2003). Recent studies by Rojas et al. (2011), using the cytochrome b gene along with the mitochondrial genes used by Baker et al. (2003), Dumont et al. (2012), using cytochrome b, COI, and the ribosomal genes used in Baker et al. (2003), Dávalos et al. (2012), using a morphological partition and molecular data partition (mtDNA and nuclear RAG2 gene); and Dávalos et al. (2014), using a matrix of 278 dental characters and nuclear (atp7a, bdnf, plcb4, rag2, stat5a, thy, ttn6) and mitochondrial (cyt b, COI, and the ribosomal genes from Baker et al., 2003) DNA, were generally supportive of the tree produced by Baker et al. (2003 — but see discussion below). The overall congruence

TABLE 1. Classifications of phyllostomid bats

Wetterer *et al*. (2000)	Baker *et al*. (2003)	This paper
Phyllostomidae	Phyllostomidae	Phyllostomidae
Desmodontidae	Macrotinae	Macrotinae
Desmodus	*Macrotus*	*Macrotus*
Diaemus	Karyovarians (unranked)	Micronycterinae
Diphylla	Micronycterinae	*Lampronycteris*
Brachyphyllinae (incertae sedis)	*Micronycteris*	*Micronycteris*
Brachyphylla	*Lampronycteris*	Desmodontinae
Hirsutaglossa (unranked)	Victivarians (unranked)	Desmodontini
Glossophaginae	Desmodontidae	*Desmodus*
Glossophagini	Desmodontini	*Diaemus*
Anoura	*Desmodus*	Diphyllini
Choeroniscus	*Diaemus*	*Diphylla*
Choeronycteris	Diphyllini[1]	Lonchorhininae
Glossophaga	*Diphylla*	*Lonchorhina*
Hylonycteris	Phyllovarians (unranked)	Phyllostominae
Leptonycteris	Lonchorhininae	Phyllostomini
Lichonycteris	*Lonchorhina*	*Gardnerycteris*
Monophyllus	Unnamed, unranked taxon	*Lophostoma*
Musonycteris	Phyllostominae	*Phylloderma*
Scleronycteris	Macrophyllini	*Phyllostomus*
Lonchophyllini	*Macrophyllum*	*Tonatia*
Lionycteris	*Trachops*	Macrophyllini
Lonchophylla	Phyllostomini	*Macrophyllum*
Platalina	*Lophostoma*	*Trachops*
Phyllonycterinae	*Tonatia*	Vampyrini
Erophylla	*Mimon*	*Chrotopterus*
Phyllonycteris	*Phylloderma*	*Mimon*
Unnamed Clade	*Phyllostomus*	*Vampyrum*
Phyllostominae	Vampyrini	Glossophaginae
Lonchorhinini	*Chrotopterus*	Choeronycterini
Lonchorhina	*Vampyrum*	Anourina
Macrophyllum	Hirsutaglossa (unranked)	*Anoura*
Mimon	Glossophaginae	Choeronycterina
Micronycterini	Glossophagini	*Choeroniscus*
Glyphonycteris	*Glossophaga*	*Choeronycteris*
Lampronycteris	*Leptonycteris*	*Dryadonycteris*
Macrotus	*Monophyllus*	*Hylonycteris*
Micronycteris	Brachyphyllini	*Lichonycteris*
Neonycteris	*Brachyphylla*	*Musonycteris*
Trinycteris	Phyllonycterini	*Scleronycteris*
Phyllostomini	*Erophylla*	Glossophagini
Phylloderma	*Phyllonycteris*	*Glossophaga*
Phyllostomus	Choeronycterini	*Leptonycteris*
Vampyrini	Anourina[1]	*Monophyllus*
Chrotopterus	*Anoura*	Brachyphyllini
Tonatia	Choeronycterina	Brachyphyllina
Trachops	*Choeroniscus*	*Brachyphylla*
Vampyrum	*Choeronycteris*	Phyllonycterina
Nullicauda (unranked)	*Hylonycteris*	*Erophylla*
Carollinae	*Lichonycteris*	*Phyllonycteris*
Carollia	*Musonycteris*	Lonchophyllinae
Rhinophylla	*Scleronycteris*	Lonchophyllini
Stenodermatinae	Dulcivarians (unranked)	*Lionycteris*
Stenodermatini	Lonchophyllinae	*Lonchophylla*
Ectophyllina[1]	*Lonchophylla*	*Platalina*
Artibeus	*Lionycteris*	*Xeronycteris*
Chiroderma	*Platalina*	Hsunycterini
Ectophylla	Nullicauda (unranked)	*Hsunycteris*
Enchisthenes	Carollinae	Glyphonycterinae
Platyrrhinus	*Carollia*	*Glyphonycteris*
Uroderma	Glyphonycterinae[1]	*Neonycteris*
Vampyressa	*Glyphonycteris*	*Trinycteris*
Vampyrodes	*Trinycteris*	Carollinae

TABLE 1. Continued

Wetterer *et al.* (2000)	Baker *et al.* (2003)	This paper
Stenodermatina	Carpovarians (unranked)	*Carollia*
Ametrida	Rhinophyllinae[1]	Rhinophyllinae
Ardops	*Rhinophylla*	*Rhinophylla*
Ariteus	Stenodermatinae	Stenodermatinae
Centurio	Sturnirini	Sturnirini
Phyllops	*Sturnira*	*Sturnira*
Pygoderma	Stenodermatini	Stenodermatini
Sphaeronycteris	Vampyressina[1]	Vampyressina
Stenoderma	*Chiroderma*	*Chiroderma*
Sturnirini	*Mesophylla*	*Mesophylla*
Sturnira	*Platyrrhinus*	*Platyrrhinus*
	Uroderma	*Uroderma*
	Vampyressa	*Vampyressa*
	Vampyriscus	*Vampyrodes*
	Vampyrodes	*Vampyriscus*
	Mesostenodermatini[2]	Enchisthenina
	Enchisthenina[1]	*Enchisthenes*
	Enchisthenes	Ectophyllina
	Ectophyllina[1]	*Ectophylla*
	Ectophylla	Artibeina
	Artibeina	*Artibeus*
	Artibeus	Stenodermatina
	Dermanura	*Ametrida*
	Stenodermatina	*Ardops*
	Ametrida	*Ariteus*
	Ardops	*Centurio*
	Ariteus	*Phyllops*
	Centurio	*Pygoderma*
	Phyllops	*Stenoderma*
	Pygoderma	*Sphaeronycteris*
	Stenoderma	
	Sphaeroncyteris	

[1]— Unavailable name when first used, [2] — Unranked. Remains unavailable (ICZN 11.7.1.1)

among these many recent studies suggests that a growing consensus is emerging regarding the relationships of the major clades of phyllostomids. This increases the likelihood that the classification proposed in Baker *et al.* (2003), and modified slightly herein, will remain relatively stable in the future.

MATERIALS AND METHODS

The clades named and described in Baker *et al.* (2016) were diagnosed with molecular rather than morphological characters; herein we provide morphological diagnoses for each taxon based on the data set of Dávalos *et al.* (2012). The morphological matrix in Dávalos *et al.* (2012) is directly based on the Wetterer *et al.* (2000) matrix, but includes additional species and characters. That data set included only extant phyllostomid species; no fossils were included. However, we do note in the comments section the positions of two fossil Miocene phyllostomids following the analysis of Dávalos *et al.* (2014).

The first sentence of each morphological diagnosis includes a general external description of the included genera and their dental formula, and is in standard font. Each of these general accounts covers slightly different features depending on the nature of the derived characters, which are given in the second section accompanied by character numbers in parentheses. Character numbers correspond to the Morphobank-accessible matrix and appear at the end of each described state. Teeth are labelled according to the following convention, with the upper toothrow in capitals and lower toothrow in lower case (I/i = incisor, C/c = canine, P/p = premolar, M/m = molar): I1, I2, C, P3, P4, M1, M2, M3/i1, i2, c, p2, p3, p4, m1, m2, m3.

For the derived features of Phyllostomidae, we used the data set of Simmons *et al.* (2008; Morphobank P104: http://www.morphobank.org/index.php/Projects/ProjectOverview/project_id/104; O'Leary and Kaufmann, 2012) mapped onto the phylogeny of Miller-Butterworth *et al.* (2007) to discover morphological synapomorphies of the family using both ACCTRAN and DELTRAN optimization. For the derived features of taxa within Phyllostomidae, we used the morphological data set of Dávalos *et al.* (2012) and published as a data matrix in Morphobank (Morphobank P947: http://www.morphobank.org/index.php/MyProjects/List/select/project_id/947;O'Leary and Kaufmann 2007) mapped onto a modified phylogeny of Baker *et al.* (2003) to discover morphological synapomorphies of clades using both ACCTRAN and DELTRAN optimization. We modified the original Baker *et al.* (2003) tree to include all taxa sampled by Dávalos *et al.* (2012) that were not originally included in the Baker *et al.* (2003) study. When an ingroup

taxon could not be placed with a congener, it was placed in a polytomy at the base of the lowest level clade we name. Relationships within Lonchophyllinae follow Parlos *et al.* (2014). Outgroup arrangement followed Miller-Butterworth *et al.* (2007). Unambiguously derived synapomorphies are shown in italic type. Unique characters that are unreversed on the tree are additionally shown in boldface type. Characters with an ambiguous optimization are in standard typeface. Both ACCTRAN and DELTRAN characters are listed in each account; DELTRAN optimization is denoted with an asterisk.

We have made no attempts to provide a complete history of the usage of each name because other sources have already done so (e.g., McKenna and Bell, 1997; Wetterer *et al.*, 2000), but we do provide commentary as appropriate for each family-level name. We have chosen here to limit the traditionally-used names to crown clades because these names are most commonly applied in this manner, and other provisions are available for including fossil species that may be stem lineages, for example. Finally, we comment on proposed unranked taxa that have value as taxonomic groups (see Pauly *et al.*, 2009; Cantino and de Quieroz, 2010), as well as names that we have rejected.

RESULTS

Family Phyllostomidae Gray 1825: 242

Type genus
Phyllostomus Lacépède 1799.

Definition
The clade arising from the last common ancestor of *Macrotus*, *Micronycteris*, *Desmodus*, *Lonchorhina*, *Phyllostomus*, *Glossophaga*, *Lonchophylla*, *Carollia*, *Glyphonycteris*, *Rhinophylla*, and *Sturnira*.

Composition
Macrotus Gray 1843, *Lampronycteris* Sanborn 1949, *Micronycteris* Gray 1866 (includes *Xenoctenes* Miller 1907, *Leuconycteris* Porter *et al.* 2007, *Schizonycteris* Porter *et al.* 2007), *Desmodus* Wied-Neuwied 1826, *Diaemus* Miller 1906, *Diphylla* Spix 1823, *Lonchorhina* Tomes 1863, *Chrotopterus* Peters 1865, *Gardnerycteris* Hurtado and Pacheco 2014 (does not include *Anthorhina* — see Simmons, 2005), *Lophostoma* d'Orbigny 1836, *Macrophyllum* Gray 1838, *Mimon* Gray 1847, *Trachops* Gray 1847, *Tonatia* Gray 1827 (sensu Lee *et al.*, 2002), *Phylloderma* Peters 1865, *Phyllostomus* Lacépède 1799, *Vampyrum* Rafinesque 1815, *Anoura* Gray 1838, *Brachyphylla* Gray 1833, *Choeroniscus* Thomas 1928, *Choeronycteris* Tschudi 1844, *Dryadonycteris* Nogueira, Lima, Peracchi, and Simmons 2012, *Erophylla* Miller 1906, *Glossophaga* E. Geoffroy 1818, *Hsunycteris* Parlos, Timm, Swier, Zeballos, and Baker 2014, *Hylonycteris* Thomas 1903, *Leptonycteris* Lydekker 1891, *Lichonycteris* Thomas 1895,

Monophyllus Leach 1821, *Musonycteris* Schaldach and McLaughlin 1960, *Phyllonycteris* Gundlach 1860, *Scleronycteris* Thomas 1912, *Hsunycteris* Parlos, Timm, Swier, Zeballos and Baker 2014, *Lonchophylla* Thomas 1903, *Lionycteris* Thomas 1913, *Platalina* Thomas 1928, *Xeronycteris* Gregorin and Ditchfield 2005, *Carollia* Gray 1838, *Glyphonycteris* Thomas 1896 (includes *Barticonycteris* Hill 1964), *Neonycteris* Sanborn 1949, *Trinycteris* Sanborn 1949, *Rhinophylla* Peters 1865, *Ametrida* Gray 1847, *Ardops* Miller 1906, *Ariteus* Gray 1838, *Artibeus* Leach 1821 (includes *Koopmania* Owen 1991 and *Dermanura* Gervais 1856), *Centurio* Gray 1842, *Chiroderma* Peters 1860, *Ectophylla* H. Allen 1892, *Enchisthenes* K. Andersen 1906, *Mesophylla* Thomas 1901, *Phyllops* Peters 1865, *Platyrrhinus* Saussure 1860, *Pygoderma* Peters 1863, *Sturnira* Gray 1842, *Stenoderma* E. Geoffroy 1818, *Sphaeronycteris* Peters 1882, *Uroderma* Peters 1866, *Vampyressa* Thomas 1900, *Vampyriscus*, Thomas 1900 (includes *Metavampyressa* Peterson 1968), *Vampyrodes* Thomas 1900.

Description and diagnosis
Small to very large bats (FA= 29–110 mm) in which the nasal processes of the premaxillae are fused to the maxillae and the nasals, and the bodies of the premaxillae are fused with each other (see Giannini and Simmons, 2007); the tragus is well-developed; the greater tuberosity of the humerus extends proximal to the humeral head, forming a double articulation with the scapula; manual digit II has a well-developed metacarpal and a small ossified proximal phalanx; manual digit III has three complete ossified phalanges; there are no fusions in the cervical, thoracic, or lumbar regions of the vertebral column; and the fibula is cartilaginous proximally. *Three lower premolars present* (7); *body of premaxilla of intermediate thickness* (13); *stapedial fossa deep and constricted* (27); *cochlea moderately enlarged* (33); *M. mylohyoideus fleshy* (47); *M. styloglossus with single muscle belly* (59); *posterior lamellae present and narrow on ribs* (81); *ventral process of manubrium at 90 degree angle* (84); *xiphisternal keel of sternum absent* (87); *anteromedial projection from tip of acromion process of scapula absent* (90); dorsal articular facet of scapula large and flat (92); infraspinous fossa of scapula with intermediate facet narrower than posterolateral facet (95)*; *sesamoid bone absent from the dorsal surface of the unciform-magnum articulation* (114); *M. biceps brachii coracoid head half the size of the glenoid head* (148); M. flexor digitorum profundus

FIG. 1. Strict consensus tree from Wetterer *et al.* (2000: redrawn after figure 49). Subfamilies are labeled according to their classification. Bootstrap support is shown, with white ≥ 75%; gray = 50–74%; and black ≤ 49%
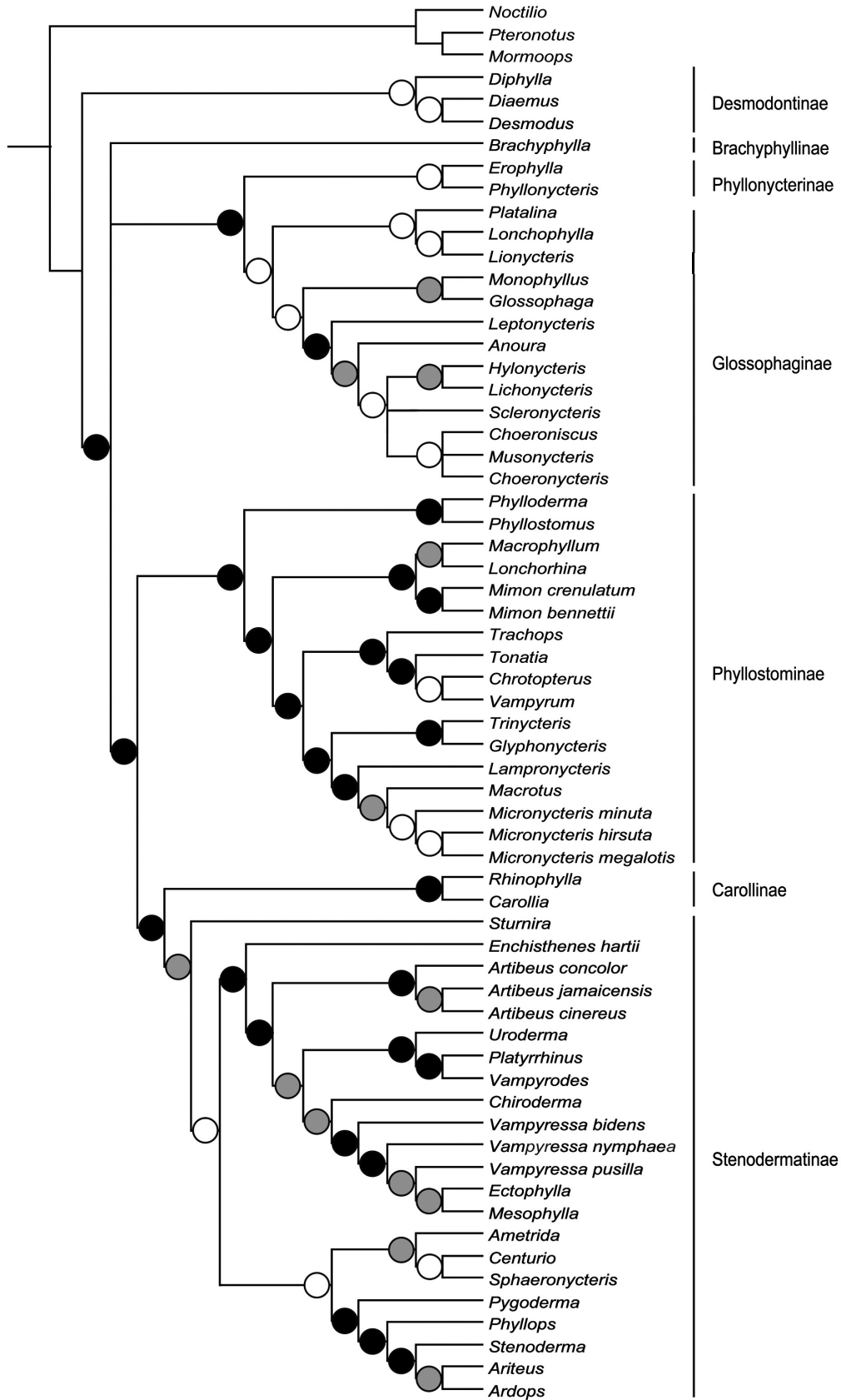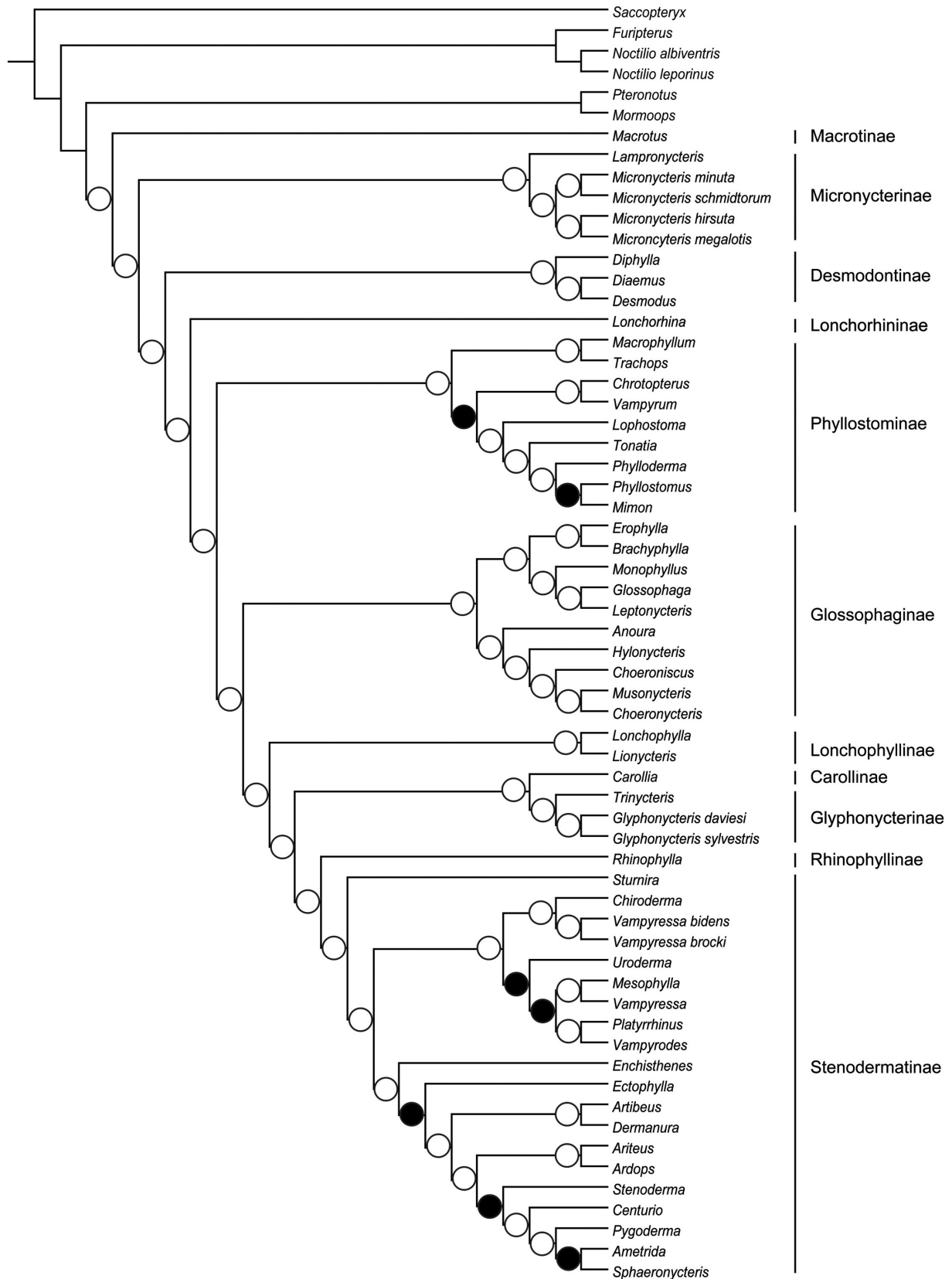
FIG. 2. Strict consensus tree from Baker *et al.* (2003: redrawn after figure 5a). Subfamilies are labelled according to their classification. Posterior probabilities are shown, with white ≥ 95% and black <95%

does not insert on manual digit V (152)*; M. psoas minor thick and fleshy (159)*; interstitial implantation present (184)*; vomeronasal epithelial tube well-developed (194)*; paraseptal cartilage C-shaped (195); ear pinnae are not funnel shaped (204); *noseleaf present* (206).

Comments

Monophyly of Phyllostomidae is strongly supported by both molecular data (e.g., Teeling *et al.*, 2005; Miller-Butterworth *et al.*, 2007) and morphological data. The composition of the family has been largely stable for many decades; for a comprehensive review, see Wetterer *et al.* (2000). The family also includes the two Miocene fossil genera *Notonycteris* and *Palynephyllum.*

Subfamily Macrotinae Van Den Bussche 1992: 36

Type genus
Macrotus Gray 1843.

Definition
The clade arising from the last common ancestor of *Macrotus waterhousii* and *Macrotus californicus.*

Composition
Macrotus Gray 1843 (includes *Otopterus* Lydekker 1891).

Description and diagnosis
Medium sized bats (FA = 45–58 mm) lacking facial and dorsal stripes or shoulder and neck spots; large rounded ears connected across the forehead by a skin band; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; lateral edge of noseleaf thin free flap; labial border of horseshoe fused to upper lip forming a thickened ridge; two dermal pads with smoothly rounded lateral margins present on the chin; long tail largely enclosed in an extensive uropatagium; hindlimbs longer than the tail; calcar present and longer than foot; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Single superciliary vibrissa present (14)*; papillated ridge or papillae is sometimes or always present in the internarial region on the spear (28); *lateral border of the pinna smoothly rounded with no concavity* (40); *interauricular band present between external pinnae* (43); deep notch in interauricular band, distinct triangular flaps present (44)*; *anterior rim of orbit terminates above anterior M2* (52); *ectotympanic bulla extends medially across 66% of cochlea* (54); *coronoid process twice the height of the condyloid process* (62); I2 and C in contact, no diastema present (69)*; *bilobed i1 occlusal margin* (72); bilobed i2 occlusal margin (73)*; *diastema sometimes or always present between P3-P4 (78); p3 subequal to p2, p4 (81); two roots on p3 (83);* M. mylohyoid clearly divided into anterior and posterior parts by pronounced break (103); 12 thoracic vertebrae (150)*; *xiphisternum flat, keel absent* (160); pit for clavicular ligaments absent from scapula (162); *fifth metacarpal longest (175); first phalanx of manual digit IV longer than second phalanx (180); tail equal to or longer than hind legs (182); M. humeropatagialis absent (191);* M. teres major inserts on ventral ridge of humerus (198); M. triceps brachii caput medial inserts into caput lateral tendon only (199)*; M. palmaris longus does not insert on manual digit II (203)*; uterine cornual lumina reduced to tubular intramural uterine cornua (216).

Comments

Macrotus has been traditionally classified within the subfamily Phyllostominae (e.g., Miller, 1907; Koopman, 1993; Wetterer *et al.*, 2000; Simmons, 2005 — Table 1). However, much data has been accumulating to suggest that this genus is the basal branch of Phyllostomidae and is not part of a monophyletic Phyllostominae (Fig. 2). These data are molecular (restrictions sites and sequences) and karyotypic — morphological analyses continue to support placement of *Macrotus* as part of a clade including species of *Micronycteris* (Dávalos *et al.*, 2012). However, the high levels of support for the basal placement of *Macrotus* seen in the molecular studies (e.g., Baker *et al.*, 2003; Rojas *et al.*, 2011) and the combined analyses of Dávalos *et al.* (2012, 2014) suggest that additional morphological data are unlikely to overturn this hypothesis.

Subfamily Micronycterinae Van Den Bussche 1992: 36

Type genus
Micronycteris Gray 1866.

Definition
The clade arising from the last common ancestor of *Micronycteris* (sensu Wetterer *et al.*, 2000; Porter *et al.*, 2007) and *Lampronycteris.*

Composition
Lampronycteris Sanborn 1949, *Micronycteris* Gray 1866 (includes *Xenoctenes* Miller 1907,

Leuconycteris Porter, Hoofer, Cline, Hoffman, and Baker 2007, *Schizonycteris* Porter, Hoofer, Cline, Hoffman, and Baker 2007; *homezorum* [not *homezi* — Solari, 2008] is a synonym of *M. minuta*, see Ochoa and Sanchez, 2005).

Description and diagnosis

Small to medium-sized bats (FA: 32–46 mm) lacking facial and dorsal stripes or shoulder and neck spots; large rounded ears connected across the forehead by a skin band in *Micronycteris*, but with pointed tips and no band in *Lampronycteris*; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear restricted to proximal part; lateral edge of noseleaf thin free flap; labial border of horseshoe fused to upper lip forming a thickened ridge; two dermal pads with smoothly rounded lateral margins present on the chin; tail of medium length — shorter than the hindlegs; extensive uropatagium lacks a fringe; calcar present and equal to or longer in length than the foot; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Ventral hairs unicolored (6); single superciliary vibrissa present (14)*; rib present on spear of noseleaf (26)*; I2 and canine always in contact, no diastema present (69)*; one horny papilla in cluster on tongue always larger than others (144)*; 13 thoracic vertebrae present (150); *suprascapular process present* (166).

Comments

Micronycteris was traditionally classified as a member of the subfamily Phyllostominae and this usage has been maintained in much of the recent literature (e.g., Koopman, 1993, 1994; Williams and Genoways, 2008). Van Den Bussche (1992: 36) introduced the name Micronycterinae for all ten species of *Micronycteris* (*sensu* Sanborn, 1949). In their morphological analysis, Wetterer *et al.* (2000) raised the subgenera of *Micronycteris* to generic standing and named Micronycterini for *Macrotus*, *Micronycteris*, *Lampronycteris*, *Glyphonycteris*, *Trinycteris*, and *Neonycteris* (see Table 1). Baker *et al.* (2003) used Micronycterinae to refer to a more restricted clade consisting only of *Micronycteris* + *Lampronycteris* (see Table 1). These studies disagreed on the position of these clades within the family. Analyses of molecular data (Van Den Bussche, 1992; Baker *et al.*, 2003 — Fig. 2) placed this clade as one of the basal groups within Phyllostomidae. Morphological data support a different position for *Micronycteris* + *Lampronycteris*. Wetterer *et al.* (2000 — Fig. 1) found that Micronycterini nested well within Phyllostomidae

as part of a monophyletic Phyllostominae, and a more recent morphological analysis (Dávalos *et al.*, 2012) supports the placement of this clade within a larger clade of 'phyllostomines'. However, the more basal position of the subfamily (and exclusion of *Macrotus*, *Glyphonycteris*, and *Trinycteris*) is strongly supported by accumulating molecular evidence (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dumont *et al.*, 2012 — Figs. 2 and 3) and moderately supported in the combined analysis of Dávalos *et al.* (2012, 2014). Consequently, we apply a subfamily level name to the clade comprising *Micronycteris* + *Lampronycteris*.

Subfamily Desmodontinae J. A. Wagner 1840: 375

Type genus

Desmodus Wied-Neuwied 1826.

Definition

The clade arising from the last common ancestor of *Desmodus* and *Diphylla*.

Composition

Desmodus Wied-Neuwied 1826, *Diaemus* Miller 1906, *Diphylla* Spix 1823.

Description and diagnosis

Medium sized bats (FA = 48–65 mm) lacking facial and dorsal stripes or shoulder and neck spots; ears taper to a blunt point in *Desmodus* and *Diaemus* but are rounded, with an expanded medial lobe in *Diphylla*; noseleaf present but reduced; smooth internarial region on noseleaf; lateral edge of noseleaf is a thin free flap; two chin pads with smoothly rounded edges present on either side of the midline of the chin; uropatagium reduced; calcar absent (*Desmodus*, *Diaemus*) or present (*Diphylla*); dental formula I1-2/2 C1/1 P1/2 M1-2/1-2 = 20–26. *Cuticular scales appressed to hair shaft* (3); *fringe of hairs on trailing edge of uropatagium* (13); *spear short, equal to or less than the height of the horseshoe* (24); *U-shaped notch in distal tip of spear* (25); spear flat, rib absent (26); no distinct boundary between the labial edge of horseshoe and upper lip (31)*; *skin ridge on dorsum of snout posterior to noseleaf* (34); anterior rim of orbit terminates above anterior M1 (52); ectotympanic bulla extends medially across 66% of cochlea (54); *basisphenoid pits present* (58); *coronoid process of mandible level with or below condyloid process* (62); *I1 occlusal margin C-shaped, forming a sharp cutting blade* (64); *I1 occludes posterior to i1 in fossa on*

mandible (74); *P3 absent* (75); *p3 absent* (81); *W-shaped ectoloph absent on M1, M2* (84); *hypocone basin and cusp absent on M1* (85); *M3 absent* (88); **m1 laterally compressed into shearing ridge** (90); lower molar with cusps and crests indistinguishable (94)*; *m3 absent* (96); lateral fibers of M. sternohyoideus do not have a manubrial origin (106); lateral fibers of M. sternohyoideus originate from first rib (108); lateral slip of M. sphincter colli profundus absent (121); M. cricopharyngeus has a single slip (123); ceratohyal tiny or absent (125); *medial circumvallate papillae absent* (128); *lateral circumvallate papillae absent* (130); *basketlike medial-posterior mechanical papillae absent* (137); **horny papillae arranged in large V-shape cluster** (143); *90 degree angle between ventral process and body of manubrium* (159); *xiphisternum flat, median keel absent* (160); tip of coracoid process same width as shaft (164); third and fourth metacarpals subequal and both longer than fifth (175)*; *sacral vertebrae fused to ischium* (181); *tail absent* (182); shaft of femur straight (185)*; *fibula well-developed* (186); *calcar present shorter than foot* (187); *calcar totally cartilaginous* (188); *M. occipitopollicalis distal muscle belly present* (192); M. occipitopollicallis with no attachment to M. pectoralis profundus (193)*; M. palmaris longus inserts on manual digit II (203); length of uterine horns 1/2 the length of the common uterine body (215).

Comments

These three species were recognized as a separate family (e.g., Miller, 1907) until the late 1960s when host-parasite associations, echolocation call structure, immunological, karyological, and morphological data (see e.g., Machado-Allison, 1967; Forman *et al.*, 1968) supported the placement of these species within Phyllostomidae. Koopman and Jones (1970) were the first to formally reduce Desmodontinae to a subfamily of Phyllostomidae. Both molecular and morphological data strongly support monophyly of Desmodontinae (see Figs. 1 and 2). We follow Kwon and Gardner (2008) in recognizing the priority of authorship of Wagner 1840, who used the name Desmodina for this group within the family Istiophora (see Wetterer *et al.*, 2000: 10), over Bonaparte 1845, who is often cited as the author of this name (e.g., Miller, 1907; Koopman, 1994; McKenna and Bell, 1997; Simmons, 2005). Although some authors (e.g, Palmer, 1904; Husson, 1962) spelled the family name as Desmodidae, Handley (1980) explained that the correct form is Desmodontinae, and that spelling has been used by all subsequent authors.

Tribe Desmodontini J. A. Wagner 1840: 375

Type genus
Desmodus Wied-Neuwied 1826.

Definition
The clade arising from the last common ancestor of *Desmodus* and *Diaemus*.

Composition
Desmodus Wied-Neuwied 1826, *Diaemus* Miller 1906.

Description and diagnosis
Medium sized bats (FA = 48–65 mm) with large thumbs, with either one or two pads on the palmar surface; leading edge of wing and wingtips sometimes (*Desmodus*) or always (*Diaemus*) white; ears taper to a blunt point; tail effectively absent; short U-shaped uropatagium with a fringe of hairs along the trailing edge; dental formula I1/2 C1/1 P1/2 M1-2/2 = 20–22. *Pelage differentiated into over and under hairs* (1); *bulb present at base of hair shaft* (2)*; *cuticular scales on hair shaft have irregular margin* (4); *single superciliary vibrissa* (14); *infraorbital foramen located above posterior P4* (51); ectotympanic bulla extends medially across 66% of cochlea (54)*; *I2 absent* (67); *i2 bilobed* (73)*; **m2 absent** (95); *cerebellar vermis completely covers medial longitudinal fissure and inferior colliculi* (101); **ventral sulcus present on tongue** (148); 12 thoracic vertebrae (150)*; pit for clavicular ligament absent (162); *calcar vestigial or absent* (187).

Comments
Although currently recognized as a valid genus, *Diaemus* was previously synonymized with *Desmodus* by Handley (1976), Koopman (1978), and Honacki *et al.* (1982). Both morphological and molecular data strongly support monophyly of this clade (e.g., Wetterer *et al.*, 2000; Baker *et al.*, 2003; Dávalos *et al.*, 2012 — Figs. 1 and 2).

Tribe Diphyllini Baker, Solari, Cirranello, and Simmons 2016: 20

Type genus
Diphylla Spix 1823.

Definition
The clade including all populations of *Diphylla ecaudata*.

Composition
   Diphylla Spix 1823.

Description and diagnosis
   Medium-sized bats (FA: 49–56 mm) with large eyes; thumb small and lacking the extra pads seen in Desmodontini; rounded tip on ears and expanded medial lobe; wing tips and leading edge always black; tail absent; uropatagium greatly reduced to a band running along the legs; calcar present; dental formula I2/2 C1/1 P1/2 M2/2 = 26. Bulb at base of hair shaft absent (2); *ventral hair unicolored* (6); *uropatagium rudimentary, present as bands along each leg* (12); *lateral proximal pinna confluent with ridge of skin running to mouth or lower lip* (41); anterior rim of orbit terminates above anterior M1 (52)*; *i1 occlusal margin with four lobes* (72); *i2 occlusal margin with more than three lobes* (73); 13 thoracic vertebrae (150); *ventral ridge on third or fourth thoracic vertebra sometimes or always present* (151); pit for clavicular ligament present on scapula (162)*; tip of coracoid process same width as shaft (164)*; dorsal articular facet of scapula large, flat (167)*; *first phalanx of manual digit I longer than metacarpal* (176); M. teres major takes origin from 25–40% of axillary border of scapula (197); *caput mediale of M. triceps brachii inserts into elbow sesamoid only* (199).

Comments
   Baker *et al.* (2003: 21) proposed the name Diphyllini for *Diphylla* as the molecular distance between *Diphylla* and Desmodontini is comparable to distances that separate subfamilies and is the greatest of any genus or pair of genera. However, the name was not made available at that time and so takes authorship from Baker *et al.* (2016). Both morphological and molecular data strongly support the position of *Diphylla* as the basal branch of Desmodontinae (e.g, Wetterer *et al.*, 2000; Baker *et al.*, 2003; Dávalos *et al.*, 2012 — Figs. 1 and 2).

   Subfamily Lonchorhininae Gray 1866: 113

Type genus
   Lonchorhina Tomes 1863.

Definition
   The clade arising from the last common ancestor of all species within the genus *Lonchorhina.*

Composition
   Lonchorhina Tomes 1863.

Description and diagnosis
   Medium-sized bats (FA: 41–59 mm) lacking facial and dorsal stripes or shoulder and neck spots; enormous pointed ears; noseleaf almost as long as ears; lateral edge of noseleaf forms thin free flap; ridge or papillae sometimes or always present on rib of spear; two dermal pads with smoothly rounded lateral margins present on the chin; long tail running to end of extensive uropatagium; fringe absent on uropatagium; calcar present and longer in length than the foot; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Bulb at base of hair shaft present (2)*; *cuticular scales on hair shaft with toothed margin* (4); *posterior edge of plagiopatagium attached to calcar* (11); *single vibrissal column adjacent to noseleaf* (17); rib runs to tip of spear (27)*; *trilobed sella present* (29); *labial edge of horseshoe is thin free flap* (31); *mastoid breadth greater than zygomatic breadth* (49); occlusal margin of i2 with three lobes (73); infraorbital foramen located above posterior M1 (51)*; height of P3 less than P4 (76)*; one root on P3 (77)*; medial longitudinal fissure and inferior colliculi fully exposed (101)*; *ridges on anterior face of manubrium define a broad triangular face* (158); pit for clavicular ligament present on scapula (162)*; *trochiter of humerus extends to level of humeral head* (171); *distal spinous process of humerus extends distally beyond trochlea* (173); *tail is equal to or longer than the hind legs* (182); shaft of femur straight (185)*.

Comments
   This tribal name was proposed by Gray (1866) for *Lonchorhina* only. Previous authors have included this genus within Phyllostominae (e.g., Smith, 1976; Griffiths, 1982; Baker *et al.*, 1989; Williams and Genoways, 2008), a position supported by morphological data (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1). While an analysis of some molecular data strongly supports the position of *Lonchorhina* as an independent lineage that branched off before most other phyllostomid clades (including phyllostomines; Baker *et al.*, 2003 — Fig. 2), the analyses of Rojas *et al.* (2011), Dumont *et al.* (2012), and Dávalos *et al.* (2012, 2014) found a slightly different position for *Lonchorhina*. In these trees (both molecular and combined for the Dávalos *et al.* studies), *Lonchorhina* appears as the sister taxon of nectar-feeders + fruit-feeders. This shift may be due to saturation at third codon positions in mitochondrial DNA; downweighting these sites reduces support for this placement (Dávalos *et al.*, 2012). Regardless of its overall placement in the tree, we recognize the

molecular and morphological distinctiveness of this taxon at the subfamily level. The content of this family-group name was expanded by Wetterer *et al.* (2000), when they used it for the clade including *Lonchorhina*, *Macrophyllum*, and *Mimon* (Table 1). Baker *et al.* (2003) restricted the name to its original content, and elevated it to a subfamily; we follow this usage here (Table 1).

Subfamily Phyllostominae Gray 1825: 242

Type genus
    Phyllostomus Lacépède 1799.

Definition
    The clade arising from the last common ancestor of *Macrophyllym*, *Vampyrum*, and *Phyllostomus*.

Composition
    Chrotopterus Peters 1865, *Gardnerycteris* Hurtado and Pacheco 2014 (does not include *Anthorhina* — see Simmons, 2005), *Lophostoma* d'Orbigny 1836, *Macrophyllum* Gray 1838, *Mimon* Gray 1847, *Tonatia* Gray 1827 (sensu Lee *et al.*, 2002), *Trachops* Gray 1847, *Phylloderma* Peters 1865, *Phyllostomus* Lacépède 1799, *Vampyrum* Rafinesque 1815.

Description and diagnosis
    Small to large-sized bats (FA: 32–110 mm) lacking facial stripes or shoulder and neck spots; dorsal stripes absent in all save *Gardnerycteris crenulatum;* large rounded ears in most species, but large and with pointed tips in *Mimon*, *Gardnerycteris*, and *Macrophyllum*, and small and pointed in *Phyllostomus* and *Phylloderma*; noseleaf with spear equal to or longer than twice the height of the horseshoe, sometimes quite long (e.g., *Gardnerycteris crenulatum*); lateral edges of horseshoe are thin free flaps, except in *Tonatia* and *Lophostoma* where they are fully confluent with the face; labial borders of horseshoe have no distinct boundary with the upper lip in *Trachops*, *Tonatia*, *Lophostoma*, and *Phylloderma*, form a thin free flap in *Macrophyllum*, *Chrotopterus*, *Vampyrum*, *Phyllostomus*, and *Gardnerycteris crenulatum*, and form a thickened ridge in *Mimon bennettii*; multiple well-developed papillae are present on the chin in most species, but two dermal pads with smoothly rounded lateral margins are present on the chin in *Chrotopterus*, *Vampyrum*, and *Mimon bennettii*; tail shorter than the hindlegs in most species, the exceptions being *Macrophyllum* in which it is longer and *Vampyrum* in which it is

absent; extensive uropatagium lacks a fringe in all species save *Macrophyllum* and *Gardnerycteris crenulatum*; calcar present and generally equal to or longer than the foot in length, except in *Trachops*, *Phylloderma*, and *Phyllostomus discolor*; dental formula I2/1-2 C1/1 P2/2-3 M3/3 = 30–34. *Single interramal vibrissa present* (16); vibrissal papillae surrounding noseleaf are small and separate (19); rib runs to spear tip (27)*; multiple well-developed papillae present on chin (36); lateral border of pinna smoothly rounded, no lateral concavity present (40); lingual cingulum present on I1 (63); *I2 and canine always in contact*, *no diastema present* (69); P4 taller than P3 (76)*; medial longitudinal fissure and inferior colliculi fully exposed (101)*; M. mylohyoideus clearly divided into anterior and posterior parts by pronounced break (103); medial fibers of M. sternohyoideus originate from medial manubrium (105); ceratohyal approximately equal in length to epihyal (125); 12 thoracic vertebrae (150)*; xiphisternum flat, median keel absent (160); *fifth metacarpal longest* (175); first and second phalanges of digit IV subequal in length (180); more than 1/3 of calcar calcified (188); M. occipitopollicalus attaches to anterior M. pectoralis profundus via tendon (193); caput mediale of M. triceps brachii inserts into elbow sesamoid only (199); M. flexor digitorum profundus inserts on second phalanx of manual digit IV (200); M. palmaris longus does not insert on manual digit V (206).

Comments
    Phyllostominae was first recognized as a subfamily by Gray (1825); however, the content of the group has changed substantially over time. *Carollia* and *Rhinophylla* were originally included in the subfamily, but were removed by Miller (1907). Through most of the 20th century, Phyllostominae was used for a suite of insectivorous and omnivorous phyllostomid genera that retain a more or less tribosphenic dentition (e.g., Miller, 1907; Hall, 1981; Koopman, 1993, 1994). Wetterer *et al.* (2000) recovered this clade in their analysis of morphological data, but support for the grouping was weak (see Fig. 1) and a subsequent analysis of a larger morphological data set (see Dávalos *et al.*, 2012) did not support monophyly of this subfamily. Previously Baker *et al.* (1989) had applied the name Phyllostominae to a large assemblage of primitive omnivores (Phyllostomini), nectarivores (Glossophagini), and frugivores (Stenodermatini), to the exclusion of *Macrotus*, *Micronycteris* (sensu lato), Desmodontinae, and Vampyrinae (Table 1), but few

researchers followed this usage since it expanded the subfamily to cover virtually all phyllostomids, including taxa representing multiple feeding guilds. Although more recent analyses of molecular data have effectively refuted monophyly of phyllostomines (e.g., Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012, 2014 — Figs. 1 and 2), confusion about the details led various workers to continue to use Phyllostominae in the inclusive traditional sense (e.g., Williams and Genoways, 2008). To resolve this problem, we here recognize Phyllostominae as the largest well-supported clade that includes the type genus (*Phyllostomus*) and hew as closely as possible to the traditional use of the name — i.e., including taxa that are insectivorous or omnivorous and not members of other guild-based subfamilies (i.e., Glossophaginae, Stenodermatinae — Table 1). Our definition of Phyllostominae thus excludes a number of taxa previously included in this subfamily but which are now recognized as separate evolutionary lineages despite sharing similar dietary habits (e.g., Macrotinae, Micronycterinae, Lonchorhininae, and Glyphonycterinae). The fossil genus *Notonycteris*, known from the Miocene of Colombia, is also included in this subfamily, following Dávalos *et al.* (2014).

Tribe Phyllostomini Gray 1825: 242

Type genus
  Phyllostomus Lacépède 1799.

Definition
  The clade arising from the last common ancestor of *Phyllostomus*, *Tonatia* and *Lophostoma*.

Composition
  Gardnerycteris Hurtado and Pacheco 2014 (does not include *Anthorhina* — see Simmons, 2005), *Lophostoma* d'Orbigny 1836, *Phylloderma* Peters 1865, *Phyllostomus* Lacépède 1799, *Tonatia* Gray 1827 (sensu Lee *et al.*, 2002).

Description and diagnosis
  Dental formula I2/1-2 C1/1 P2/2-3 M3/3 = 30–34. Over and under hairs present (1); irregular cuticular scale margin on hair shafts (4); lateral edges of horseshoe confluent with face along entire length (30); no distinct boundary between labial edge of horseshoe and lip (31)*; multiple well-developed papillae present on chin (36)*; *two lobes on i1 occlusal margin* (72); one root on P3 (77)*; *p3 reduced

and less than 1/3 the height of p2, p4 with well-developed cusps* (81); postcanine teeth including p3 aligned in a row (82); no keel on xiphisternum (160)*; first and second phalanges of digit 3 of wing subequal (178).

Comments
  Baker *et al.* (1989) resurrected the use of Phyllostomini as a tribal name (Table 1), including the genus *Mimon*, which then included *Gardnerycteris*. Wetterer *et al.* (2000) restricted use of the name to *Phyllostomus* and *Phylloderma* (see Table 1) but we do not follow that usage here. This clade is recognized on the basis of molecular data (e.g., Baker *et al.*, 2003; Dumont *et al.*, 2012 — Fig. 2); morphological data provide only weak support for relationships among 'phyllostomine' species (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1).

Tribe Macrophyllini Gray 1866: 113

Type genus
  Macrophyllum Gray 1838.

Definition
  The clade arising from the last common ancestor of *Macrophyllum* and *Trachops*.

Composition
  Macrophyllum Gray 1838, *Trachops* Gray 1847.

Description and diagnosis
  Small to large-sized bats (FA: 34–65 mm), both species bearing wartlike excrescences — *Trachops* on the face, and *Macrophyllum* underneath the uropatagium; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Multiple well-developed papillae present on chin (36)*; lingual cingulum absent on I1 (63)*; i2 trilobed (73); one root on P3 (77)*; pit for clavicular ligaments present on scapula (162); cornual lumina distinct, join immediately with common uterine body (216).

Comments
  Gray (1866) originally proposed this tribe for *Macrophyllum* only. A close relationship between *Macrophyllum* and *Trachops* is strongly supported by molecular data (Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012; Fig. 2). Morphological data instead weakly support either a sister taxon relationship between *Macrophyllum* and *Lonchorhina* (Wetterer *et al.*, 2003 —

Fig. 1), or between *Macrophyllum* and *Gardnerycteris crenulatum* (Dávalos *et al.*, 2012). Combined analyses that include both morphological and molecular data recover a *Macrophyllum + Trachops* clade (Dávalos *et al.*, 2012, 2014). Accordingly, we follow Baker *et al.* (2003) in applying the name Macrophyllini to *Macrophyllum + Trachops* (Table 1).

Tribe Vampyrini Bonaparte 1838: 112

Type genus
    Vampyrum Rafinesque 1815.

Definition
    The clade arising from the last common ancestor of *Mimon* and *Vampyrum*.

Composition
    Chrotopterus Peters 1865, *Mimon* Gray 1847, *Vampyrum* Rafinesque 1815.

Description and diagnosis
    Medium to large-sized bats (FA: 53–110 mm); dental formula I2/1-2 C1/1 P2/2-3 M3/3 = 30–34. *Interramal vibrissae absent* (16); globular sella present on noseleaf (29); labial edge of horseshoe is a thin, free flap (31); free edge of labial horse-shoe is cupped around nostrils (32); two dermal pads present on either side of the midline on the chin (36); lingual cingulum present on I1 (63); two roots present on P3 (77); flexor sheet distal to tendon lock retinaculum is platelike and plicated (208).

Comments
    This clade is well-supported by recent molecular (Dávalos *et al.*, 2014; Rojas *et al.*, In press) data sets. Morphological data strongly support the sister taxon relationship between *Chrotopterus* and *Vampyrum*, but do not place *Mimon* with this clade (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1). Baker *et al.* (1989) used this name at the subfamily level and included *Trachops*, whereas Wetterer *et al.* (2000) used the name at the subfamily level and included both *Trachops* and *Tonatia* (sensu lato — Table 1). We instead restrict Vampyrini to the smaller clade in recognition of the strong support for this grouping seen in recent molecular analyses that have a more complete taxon sample (e.g., Dávalos *et al.*, 2014; Rojas *et al.*, In press). The fossil genus *Notonycteris*, known from the Miocene of Colombia, is also included in this tribe (Dávalos *et al.*, 2014).

Subfamily Glossophaginae Bonaparte 1845: 5

Type genus
    Glossophaga E. Geoffroy 1818.

Definition
    The clade arising from the last common ancestor of *Glossophaga*, *Brachyphylla*, *Phyllonycteris*, and *Choeronycteris*.

Composition
    Anoura Gray 1838, *Brachyphylla* Gray 1833, *Choeroniscus* Thomas 1928, *Choeronycteris* Tschudi 1844, *Dryadonycteris* Nogueira, Lima, Peracchi, and Simmons 2012, *Erophylla* Miller 1906, *Glossophaga* E. Geoffroy 1818, *Hylonycteris* Thomas 1903, *Leptonycteris* Lydekker 1891, *Lichonycteris* Thomas 1895, *Monophyllus* Leach 1821, *Musonycteris* Schaldach and McLaughlin 1960, *Phyllonycteris* Gundlach 1860, and *Scleronycteris* Thomas 1912.

Description and diagnosis
    Small to medium-sized bats (FA: 31–69 mm) lacking facial and dorsal stripes or shoulder and neck spots; small rounded ears; noseleaf present and either simple with spear longer than twice the height of the horseshoe in most species or reduced with the spear equal to or less than twice the height of the horseshoe in *Brachyphylla*, *Erophylla*, and *Phyllonycteris*; most species with a pointed or rounded spear tip, except *Brachyphylla* and *Phyllonycteris* which sport a U-shaped notch in the distal tip of the spear; internarial region has a ridge or papilla in most taxa, but this is absent in *Brachyphylla*, *Erophylla*, and *Phyllonycteris*; lateral edge of noseleaf may be a thin free flap (*Brachyphylla*, *Erophylla*, *Phyllonycteris*), partially confluent with the face (*Hylonycteris*, *Lichonycteris*, *Scleronycteris*, *Cheoronycteris*, *Choeroniscus*, *Musonycteris*) or fully confluent with the face (*Anoura*, *Glossophaga*, *Monophyluus*, *Leptonycteris*); labial border of horseshoe grades into upper lip and no distinct boundary is present; tail present and shorter than the hindlegs in most species, but absent in *Leptonycteris yerbabuenae*, *Brachyphylla cavernarum* and *Anoura geoffroyi*; uropatagium of moderate length in most species, but rudimentary in *Anoura*; calcar present and shorter than the foot in most species, except *Brachyphylla* and *Phyllonycteris* where it is vestigial or absent; dental formula I2/0-2 C1/1 P2-3/2-3 M2-3/2-3 = 26–34. Single genal vibrissa present (15)*; *rib on spear absent* (26); chin pads with scalloped lateral edges (37)*; *slight to deep cleft on*

chin present (38); infraorbital foramen located above posterior P4 (51)*; infraorbital foramen located above anterior P4 (51); basisphenoid pits present (58); basioccipital pits absent (59); coronoid process of mandible level with or below condyloid process (62); I1 and I2 subequal (68); i1 occlusal margin smoothly rounded or straight, no lobes (72); i2 occlusal margin smoothly rounded or straight, no lobes (73); diastema sometimes or always present between P3-P4 (78)*; ectoloph on M3 W-shaped (89)*; lower molar nyctalodont (94)*; medial fibers of M. sternohyoideus originate from mesosternum (105)*; lateral fibers of M. sternohyoideus lack a manubrial origin (106); lateral fibers of M. sternohyoideus take origin from rib 1 (108); M. styloglossus inserts on posterolateral corner of tongue (117); M. genioglossus inserts into posterior quarter of ventral tongue (118); *anterolateral slip of M. sphincter colli profundus absent* (120); M. cricopharyngeus has more than three slips (123); basketlike medial-posterior mechanical papillae absent (137); brush of hairlike papillae present around distal margin of tongue (138)*; ***position of hair-like papillae on lateral margin and dorsum of distal third of tongue; not in single line*** (139); ***hairlike papillae fleshy and conical with filamentous tips*** (140); horny papillae located well proximal to tongue tip (142); *single midline artery present; lingual veins enlarged* (149); 13 thoracic vertebrae (150); *90 degree angle between ventral process and body of manubrium* (159); *M. spinodeltoideus originates from scapula* (196); caput mediale of M. triceps brachii inserts into caput laterale tendon only (199)*; M. palmaris longus inserts on manual digit II (203); M. palmaris longus does not insert on manual digit IV (205).

Comments

Glossophaginae has been the subject of considerable debate. Glossophaginae has typically been restricted to *Anoura*, *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, *Lichonycteris*, *Scleronycteris*, *Musonycteris*, *Glossophaga*, *Monophyllus*, and *Leptonycteris*, although the subfamily has often included lonchophylline species (e.g., Wetterer *et al.*, 2000; Carstens *et al.*, 2002; Simmons, 2005), phyllonycterine species (e.g., Baker and Bass, 1979; McKenna and Bell, 1997), and/or *Brachyphylla* (Baker and Bass, 1979; McKenna and Bell, 1997). Based on detailed anatomical descriptions of the hyoid region, Griffiths (1982) first proposed that Glossophaginae (sensu Jones and Carter, 1976, Wetterer *et al.*, 2000, and Simmons, 2005) was not monophyletic.

Griffiths (1982) proposed that nectar-feeding phyllostomids constituted two separate evolutionary lineages: glossophagines and lonchophyllines. Wetterer *et al.* (2000) and Dávalos *et al.* (2012) found strong support for a monophyletic Glossophaginae including the lonchophylline species (Fig. 1) using morphological data. However, although some molecular data have refuted this finding, indicating that Glossophaginae, as Griffiths (1982) originally proposed, is not monophyletic (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011), analyses of molecular data by Dumont *et al.* (2012) and Dávalos *et al.* (2012) recovered a weakly supported clade including all nectar-feeders. This node was also strongly supported in a combined analysis of morphological and molecular data (Dávalos *et al.*, 2012; see also Dávalos *et al.*, 2014). The reasons for these varying results are complex, but Dávalos *et al.* (2012) suggested that character construction (i.e., stressing the similarities among certain nectar feeding related characters rather than the differences), adaptive convergence in features related to nectar feeding, incongruence between mitochondrial and nuclear gene trees, and potentially adaptive convergence in regions of cytochrome *b* and CO1 caused recovery of what they consider to be a spurious node (i.e., a clade that includes all nectar-feeders). Studies that have more widely sampled nuclear DNA do not recover the nectar-feeder clade (Datzmann *et al.*, 2010), and removing potentially convergent morphological characters and downweighting saturated molecular data reduces support for these nodes. Consequently, we support the idea that lonchophyllines are not closely related to other nectar feeding taxa (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011 — Fig. 2), and that phyllonycterines and *Brachyphylla* actually nest within Glossophaginae (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2). Given the current understanding of relationships within this group, we expand the definition of Glossophaginae to include *Brachyphylla*, *Phyllonycteris*, and *Erophylla* (see Table 1 and Baker *et al.*, 2016). Our usage of this name thus differs from that of Griffiths (1982) and Griffiths and Gardner (2008), who excluded lonchophyllines from Glossophaginae.

Tribe Choeronycterini Solmsen 1998: 97

Type genus
Choeronycteris Tschudi 1844.

Definition

The clade arising from the last common ancestor of *Choeronycteris* and *Anoura.*

Composition

Anoura Gray 1838, *Choeroniscus* Thomas 1928, *Choeronycteris* Tschudi 1844, *Dryadonycteris* Nogueira, Lima, Peracchi, and Simmons 2012, *Hylonycteris* Thomas 1903, *Lichonycteris* Thomas 1895, *Musonycteris* Schaldach and McLaughlin 1960, and *Scleronycteris* Thomas 1912.

Description and diagnosis

Small to medium sized bats (FA= 31–49) with an elongate muzzle; lower jaw slightly to markedly longer than upper jaw; dental formula I2/0 C1/1 P2-3/3 M2-3/2–3 = 26–32. *Hairs in ventral fur unicolored* (6); lateral edges of horseshoe confluent with face inferiorly, superior edges free (30)*; infraorbital foramen located above anterior P4 (51)*; coronoid process of mandible level with or below condyloid process (62)*; I1 and I2 subequal (68)*; ***i1 absent*** (70); *i2 absent* (71); diastema between P4-M1 sometimes or always present (80)*; p3 subequal in height with p2, p4 (81)*; medial fibers of m.sternohyoideus take origin from the xiphoid process of the sternum (105)*; M. sternohyoideus inserts into fibers of M. hyoglossus and M. genioglossus (109)*; M. hyoglossus takes origin from raphe which forms insertion of M. sternohyoideus (113)*; M. geniohyoideus splits — deep insertion on basihyal, superficial insertion with M. hyoglossus (114)*; *superficial fibers of M. geniohyoideus insert in loop around the intersection of M. hyoglossus and M. sternohyoideus* (115); M. styloglossus inserts on posterolateral corner of tongue (117)*; M. genioglossus inserts on posterior quarter of ventral tongue (118)*; M. cricopharyngeus with more than three slips (123)*; *medial circumvallate papillae absent* (128); horny papillae located well proximal to tongue tip (142)*; pit for clavicular ligament present on scapula (162); M. humeropatagialis absent (191).

Comments

Allen (1898*a*) first applied the adjective 'choeronycterine' to one of three 'alliances' within Glossophaginae. The 'choeronycterine alliance' included *Choeronycteris*, *Lonchoglossa*, and *Anoura*. However, the term 'choeronycterine' was not used by Allen (1898*a*) as a formal taxonomic name. The formal taxonomic name that Allen choose for this group appears to be Lonchoglossi (Allen, 1898*a*: 240), but the genera included within

Lonchoglossi are not listed in the text. Several clues within the text suggest that Lonchoglossi is the formal name while choeronycterine is not. For example, Allen (1898*a*: 240) refers to formal taxonomic groups below the level of the subfamily in plain (non-italicized) text and preceeds all formal names with 'the' throughout the text: "Now it has been seen that the *Glossophaginae* yield two groups — that of the Glossophagi and that of the Lonchoglossi…The Glossophagi agree with the Vampyri…while the Lonchoglossi are much nearer the Phyllostomi." Allen (1898*a*: 258) also formally names Brachyphyllina for *Phyllonycteris* and *Brachyphylla*, but earlier in the text, he states that *Phyllonycteris* is the only member of the phyllonycterine alliance (Allen, 1898*a*: 237), again indicating to us that the names applied to the three alliances within Glossophagine are used informally. Part of the confusion may be due to the paper's posthumous publication, depriving the author of the chance to revise the paper before it appeared in press (Allen, 1898*a*: 264 Note).

The International Code of Zoological Nomenclature (1999: 11.7.1.2.) states that a name must be "clearly used as a scientific name to denote a supra-generic taxon and not merely as a plural noun or adjective referring to the members of a genus." Allen's usage of choeronycterine is at odds with this rule. Furthermore, the name choeronycterine does not conform with ICZN 11.7.2: "If a family-group name was published before 1900, in accordance with the above provisions of this Article but not in latinized form, it is available with its original author and date only if it has been latinized by later authors and has been generally accepted as valid by authors interested in the group concerned and as dating from that first publication in vernacular form." The name choeronycterine was not used widely for more than a century.

The author of the name Choeronycterini is Solmsen (1998: 97), who formally named the group for the genera *Choeroniscus*, *Choeronycteris* (with *Musonycteris* as a subgenus), and *Hylonycteris*. The name was used again, informally, by Carstens *et al.* (2002) who updated its composition to include the same seven genera we include here: *Anoura*, *Choeroniscus*, *Choeronycteris*, *Musonycteris*, *Hylonycteris*, *Lichonycteris*, and *Scleronycteris.* Baker *et al.* (2003 — Table 1) used the name for the same clade, which is generally strongly supported by both molecular (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2), and morphological data (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1).

Subtribe Anourina Baker, Solari, Cirranello, and Simmons 2016: 27

Type genus
Anoura Gray 1838.

Definition
The clade arising from the last common ancestor of all *Anoura* species.

Composition
Anoura Gray 1838 (includes *Lonchoglossa* Peters 1868).

Description and diagnosis
Medium sized bats (FA= 34–48) with tail vestigial or absent; muzzle elongate; lower jaw noticeably longer than upper jaw; dental formula I2/0 C1/1 P3/3 M3/3 = 32. *Cuticular scales on hair shaft with toothed scale margins* (4); *uropatagium rudimentary, present as a separate band along each leg* (12); *fringe of hair present along trailing edge of the uropatagium* (13); *lateral edges of horseshoe confluent with face along entire length* (30); M. ceratohyoideus inserts in part on stylohyal (112); basketlike medial mechanical papillae absent (137)*.

Comments
Baker *et al.* (2003: 24) divided Choeronycterini into two clades: Anourina (for *Anoura* only) and Choeronycterina (see below) based on the large genetic divergence between them (Table 1). *Anoura* appears as the sister taxon of the remaining Cheoronycterini in both morphological (Wetterer *et al.*, 2000; Carstens *et al.*, 2002; Dávalos *et al.*, 2012 — Fig. 1) and molecular trees (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2); monophyly of the remaining Choeronycterini taxa is often strongly supported. This name was made available in Baker *et al.* (2016).

Subtribe Choeronycterina, Solmsen 1998: 97

Type genus
Choeronycteris Tschudi 1844.

Definition
The clade arising from the last common ancestor of *Choeronycteris*, *Hylonycteris* and *Scleronycteris*.

Composition
Choeroniscus Thomas 1928, *Choeronycteris* Tschudi 1844, *Dryadonycteris* Nogueira, Lima, Peracchi, and Simmons 2012, *Hylonycteris* Thomas 1903, *Lichonycteris* Thomas 1895, *Musonycteris* Schaldach and *Scleronycteris* Thomas 1912.

Description and diagnosis
Small to medium sized bats (FA= 30–47), with tail present but not extending beyond edge of uropatagium; dental formula I2/0 C1/1 P2/3 M2-3/2-3 = 26–30. *Zygomatic arch sometimes or always incomplete* (48); *ectotympanic bulla extends medially across 34–49% of cochlea* (54); basisphenoid pits present (58)*; basioccipital pits absent (59)*; *W-shaped ectoloph absent on M1, M2* (84); *M1-M2 diastema sometimes or always present* (87); M. ceratohyoideus inserts in part on stylohyal (112)*; basketlike medial mechanical papillae present (137); *two horny papillae larger than others in cluster* (144); *no horny papillae anterior to largest papillae in cluster* (146); anterior lamina present on ribs (154); pit for clavicular ligament present on scapula (162)*.

Comments
See comments under Choeronycterini and Anourina above.

Tribe Glossophagini Bonaparte 1845: 5

Type genus
Glossophaga E. Geoffroy 1818.

Definition
The clade arising from the last common ancestor of *Glossophaga*, *Monophyllus*, and *Leptonycteris*.

Composition
Glossophaga E. Geoffroy 1818, *Leptonycteris* Lydekker 1891, *Monophyllus* Leach 1821.

Description and diagnosis
Small to medium sized bats (FA=32–57) in which the lower incisors are present; dental formula I2/2 C1/1 P2/3 M2-3/2-3 = 30–34. Genal vibrissae absent (15); *lateral edges of horseshoe confluent with face along entire length* (30); infraorbital foramen located above anterior P4 (51)*; *anterior rim of orbit terminates above posterior M1* (52); ectotympanic bulla extends medially across 34–49% of cochlea (54); basisphenoid pits absent (58); basioccipital pits present (59); I1 and I2 subequal (68)*;

i1 occlusal margin smoothly rounded or straight, no lobes (72)*; i2 occlusal margin smoothly rounded or straight, no lobes (73)*; p3 subequal in height with p2, p4 (81)*; medial fibers of M. sternohyoideus take origin from xiphoid process of sternum (105)*; M. sternohyoideus inserts into the fibers of M. hyoglossus and M. geniohyoideus (109)*; M. ceratohyoideus inserts in part on stylohyal (112); M. hyoglossus originates from raphe that forms the insertion of M. sternohyoideus (113)*; M. geniohyoideus has split insertion, deep insertion onto basihyal, superficial insertion with M. hyoglossus and M. sternohyoideus (114)*; M. styloglossus inserts on posterolateral corner of tongue (117)*; M. genioglossus inserts onto posterior quarter of ventral tongue (118)*; M. stylohyoideus sometimes or always present (119)*; M. cricopharyngeus with more than three slips (123)*; basket-like medial mechanical papillae absent (137)*; horny papillae located well proximal to tongue tip (142)*; *two horny papillae larger than others in cluster* (144); single horny papilla anterior to largest papilla in cluster (145)*; *no horny papillae posterior to largest papillae in cluster* (146); *papillae flanking largest horny papillae sometimes or always absent* (147).

Comments

We follow Carstens *et al.* (2002) who informally termed these taxa 'glossophagines' and Baker *et al.* (2003 — Table 1) who named a tribe for these taxa. Morphological data do not support the monophyly of this group (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1); however, there is strong support for this clade in molecular analyses (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012; — Fig. 2), as well as a combined analysis (Dávalos *et al.*, 2012, 2014). These taxa were thought to be part of a monophyletic group that additionally included only Choeronycterini; however, it has become clear that these three Glossophagini genera may be sister taxa to Brachyphyllini.

Tribe Brachyphyllini, Gray 1866: 115

Type genus

Brachyphylla Gray 1833.

Definition

The clade arising from the last common ancestor of *Brachyphylla* and *Phyllonycteris*.

Composition

Brachyphylla Gray 1833, *Erophylla* Miller 1906, and *Phyllonycteris* Gundlach 1860.

Description and diagnosis

Medium to large bats (FA= 45–69) with noseleaf reduced to a low flap with little or no projection above the rostrum; dental formula I2/2 C1/1 P2/2 M3/3 = 32. *Pelage differentiated into over and under hairs* (1); **padlike or flaplike vibrissal papillae in contact across the dorsum of the snout** (20); *spear of noseleaf equal to or less than the height of the horseshoe* (24); *internarial region smooth* (28); entire lateral edge of horseshoe forms thin free flap (30); infraorbital foramen located above posterior P4 (51); *ectotympanic bulla extends medially across 66% of cochlea* (54); basioccipital pits absent (59)*; coronoid process of mandible is 1.5 times the height of the condyloid process (62); I1 noticeably larger than I2 (68); *height of P3 less than P4* (76); *P3 single rooted* (77); *p3 absent* (81); *W-shaped ectoloph on M1, M2 absent* (84); *paraconid on m1 sometimes or always absent* (91); lower molars with cusps or crest indistinguishable (94); vomeronasal tube rudimentary, neuroepithelial lining absent (97); vomeronasal cartilage bar-shaped (98); accessory olfactory bulb absent (100); *M. mylohyoideus partially divided into anterior and posterior parts by aponeurosis* (103); medial fibers of M. sternohyoideus take origin from mesosternum (105); M. sternohyoideus inserts on basihyal (109); M. ceratohyoideus does not insert on stylohyal (112)*; M. hyoglossus originates from basihyal (113); M. geniohyoideus has single insertion via tendon to basihyal or basihyal raphe (114); M. styloglossus inserts on lateral surface of tongue (117); M. genioglossus inserts on ventral tongue along more than half its length (118); *M. cricopharyngeus with two slips* (123); hairlike papillae with ellipse shaped distal ends (140); horny papillae located near tongue tip (142); *third and fifth metacarpals subequal in length, both longer than fourth* (175); calcar vestigial or absent (187); Brunner's glands absent at gastroduodenal juncture (210).

Comments

Many recent classifications have not provided a name for this clade, but instead placed *Brachyphylla* and phyllonycterines (*Phyllonycteris* + *Erophylla*) into separate subfamilies (e.g., Koopman, 1994; but see McKenna and Bell, 1997 — Table 1) despite their close relationship. Although that was an option here, we choose instead to emphasize the

relationship between these two groups, subsuming subtribes within Brachyphyllini. Previous morphological, immunological, and molecular work has often indicated strong support for a close relationship of *Brachyphylla* with Phyllonycterinae (e.g., Taboada and Pine, 1969; Baker and Lopez, 1970; Baker and Bass, 1979; Baker *et al.*, 1981, 2003; Carstens *et al.*, 2002; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2). Wetterer *et al.* (2000) found that their morphological data were unable to resolve the position of *Brachyphylla* and they placed this taxon *incertae sedis* in their classification (Table 1). An expanded morphological data set places *Brachyphylla* as sister taxon to desmodontines with weak support (Dávalos *et al.*, 2012). Combined analyses of molecular and morphological data provide strong support for Brachyphyllini (Dávalos *et al.*, 2012, 2014).

Subtribe Brachyphyllina, Gray 1866: 115

Type genus
  Brachyphylla Gray 1833.

Definition
  The clade arising from the last common ancestor of all species of *Brachyphylla*.

Composition
  Brachyphylla Gray 1833.

Description and diagnosis
  Large bats (FA = 56–69 mm). *Spear tip with U-shaped notch in distal tip* (25); *multiple well-developed papillae present on chin* (36); *central chin cleft absent* (38); *infraorbital foramen above anterior M1* (51); basisphenoid pits present (58)*; *lingual cingulum on I1* (63); i1 occlusal margin with three lobes (72); i2 occlusal margin with three lobes (73); *P3-P4 always in contact, diastema absent* (78); P4-M1 always in contact, diastema absent (80); lower molar cusps or crests indistinguishable (94)*; vomeronasal tube rudimentary, neuroepithelial lining absent (97)*; vomeronasal cartilage bar-shaped (98)*; accessory olfactory bulb absent (100)*; lateral fibers of M. sternohyoideus do not take origin from manubrium (106)*; lateral fibers of M. sternohyoideus take origin from first rib (108)*; M. stylohyoideus absent (119); *anterolateral slip of M. sphincter colli profundus present* (120); *lateral circumvallate papillae absent* (130); basketlike medial mechanical papillae present (137); *brush of

hairlike papillae absent around distal margin of tongue* (138); three papillae anterior to largest horny papilla (145); *paired lingual arteries present, lingual veins not enlarged* (149); *angle between ventral process and body of manubrium less than 90 degrees* (159); *tail effectively absent* (182); calcar vestigial or absent (187)*; Brunner's glands at gastroduodenal juncture absent (210)*.

Comments
  This name has been accorded subfamily rank in previous classifications (e.g., McKenna and Bell, 1997; Wetterer *et al.*, 2000 — Table 1), and includes a single genus, *Brachyphylla*, with a distinctive morphology (Miller 1907) that validates its separation from other genera. *Brachyphylla* was included within Stenodermatinae by H. Allen (1898*b*) and Miller (1907).

Subtribe Phyllonycterina Miller 1907: 171

Type genus
  Phyllonycteris Gundlach 1860.

Definition
  The clade arising from the last common ancestor of *Phyllonycteris* and *Erophylla*.

Composition
  Erophylla Miller 1906 and *Phyllonycteris* Gundlach 1860.

Description and diagnosis
  Medium-large bats (FA = 44–50 mm). Lower i1 occlusal margin smoothly rounded or straight, no lobes (72)*; i2 occlusal margin smoothly rounded or straight, has no lobes (73)*; P4-M1 diastema sometimes or always present (80)*; *metaconid on m1 absent* (92); *entoconid on m1 absent* (93); *medial longitudinal fissure covered by cerebellar vermis, inferior colliculi partially exposed* (101); M. stylohyoideus sometimes or always present (119)*; *lateral slip of M. sphincter colli profundus absent* (121); basketlike medial mechanical papillae absent (137)*; hairlike papillae cylindrical with ellipse shaped distal end (140)*; *no horny papillae anterior to largest papilla in cluster* (145); *second costal cartilage articulates with manubrial-mesosternal joint* (156): *first and second phalanges of manual digit III subequal* (178).

Comments
  Miller (1907) introduced the subfamily Phyllonycterinae for *Phyllonycteris* and *Erophylla* and this

usage and composition was followed by many subsequent authors (e.g., Koopman 1993; Wetterer *et al.*, 2000; and see McKenna and Bell 1997 for an arrangement using this name at the tribal level — Table 1). *Erophylla* was considered a synonym of *Phyllonycteris* by Varona (1974), in recognition of the close relationship between these two genera strongly suggested by morphological data (Wetterer *et al.*, 2000; Carstens *et al.*, 2002; Dávalos *et al.*, 2012 — Fig. 1). Intriguingly, Datzmann *et al.* (2010), in an analysis of molecular data, found that *Brachyphylla* nested within Phyllonycterinae as the sister taxon of *Phyllonycteris*. However, subsequent molecular analyses have strongly supported the monophyly of *Phyllonycteris* + *Erophylla* (Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012).

Subfamily Lonchophyllinae Griffiths 1982: 43

Type genus
   Lonchophylla Thomas 1903.

Definition
   The clade arising from the last common ancestor of *Hsunycteris*, *Lonchophylla*, *Lionycteris*, *Platalina*, and *Xeronycteris*.

Composition
   Hsunycteris Parlos, Timm, Swier, Zeballos, and Baker 2014, *Lionycteris* Thomas 1913, *Lonchophylla* Thomas 1903, *Platalina* Thomas 1928, *Xeronycteris* Gregorin and Ditchfield 2005.

Description and diagnosis
   Small to medium-sized bats (FA: 32–61 mm) lacking facial and dorsal stripes or shoulder and neck spots; small rounded ears; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear present (in all but *Platalina*) and restricted to proximal part; internarial region bearing a ridge or papilla in all taxa save *Platalina*; no distinct boundary between labial border of horseshoe and upper lip; tail of medium length — shorter than the hindlegs; uropatagium present, of medium length, and lacking a fringe; calcar present and shorter than the foot; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Genal vibrissae absent (15); single genal vibrissa present (15)*; *three interramal vibrissae present* (16); *lateral edges of horseshoe confluent with face along entire length* (30); chin pads with scalloped lateral edges (37)*; zygomatic arch

sometimes or always incomplete (48)*; infraorbital foramen located above posterior P4 (51)*; two lobes on i2 occlusal margin (73)*; P3-P4 diastema sometimes or always present (78)*; P4-M1 diastema sometimes or always present (80)*; p3 subequal in height with p2, p4 (81)*; M3 ectoloph W-shaped (89)*; M. cricopharyngeus with two slips (123); *patch of anteriorly directed medial-posterior mechanical papillae sometimes or always absent* (134); brush of hair-like papillae along distal margin of tongue (138)*; *no horny papillae anterior to largest papillae in cluster* (145); *papillae flanking largest horny papillae in cluster sometimes or always absent* (147); *lateral sulcus present on tongue* (148).

Comments
   Lonchophylline species traditionally have been included within Glossaphagine along with other nectar-feeding phyllostomids (e.g., Miller, 1907). However, on the basis of tongue morphology, Griffiths (1982) suggested that lonchophyllines were not closely related to other nectar feeding taxa. Despite this evidence, many authors continued to include lonchophyllines in the subfamily Glossaphagine based on more comprehensive analyses of morphological data from a number of anatomical systems, which provided some support for a sister-group relationship between glossaphagines (sensu stricto) and lonchophyllines (Wetterer *et al.*, 2000; Carstens *et al.*, 2002; Dávalos *et al.*, 2012 — Fig. 1 and Table 1). Recent molecular work, however, suggests that lonchophyllines are more closely related to taxa typically included in Carolliinae, Stenodermatinae, and a few taxa formerly included in Phyllostominae than they are to Glossophaginae (Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011 — Fig. 2; but see discussion under Glossophaginae above and Dávalos *et al.*, 2012 and Dumont *et al.*, 2012). The fossil genus *Palynephyllum*, known from the Miocene of Colombia, is also included in this subfamily, following Dávalos *et al.* (2014).

Tribe Lonchophyllini Griffiths 1982: 43

Type genus
   Lonchophylla Thomas 1903.

Definition
   The clade arising from the last common ancestor of *Lonchophylla*, *Lionycteris*, *Platalina*, and *Xeronycteris*.

Composition

   Lionycteris Thomas 1913, *Lonchophylla* Thomas 1903, *Platalina* Thomas 1928, *Xeronycteris* Gregorin and Ditchfield 2005.

Description and diagnosis

   Small to medium sized bats (FA: 32–61 mm). Medial fibers of M. sternohyoideus orginate from xiphoid process of sternum (105)*; M. sternohyoideus inserts into the fibers of M. hyoglossus and M. geniohyoideus (109)*; M. hyoglossus takes origin from raphe which forms the insertion of M. sternohyoideus (113)*; M. geniohyoideus with deep insertion on basihyal and superficial insertion with M. hyoglossus and M. sternohyoideus (114)*; M. genioglossus insets on posterior half to third of ventral tongue (118)*; M. cricopharyngeus with two muscular slips (123)*; 90 degree angle between ventral process and body of manubrium (159).

Comments

   All of these genera were previously classified within Lonchophyllinae and no tribes were recognized within (Baker *et al.*, 2003). However, several authors found that *Lonchophylla* as previously defined did not appear to be monophyletic (e.g., Dávalos and Jansa, 2004; Woodman and Timm, 2006; Woodman, 2007). Parlos *et al.* (2014), on the basis of a multigene analysis, defined two tribes within Lonchophyllinae, resolving some of the problems with *Lonchophylla* by recognizing *Hsunycteris* and Hsunycterini for what had been previously called the '*L. thomasi* complex.' Morphological data have not been applied to this problem recently. Additional work is needed to clarify relationships within Lonchophyllini (Parlos *et al.*, 2014; Rojas *et al.*, In press) and the relationships and position of several newly recognized species.

Tribe Hsunycterini Parlos, Timm, Swier, Zeballos, and Baker 2014: 14

Type genus

   Hsunycteris Parlos, Timm, Swier, Zeballos, and Baker 2014.

Definition

   The clade arising from the last common ancestor of all species of *Hsunycteris*.

Composition

   Hsunycteris Parlos, Timm, Swier, Zeballos, and Baker 2014.

Description and diagnosis

   Small bats (FA: 30–34 mm). Genal vibrissae absent (15)*; *infraorbital foramen above anterior P4* (51).

Comments

   Additional support for recognition of Hsunycterini comes from karyotypic data (Parlos *et al.*, 2014; Almeida *et al.*, 2016). See comments under Lonchophyllini above.

Subfamily Glyphonycterinae Baker, Solari, Cirranello, and Simmons 2016: 16

Type genus

   Glyphonycteris Thomas 1896.

Definition

   The clade arising from the last common ancestor of *Glyphonycteris*, *Neonycteris*, and *Trinycteris*.

Composition

   Glyphonycteris Thomas 1896 (includes *Barticonycteris* Hill 1964), *Neonycteris* Sanborn 1949, *Trinycteris* Sanborn 1949.

Description and diagnosis

   Small to large-sized bats (FA: 37–58 mm) lacking facial stripes and shoulder and neck spots, dorsal stripe sometimes present (only in *Trinycteris)*, medium to larger sized ears with pointed tips; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear restricted to proximal part; lateral edge of noseleaf forms a thin free flap; no distinct boundary between the labial border of horseshoe and the upper lip; two dermal pads with smoothly rounded lateral margins present on the chin; tail shorter than the hindlegs; moderate length uropatagium lacks a fringe; calcar present and shorter than the foot; dental formula I2/2 C1/1 P2/3 M3/3 = 34. Two vibrissal columns present adjacent to noseleaf (17); chin smooth just ventral to midline of lower lip, central papilla absent (39); zygomatic arch complete (48); *infraorbital foramen located above posterior M1* (51); anterior rim of orbit terminates above anterior M2 (52); ectotympanic bulla extends medially across 50% of cochlea (54); coronoid process of mandible 1.5 times the height of condyloid process (62); *lingual cingulum on I1 absent* (63); *I2-canine always in contact diastema, absent* (69); *p3 reduced, less than 1/4 the height of p2*, p4 (81); W-shaped ectoloph present on M1, M2 (84); *hypocone basin present*

on M1, cusp indistinct to well-developed (85); medial longitudinal fissure covered by cerebellar vermis, inferior colliculi partially exposed (101); M. mylohyoideus clearly divided into anterior and posterior parts by pronounced break (103); M. ceratohyoideus inserts, in part, on stylohyal (112); *four ribs articulate with mesosternum* (157); pit for clavicular ligaments present on scapula (162); ischial tuberosity large (183); compact white anteromedial body in male accessory gland absent (212).

Comments

All of these genera were traditionally classified within Phyllostominae as subgenera of *Micronycteris* (sensu Sanborn 1949). Wetterer *et al.* (2000) raised the subgenera to generic rank and included them within the tribe Micronycterini (see Table 1). Support for the relationships within Glyphonycterinae and of this taxon with other phyllostomids were only weakly supported by the Wetterer *et al.* (2000) data set (Fig. 1). Morphological data do not provide support for this clade (Dávalos *et al.*, 2012). However, recent molecular analyses have confirmed the placement of *Glyphonycteris* and *Trinycteris* as part of a clade including *Carollia* (Carolliinae, sensu stricto), with high levels of support (e.g., Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — see Fig. 2). Baker *et al.* (2003) used the name Glyphonycterinae for this clade (Table 1), which was made available in Baker *et al.* (2016). The inclusion of *Neonycteris* within this subfamily is based on the combined analysis of Dávalos *et al.* (2014).

Subfamily Carolliinae Miller 1924: 53

Type genus
    Carollia Gray 1838.

Definition
    The clade arising from the last common ancestor of species of *Carollia.*

Composition
    Carollia Gray 1838.

Description and diagnosis
    Small to medium-sized bats (FA: 34–45 mm), lacking facial stripes, dorsal stripes, and shoulder and neck spots; medium sized ears with pointed tips; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear present and restricted to proximal part of spear;

lateral edge of noseleaf thin free flap; no distinct boundary between labial border of horseshoe and upper lip; tail shorter than the hindlegs and shorter than the medium length uropatagium; uropatagium lacks a fringe; calcar present and shorter than the foot; dental formula I2/2 C1/1 P2/2 M3/3 = 32. *Tricolored ventral hairs present*, *base pale*, *dark median band*, *pale tip* (6); *genal vibrissae absent* (15); single vibrissal column lateral to noseleaf (17)*; *multiple well-developed papillae present on chin* (36); central papilla present just ventral to midline of lower lip (39)*; zygomatic arch sometimes or always incomplete (48)*; anterior rim of orbit terminates above posterior M1 (52)*; *ectotympanic bulla extends medially across 33% of cochlea* (54); coronoid process of mandible twice the height of the condyloid process (62)*; *i1 occlusal margin bilobed* (72); *i2 occlusal margin bilobed* (73); p3 absent (81)*; W-shaped ectoloph absent on M1, M2 (84)*; M. stylohyoideus sometimes or always present (119); suprascapular process present (166)*; *third and fifth metacarpals subequal in length*, *both longer than fourth* (175); *first and second phalanges of manual digit IV subequal* (180); *XX/XY1Y2 sex determining system sometimes or always present*, *X translocated to autosome* (220).

Comments

This subfamily was originally proposed as Hemiderminae by Miller (1907) for the genera *Hemiderma* (=*Carollia*) and *Rhinophylla*, which had been previously included in Phyllostominae. Most subsequent classifications have recognized this taxon, albeit at slightly different taxonomic levels (e.g., subfamilial level by Koopman, 1993, and McLellan and Koopman, 2008; tribal level by McKenna and Bell, 1997). However, taxonomic confusion has surrounded this grouping since the late 1960s, when Baker (1967) and Baker and Bleier (1971) described karyotypic data placing *Carollia* as a close relative of *Choeroniscus*, and Owen *et al.* (1984) placed *Carollia* in Glossophaginae. More recently, explicit phylogenetic analyses based on morphology provided weak support for carolliine monophyly including *Rhinophylla* (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1). However, molecular studies unequivocally indicate that Carolliinae as traditionally recognized is polyphyletic (Baker *et al.*, 2000, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012); *Rhinophylla* appears to be more closely related to Stenodermatinae, while *Carollia* is the sister taxon of a clade including

Glyphonycteris, *Neonycteris*, and *Trinycteris* (Fig. 2). Accordingly, we here restrict Carolliinae to *Carollia* only, following Baker *et al.* (2003 — see Table 1).

Subfamily Rhinophyllinae Baker, Solari, Cirranello, and Simmons 2016: 17

Type genus
  Rhinophylla Peters 1865.

Definition
  The clade arising from the last common ancestor of all recognized species of *Rhinophylla*.

Composition
  Rhinophylla Peters 1865.

Description and diagnosis
  Small bats (FA: 29–38 mm) lacking facial stripes, dorsal stripes, and shoulder and neck spots; small ears with a rounded tip; simple noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear restricted to proximal part; lateral edge of noseleaf thin free flap; no distinct boundary between labial border of horseshoe and upper lip; two dermal pads with smoothly rounded lateral margins present on the chin; papilla present in center of chin between lateral dermal pads; tail absent; medium length uropatagium lacks a fringe; calcar present and shorter than the foot; dental formula I2/2 C1/1 P2/2 M3/3 = 32. Posterior edge of plagiopatagium attaches to lateral metatarsal (11)*; *vibrissal papillae surrounding noseleaf joined to form a skin flap* (19); zygomatic arch sometimes or always incomplete (48)*; ectotympanic bulla extends medially across 34–49% of cochlea (54)*; coronoid process of mandible twice the height of condyloid process (62)*; *I1 occlusal margin bifid, both lobes approximately the same size* (64); P3 lower in height than P4 (76)*; *diastema between P3-P4 sometimes or always present* (78); *diastema between P4-M1 sometimes or always present* (80); *diastema between M1-M2 sometimes or always present* (87); *accessory olfactory bulb absent* (100); *all horny papilla subequal in size* (144); second costal cartilage articulates with manubrium only (156); *90 degree angle between ventral process and body of manubrium* (159); suprascapular process present (166)*; *first and second phalanges of manual digit IV subequal in length* (180); calcar completely cartilaginous (188)*.

Comments
  The genus *Rhinophylla* was previously associated with *Carollia* (e.g., Miller 1907) in the subfamily Carolliinae. Although karyotypic (Baker and Bleier, 1971) and genetic distance data for the cytochrome *b* gene (Wright *et al.*, 1999) supported the distinctiveness of *Rhinophylla*, morphological work (e.g., Wetterer *et al.*, 2000; Dávalos *et al.*, 2012) continued to recover Carolliinae, albeit with weak support (Fig. 1). Molecular analysis (e.g., Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012) generally provides strong support for placement of *Rhinophylla* as the sister taxon of Stenodermatinae (Fig. 2). Baker *et al.* (2003) named Rhinophyllinae for *Rhinophylla* (Table 1), and Baker *et al.* (2016) made this name available. We follow Baker *et al.* (2003) in recognizing Rhinophyllinae as a subfamily, rather than subsuming it within Stenodermatinae, a taxon with a long history, stable composition, and strong support from both molecular and morphological work.

Subfamily Stenodermatinae Gervais, in de Castelnaeu 1855: 32n

Type genus
  Stenoderma E. Geoffroy 1818.

Definition
  The clade arising from the last common ancestor of *Sturnira*, *Vampyressa*, and *Stenoderma*.

Composition
  Ametrida Gray 1847, *Ardops* Miller 1906, *Ariteus* Gray 1838, *Artibeus* Leach 1821, *Centurio* Gray 1842, *Chiroderma* Peters 1860, *Ectophylla* H. Allen 1892, *Enchisthenes* K. Andersen 1906, *Mesophylla* Thomas 1901, *Phyllops* Peters 1865, *Platyrrhinus* Saussure 1860, *Pygoderma* Peters 1863, *Sturnira* Gray 1842, *Stenoderma* E. Geoffroy 1818, *Sphaeronycteris* Peters 1882, *Uroderma* Peters 1866, *Vampyressa* Thomas 1900, *Vampyriscus*, Thomas 1900 (includes *Metavampyressa* Peterson 1968), *Vampyrodes* Thomas 1900.

Description and diagnosis
  Small to medium-sized bats (FA: 33–46 mm); facial stripes present in some or all species of *Artibeus*, *Enchisthenes*, *Chiroderma*, *Vampyressa*, *Vampyriscus*, *Uroderma*, *Vampyrodes*, and *Platyrrhinus*; shoulder patch present in *Ametrida*, *Centurio*, *Pygoderma*, *Phyllops*, *Sphaeronycteris*, and *Stenoderma*; white spot on shoulder present in

Ametrida, *Ardops*, *Ariteus*, *Centurio*, *Pygoderma*, *Phyllops*, *Sphaeronycteris*, and *Stenoderma;* dorsal stripes present in some or all species of *Chiroderma*, *Platyrrhinus*, *Uroderma*, *Vampyrodes*, *Vampyriscus*; small ears often with pale bands along the edges; noseleaf present in all species except *Centurio* in which it is highly modified; noseleaf with spear equal to or longer than twice the height of the horseshoe; rib of spear runs to the distal tip; lateral edge of noseleaf thin free flap; labial border of horseshoe is a thin free flap (*Ametrida*, *Artibeus Chiroderma*, *Ectophylla*, *Mesophylla*, *Platyrrhinus*, *Stenoderma*, *Uroderma*, *Vampyrodes*, *Vampyressa*, and *Vampyriscus*), or thickened ridge present between labial horseshoe and upper lip (*Ardops*, *Ariteus*, *Phyllops*, and *Pygoderma*), or no distinct boundary present between the labial edge of the horseshoe and the upper lip (*Sturnira*, *Enchisthenes*, and *Sphaeronycteris*); multiple well-developed papillae surround a large central papilla on chin, except in *Centurio* and *Sphaeronycteris* where the chin is smooth; tail absent; uropatagium present and of medium length except in *Sturnira* in which it is rudimentary; a fringe of hairs along the trailing edge of the uropatagium in *Ardops*, *Ariteus*, *Ametrida*, *Centurio*, *Phyllops*, *Pygoderma*, *Sphaeronycteris*, *Stenoderma*, *Enchisthenes*, *Vampyrodes caraccioli*, *Sturnira*, some species of *Artibeus* and some species of *Platyrrhinus*; calcar present and shorter than the foot, except in *Sturnira* where the calcar is vestigial or absent; dental formula I2/1-2 C1/1 P2/2 M2-3/2-3 = 26–32. *Multiple well-developed papillae present on chin* (36); zygomatic arch complete (48); *infraorbital foramen located above posterior P4* (51); anterior rim of orbit terminates above anterior M1 (52); basioccipital pits absent (59); I2 and canine always in contact, diastema absent (69); **papillae present on inner surface of lips and cheeks** (126); *lateral circumvallate papillae present on dorsolateral border of tongue, between dorsal and lateral surfaces* (131); second costal cartilage articulates with manubrial-mesosternal joint (156)*; *elevated ridges define broad triangular face of manubrium* (158); suprascapular process absent (166); *sacral vertebrae sometimes or always articulate with ischium* (181); *ischial tuberosity large* (183); M. palmaris longus does not insert on manual digit III (204)*; *cornual lumina of uterus absent* (216); *oviducts with fundic medial entry to uterus* (218).

Comments

Monophyly of Stenodermatinae is very strongly supported in analyses of both molecular (Van Den Bussche, 1992; Baker *et al.*, 2000, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2) and morphological data (Wetterer *et al.*, 2000; Dávalos *et al.*, 2012 — Fig. 1). *Sturnira* has occasionally been considered as a distinct subfamily (Sturnirinae Miller, 1907; Baker, 1967) due to its morphological differences from other stenodermatine species; however, karyological (e.g., Baker, 1967), immunological (e.g., Gerber, 1968; Gerber and Leone, 1971), molecular (e.g., Baker *et al.*, 2003), and morphological data (e.g., Wetterer *et al.*, 2000; Dávalos *et al.*, 2012) support a sister taxon relationship between *Sturnira* and Stenodermatini bats (Figs. 1 and 2). We follow recent classifications (e.g., Koopman, 1993, 1994; Gardner, 2008) and retain *Sturnira* within Stenodermatinae to recognize the close relationship and historical association of this taxon with other stenodermatines.

Tribe Sturnirini Miller 1907: 38

Type genus
    Sturnira Gray 1842.

Definition
    The clade arising from the last common ancestor of all species of *Sturnira*.

Composition
    Sturnira Gray 1842.

Description and diagnosis
    Medium to large sized bats (FA= 34–61 mm), with large adult males of most species bearing epaulettes, conspicuous tufts of yellow or reddish hairs on the shoulders; dental formula I2/1-2 C1/1 P2/2 M3/3 = 30–32. *Pelage differentiated into over and under hairs* (1); *dorsal fur with tricolored hairs, dark base, pale median band, dark tip* (5); posterior edge of plagiopatagium attaches to ankle or lower leg (11); *uropatagium rudimentary, present as a separate band along each leg* (12); *fringe of hairs present along trailing edge of uropatagium* (13); ectotympanic bulla extends medially across 50% of cochlea (54); *basisphenoid pits present* (58); basioccipital pits absent (59)*; *width of basiocciput between cochlea sometimes or always 1/3 the width of the foramen magnum* (60); coronoid process of mandible 1.5 times the height of condyloid process (62); *lingual cingulum present on I1* (63); I2 and canine always in contact, diastema absent (69)*; P3 subequal to P4 in height (76); *lateral fibers*

of *M. sternohyoideus do not originate from clavicle* (107); *lateral slip of M. sphincter colli profundus absent* (121); *four ribs articulate with mesosternum* (157); *pit for clavicular ligaments present on scapula* (162); *calcar vestigial or absent* (187).

Comments

Although most workers include the subgenus *Corvira* within *Sturnira* (e.g, Simmons, 2005), Owen (1987) recognized Corvirini for the genus *Corvira* and Sturnirini for *Sturnira* sensu stricto. Although species of *Sturnira* (*Corvira*) appear to fall outside the clade that includes all species of *Sturnira* (*Sturnira*), the two *Corvira* species may not form a monophyletic group (see Pacheco and Patterson, 1991; Villalobos and Valerio, 2002; Velazco and Patterson, 2013). Accordingly, we do not use the name Corvirini and apply the name Sturnirini to include all species of *Sturnira* sensu lato.

Tribe Stenodermatini Gervais, in de Castelnaeu 1855: 32n

Type genus
Stenoderma E. Geoffroy 1818.

Definition

The clade arising from the last common ancestor of *Stenoderma*, *Artibeus*, *Enchisthenes*, *Ectophylla*, and *Vampyressa*.

Composition

Ametrida Gray 1847, *Ardops* Miller 1906, *Ariteus* Gray 1838, *Artibeus* Leach 1821, *Centurio* Gray 1842, *Chiroderma* Peters 1860, *Ectophylla* H. Allen 1892, *Enchisthenes* K. Andersen 1906, *Mesophylla* Thomas 1901, *Phyllops* Peters 1865, *Platyrrhinus* Saussure 1860, *Pygoderma* Peters 1863, *Stenoderma* E. Geoffroy 1818, *Sphaeronycteris* Peters 1882, *Uroderma* Peters 1866, *Vampyressa* Thomas 1900, *Vampyriscus*, Thomas 1900 (includes *Metavampyressa* Peterson 1968), *Vampyrodes* Thomas 1900.

Description and diagnosis

Dental formula I2/1-2 C1/1 P2/2 M2-3/2-3 = 26–32. *toothed margin on cuticular scales on hair shaft* (4); *facial stripes present* (7); posterior edge of plagiopatagium attaches to lateral metatarsal (11)*; interramal vibrissae absent (16); *rib runs to tip of spear* (27); labial edge of horseshoe forms a thin free flap (31); infraorbital foramen located above anterior P4 (51); anterior rim of orbit terminates

above anterior M1 (52)*; coronoid process of mandible twice the height of the condyloid process (62)*; i1 occlusal margin bilobed (72); i2 occlusal margin bilobed (73); *I1 and i1 widely separated when cheek teeth occlude* (74); P3 lower in height than P4 (76)*; *M3 absent* (88); *m1 paraconid sometimes or always absent* (91); *M. mylohyoideus clearly divided into anterior and posterior parts by pronounced break* (103); lateral slip of M. sphincter colli profundus passes laterally and anteriorly to insert on the skin of the cervical region (122)*; *medial posterior mechanical papillae inclined toward the tongue tip* (133); band of long-tipped bifid anterior mechanical papillae present at juncture between anterior and medial-posterior mechanical papillae (135); *basketlike medial posterior mechanical papillae absent* (137); *third and fourth metacarpals subequal in length and longer than fifth* (175); Brunner's glands absent at gastroduodenal juncture (210); compact white anteromedial body in male accessory gland absent (212).

Comments

Monophyly of Stenodermatini as recognized here is strongly supported by both molecular and morphological data sets (Wetterer *et al.*, 2000; Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Figs. 1 and 2). The name Stenodermatini historically has been applied to many different groupings of stenodermatine species. The name was restricted to the 'short-faced' fruit bats by H. Allen (1898*b*; Stenodermini); it was used to apply to all of what we call Stenodermatinae by Baker *et al.* (1989) and McKenna and Bell (1997). Owen (1987) applied this name to either a clade that included only the short-faced stenodermatines, or to a clade that included the short-faced stenodermatines plus *Enchisthenes*, *Dermanura*, and *Koopmania* (Owen, 1987). This name was also applied to non-*Sturnira* stenodermatines by Koopman (1993, 1994) and Wetterer *et al.* (2000 — Table 1). This last usage provides a means of distinguishing between *Sturnira* and other stenodermatines while preserving the traditional use of subfamily names, so we use it in this sense here.

Subtribe Vampyressina Baker, Solari, Cirranello, and Simmons 2016: 29

Type genus
Vampyressa Thomas 1900 (as restricted by Hoofer and Baker, 2006).

Definition

The clade arising from the last common ancestor of *Chiroderma*, *Platyrrhinus*, *Vampyrodes*, *Uroderma*, *Mesophylla*, *Vampyressa*, and *Vampyriscus*.

Composition

Chiroderma Peters 1860, *Mesophylla* Thomas 1901, Peterson 1868, *Platyrrhinus* Saussure 1860 (*Vampyrops* Peters 1865 is a synonym; Gardner and Ferrell, 1990), *Uroderma* Peters 1866, *Vampyressa* Thomas 1900, *Vampyriscus* Thomas 1900, (*Metavampyressa* Peterson 1868 is a synonym) and *Vampyrodes* Thomas 1900.

Description and diagnosis

Small to medium sized bats (FA = 29–64 mm) with a somewhat longer rostrum than other stenodermatine bats, and generally at least a supraocular facial stripe; dental formula I2/1-2 C1/1 P2/2 M2-3/2-3 = 26–32. Single dorsal stripe present (10); interramal vibrissae absent (16)*; noseleaf bicolored, light patches on edges of spear and horseshoe, center of noseleaf brown (22); labial edge of horseshoe forms a thin free flap (31)*; *ectotympanic bulla extends medially across 33% of cochlea* (54); basioccipital pits present (59); diastema sometimes or always present between I2 and canine (69); i1 occlusal margin bilobed (72)*; i2 occlusal margin bilobed (73)*; *diastema between P3-P4 sometimes or always present* (78); *metaconid absent on m1* (92); M. ceratohyoideus inserts in part on stylohyal (112); 13 thoracic vertebrae present (150); distal tip of clavicle suspended between coracoid and acromion processes by ligaments (161); Brunner's glands absent at gastroduodenal juncture (210)*.

Comments

Owen (1987: 62) originally proposed the name Vampyressatini for *Vampyressa pusilla*, *V. brocki*, and *V. bidens* only, and Ferrarezi and Gimenez (1996) expanded this group to include *Mesophylla* and *Ectophylla*. Baker *et al.* (2003 — Fig. 2) found strong support for a somewhat larger clade excluding *Ectophylla* and named that clade Vampyressina. Wetterer *et al.* (2000) and Dávalos *et al.* (2012) did not find this clade based on their analysis of morphological data; instead they found that *Ectophylla* nested within the clade of Vampyressina genera (Fig. 1). However, support values were low for all relevant clades in that analysis, and both molecular (e.g, Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012) and combined analyses (Dávalos *et al.*, 2012) favor

the arrangement of Baker *et al.* (2003). This name was made available in Baker *et al.* (2016).

Subtribe Enchisthenina Baker, Solari, Cirranello, and Simmons 2016: 30

Type genus

Enchisthenes K. Andersen 1906.

Definition

The clade arising from the last common ancestor of all populations of *Enchisthenes*.

Composition

Enchisthenes K. Andersen 1906.

Description and diagnosis

Dental formula I2/2 C1/1 P2/2 M3/3. *Fringe of hair present along trailing edge of uropatagium* (13); two interramal vibrissae present (16); no distinct boundary between horseshoe and lip (31); infraorbital foramen located above anterior P4 (51)*; ectotympanic bulla extends medially across 50% of cochlea (54); I2 and canine always in contact, diastema absent (69)*; i1 occlusal margin trilobed (72); i2 occlusal margin trilobed (73); hypocone basin present, cusp indistinct to well-developed (85)*; band of long-tipped bifid anterior mechanical papillae present at juncture between anterior and medial-posterior mechanical papillae (135)*; *90 degree angle between ventral process of manubrium and body* (159); *third, fourth, and fifth metacarpals subequal in length* (175); XX/XY1Y2 sex determining system sometimes or always present, X translocated to autosome (220)*.

Comments

The name for this group was originally proposed as Enchistheneini by Owen (1987:61) to include *Enchisthenes* only. Wetterer *et al.* (2000), based on their analysis of morphological data, included *Enchisthenes* in Ectophyllina (Table 1). However, Baker *et al.* (2003), using molecular data, found stronger support for an alternative topology in which *Enchisthenes* is one of several successive sister taxa to 'short-faced' stenodermatines, and consequently restricted Enchisthenina to only *Enchisthenes*, which we follow here (Fig. 1 and Table 1). This topology is supported by most molecular analyses (e.g., Dumont *et al.*, 2012) and the combined analysis of Dávalos *et al.* (2012). Morphological data also support the uniqueness of *Enchisthenes* relative to other stenodermatine bats (see Dávalos *et al.*,

2012). This name was made available in Baker *et al*. (2016).

Subtribe Ectophyllina Baker, Solari, Cirranello and Simmons 2016: 30

Type genus
Ectophylla H. Allen 1892.

Definition
The clade arising from the last common ancestor of all populations of *Ectophylla.*

Composition
Ectophylla H. Allen 1892.

Description and diagnosis
Small bats (FA: 29 to 32 mm), with yellow ears, a white head and shoulders, and a brownish lower body; dental formula I2/2 C1/1 P2/2 M2/2 = 28. *Scale margins entire on cuticular scales on hair shaft* (4); *noseleaf yellow* (22); labial edge of horseshoe forms a thin free flap (31)*; *I1 and i1 in contact or slightly separated when cheek teeth occlude* (74); *diastema between P3-P4 sometimes or always present* (78); *diastema sometimes or always present between P4-M1* (80); hypocone basin and cusp both indistinct or absent on M1 (85); *diastema sometimes or always present between M1-M2* (87); *metaconid absent on m1* (92); *entoconid absent on m1* (93); *m3 absent* (96); *pharyngeal region of tongue covered with papillae* (132); *wide posterior laminae present on ribs* (155); four ribs articulate with mesosternum (157)*; *first and second phalanges of manual digit four subequal in length* (180); XX/XY sex determining system (220).

Comments
This name was originally proposed by Wetterer *et al*. (2000) based on their analysis of morphological data, for a group that included the genera *Artibeus*, *Chiroderma*, *Dermanura*, *Ectophylla*, *Enchisthenes*, *Koopmania*, *Mesophylla*, *Platyrrhinus*, *Uroderma*, *Vampyressa*, and *Vampyrodes* (Table 1). Although the name was subsequently used by some authors (e.g., Baker *et al*., 2003; Gardner, 2008), the name was unavailable. The ICZN (1999: 16.2) states that all new family group names must include reference to a type genus: "In addition to satisfying the provisions of Articles 13–15, a new family-group name published after 1999 must be accompanied by citation of the name of the type genus (i.e. the name from which the family-group name is formed)."

Although Wetterer *et al*. (2000: 140) state: "We define Ectophyllina as the clade of genera within Stenodermatini that share a more recent common ancestor with *Ectophylla* than with *Centurio*," this is not an explicit enough statement to fully satisfy the provision of the ICZN to cite the name from which the family group is formed.

Here, we apply the name to *Ectophylla* only as molecular (Hoofer and Baker 2006; Rojas *et al*., 2011; Dávalos *et al*., 2012; Dumont *et al*., 2012) and combined analyses (Dávalos *et al*., 2012) support the position of this taxon as one of several successive sister taxa to the short-faced stenodermatines. Wetterer *et al*. (2000) synonymized *Mesophylla* with *Ectophylla*; however, molecular work (e.g., Baker *et al*., 2003; Hoofer and Baker, 2006; Dávalos *et al*., 2012) indicates that these two genera are not closely related. Consequently, we do not include *Mesophylla* within *Ectophylla*, nor within Ectophyllina.

Subtribe Artibeina H. Allen 1898[*b*]: 269

Type genus
Artibeus Leach 1821.

Definition
The clade arising from the last common ancestor of *Artibeus* and *Artibeus* (*Dermanura).*

Composition
Artibeus Leach 1821 (includes the valid subgenus *Dermanura* Gervais 1856 and *Koopmania* Owen 1991, which we treat as a synonym of *Artibeus*).

Description and diagnosis
Small to large bats (FA=35–76) with paired faint to prominent facial stripes but lacking a dorsal stripe; dental formula I2/2 C1/1 P2/2 M2-3/2-3 = 28–32. Labial edge of horseshoe forms a thin free flap (31)*; occlusal margin of I1 bifid, lobes subequal (64)*; diastema sometimes or always present between I2 and canine (69); *band of long-tipped bifid anterior mechanical papillae present at juncture between anterior and medial-posterior mechanical papillae* (135); *13 thoracic vertebrae present* (150); five ribs articulate with mesosternum (157); 90 degree angle between ventral process and body of manubrium (159); *xiphisternum flat, median keel absent* (160); *sacral vertebrae do not contact ischium* (181); ischial tuberosity is small or absent (183); M. teres major takes origin from 25–40% of

axillary border of scapula (197); Brunner's glands present at gastroduodenal juncture (210).

Comments

The genus *Artibeus* is currently comprised of two subgenera: *Artibeus* and *Dermanura* (e.g., Hoofer *et al.*, 2008; Larsen *et al.*, 2010). *Enchisthenes* was formerly included in this genus, but both morphological and molecular studies (Wetterer *et al.*, 2000; Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012) do not support its inclusion in this clade (Figs. 1 and 2). Numerous authors (e.g., Owen, 1987; Baker *et al.*, 2003) have raised the subgenera to generic rank. However, we have chosen to preserve traditional usage to recognize the close phylogenetic affinities of the subgenera within *Artibeus*.

The name Artibeina was first used by H. Allen (1898*b*) for a group that included *Artibeus*, *Dermanura*, *Sturnira*, and *Uroderma*. Owen (1987: 62) also used this name at both the tribal and a subtribal levels. Tribe Artibeini included five subtribes: one unnamed for *V. melissa*, Vampyressatini (see above), Mesophyllatini (*Mesophylla*, *Vampyressa nymphaea*), Chirodermini (*Chiroderma*, *Vampyrodes*, *Vampyrops* = *Platyrrhinus*), and Artibeini (*Ectophylla*, *Uroderma*, *Artibeus*). The name was also used by Ferrarezi and Gimenez (1996) for *Artibeus*, *Dermanura*, and *Uroderma*. Recent morphological analyses provide alternative resolutions of this clade (Dávalos *et al.*, 2012). Previously, a smaller morphological data set indicated that *Artibeus* was a member of a larger clade of 'long-faced' stenodermatines (see Wetterer *et al.*, 2000 — Fig. 1), but this relationship received little support. In contrast, strong molecular support (Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012 — Fig. 2) exists for the current position of *Artibeus* as one of three successive sister taxa to the clade of so-called 'short-faced' stenodermatines, the subtribe Stenodermatina.

Subtribe Stenodermatina Gervais, in de Castelnaeu 1855: 32n

Type genus
Stenoderma E. Geoffroy 1818.

Definition

The clade arising from the last common ancestor of *Stenoderma*, *Ardops*, *Centurio*, *Pygoderma*, *Phyllops*, and *Ametrida*.

Composition

Ametrida Gray 1847, *Ardops* Miller 1906, *Ariteus* Gray 1838, *Centurio* Gray 1842, *Phyllops* Peters 1865, *Pygoderma* Peters 1863, *Stenoderma* E. Geoffroy 1818, *Sphaeronycteris* Peters 1882.

Description and diagnosis

Small to medium sized bats (FA = 25–54 mm) with a short rostrum; dental formula I2/2 C1/1 P2/2 M2-3/2-3 = 28–32. *Dorsal fur with tricolored hairs with a dark base, pale median band, and dark tip* (5); *facial stripes absent* (7); white neck patch present (8); **white shoulder patch present** (9); *fringe of hairs present on trailing edge of uropatagium* (13); *vibrissal papillae connected to form skin flap* (19); labial edge of horseshoe is thickened ridge (31); *posterior hard palate with deep emargination extending minimally to M1* (55); *I1 with pointed main cusp* (64); *I2 and C always in contact, diastema absent* (69)*; **buccal papillae cover entire inner surface of cheek** (127); *pharyngeal region of tongue unpapillated* (132); *two horny papillae larger than others* (144); *no horny papillae anterior to largest* (146); four ribs articulate with mesosternum (157)*; tip of coracoid process of scapula same width as shaft of coracoid (164).

Comments

The so called 'short-faced' stenodermatines have been recognized as a distinct group by numerous authors (e.g., Miller, 1907; Smith, 1976; Owen, 1987; Lim, 1993; Gardner, 2008). Owen applied the name Stenodermatini to the 'short-faced' group of stenodermatine species. Wetterer *et al.* (2000: 140) proposed recognizing the short-faced clade as a subtribal taxon, Stenodermatina, based on their analysis of morphological data, which strongly supported monophyly of this clade (Fig. 1 and Table 1). An expanded morphological data set continues to provide robust support for this group (Dávalos *et al.*, 2012). Molecular analyses (Baker *et al.*, 2003; Rojas *et al.*, 2011; Dávalos *et al.*, 2012; Dumont *et al.*, 2012) also strongly support the monophyly of this clade (Fig. 2). We recognize the unique morphology and biogeographic patterns of this group, which are of great interest to biologists, and choose to name only the 'short-faced' clade rather than the larger clade to which it belongs (Stenodermatina + *Artibeus* + *Enchisthenes* + *Ectophylla*) to facilitate discussions and avoid an abundance of named and ranked taxa (see Baker *et al.*, 2016).

Wetterer *et al.* (2000) had previously used a stem-based approach to defining this group, indicating

that the name Stenodermatina should be applied to those genera within Stenodermatini that share a more recent common ancestor with *Centurio* than with *Ectophylla*. Such phylogenetic definitions are not accepted by the PhyloCode prior to its publication, and the case of Wetterer *et al.* (2000) should indicate that a level of caution is needed when using a stem-based approach. In this instance, the position of several genera of Stenodermatini bats has changed so radically with the introduction of molecular data that *Ectophylla* is now part of a clade that includes the short-faced taxa and *Artibeus* and *Enchisthenes*. Given this change, it is difficult to see how the stem-based definition proposed by Wetterer *et al.* (2000) could be productively applied to the clades within Stenodermatini. Accordingly, we use a crown-based definition for Stenodermatina.

Unranked names

Unranked taxonomic names for various higher-level clades of phyllostomids have been proposed by Wetterer *et al.* (2000: Hirsutaglossa p. 136; Nullicauda p. 139) and Baker *et al.* (2003: Karyovarians p. 20; Victivarians, Phyllovarians p. 21; Hirsutaglossa p. 22; Nullicauda, Dulcivarians p. 24; Carpovarians p. 25; Mesostenodermatini p. 26). Although the ICZN allows for inclusion of as many ranks as necessary or desired (Art. 35.3), names must be formed from the stem of an available valid genus name (Arts. 11.7.1, 13.2); consequently, these names are not valid within Linnean system. However, these names could be validated under the PhyloCode (Cantino and de Queiroz, 2010). Names governed under the PhyloCode cannot be established before the actual publication of the Code and its companion volume (Art. 7).

Hirsutaglossa was originally defined as the clade arising from the last common ancestor of Glossophaginae (sensu Wetterer *et al.*, 2000) and Phyllonycterinae, thus incorporating all nectar feeding taxa. Results of many molecular analyses (Baker *et al.*, 2003; Datzmann *et al.*, 2010 — see discussion under Glossophaginae above) indicate, with strong support, that Lonchophyllinae is not closely related to other nectar-feeding taxa and that Brachyphyllini nests within Glossophaginae. Consequently, Baker *et al.* (2003) recommended expanding the definition to include last common ancestor of the Glossophaginae, Lonchophyllinae, and Nullicauda (see emended definition below). However, we feel that this definition clashes with the intended use of the name as proposed by Wetterer *et al.* (2000). The name Hirsutaglossa means 'hairy tongue' and was

meant to apply only to those taxa that comprised the nectar feeding clade. Given the topology of the current best estimate of phyllostomid relationships, we have used the name Glossophaginae to apply to the clade that could best be called Hirsutaglossa. To avoid confusion, we do not recommend applying Hirsutaglossa to any group at the present time.

Wetterer *et al.* (2000) originally applied the name Nullicauda to the clade arising from the last common ancestor of Carolliinae (sensu Wetterer *et al.*, 2000) and Stenodermatinae. Based on the topology produced by their analysis of molecular data, Baker *et al.* (2003) defined this group as the clade arising from the last common ancestor of Carolliinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae. The relationship of these subfamilies is strongly supported by molecular data (e.g., Baker *et al.*, 2003; Datzmann *et al.*, 2010; Rojas *et al.*, 2011; Dumont *et al.*, 2012), and, although Glyphonycterinae is comprised of species with long tails, we feel that the expansion of this name to include these few additional species will cause substantially less confusion than the expansion of the definition of Hirsutaglossa would. Furthermore, we have no name to apply to the clade that includes Carolliinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae. Consequently, we recommend use of the name Nullicauda for this group.

DISCUSSION

Classifications enable biologists to communicate more easily about the organisms they study. In recent years, attention in phylogenetics has focused on the growing number of studies based on molecular data and how their results differ from morphological studies, and sometimes from each other. These differences have led to widespread confusion, especially when multiple classifications based on trees produced by different data subsets (morphology: Wetterer *et al.*, 2000; Carstens *et al.*, 2002; molecules: Baker *et al.*, 2003; Datzmann *et al.*, 2010) or with different techniques (supertree analysis: Jones *et al.*, 2002; parsimony: Wetterer *et al.*, 2000; Bayesian analysis: Baker *et al.*, 2003) are available. The incongruence between molecules and morphology has also led some researchers to prefer the hypotheses generated by one data type (usually molecules) over another data type (usually morphology). As a relevant example for phyllostomids, Baker *et al.* (2003) proposed three potential explanations for the incongruence between the morphological study of Wetterer *et al.* (2000) and their molecular results:

(1) the molecular data most accurately reflect phyllostomid phylogeny, while the morphological data were flawed, (2) the morphological data most accurately reflect the phylogeny, while the molecular data were flawed, or (3) that both data sets failed to reflect accurately phyllostomid phylogeny. Baker *et al.* (2003: 15) then dismissed the morphological data and adopted the first explanation, claiming that "congruent data from the mitochondrial or nuclear genomes are among the most robust for systematic studies." In fact, a close examination of the causes of incongruence in the existing data sets for phyllostomids suggest that the real situation is much more complex, with both data types contributing to the existing incongruence (see Dávalos *et al.*, 2012). Here, we adopt a more satisfying fourth hypothesis: that both the morphological and molecular data, even though incongruent, might make important contributions to our understanding of phylogeny and consequently, classification. Accordingly, we have sought to reconcile morphological and molecular data sets for phyllostomids, assessing the weight of the evidence through measures of clade support to produce a higher-level classification of phyllostomid bats that reflects all the available data and recognizes only well-supported monophyletic groups. Both molecular and morphological data strongly support more than half the clades we recognize here. While critically examining as many sources of evidence as possible and emphasizing consensus, we hope to produce a more robust and stable classification of phyllostomids that will be of use for many years, even as more data are collected.

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