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Higher level classification of phyllostomid bats with a summary of DNA synapomorphies

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The family Phyllostomidae is recognized as representing the most extensive radiation known in any mammalian family. Creating a Linnaean classification for this clade has been difficult and controversial. In two companion papers, we here propose a revised classification drawing on the strengths of genetic and morphological data and reflecting current ideas regarding phylogenetic relationships within this monophyletic clade. We recognize 11 subfamilies (Macrotinae, Micronycterinae, Desmodontinae, Phyllostominae, Glossophaginae, Lonchorhininae, Lonchophyllinae, Glyphonycterinae, Carolliinae, Rhinophyllinae, and Stenodermatinae), 12 tribes (Diphyllini, Desmodontini, Macrophyllini, Phyllostomini, Vampyrini, Glossophagnini, Brachyphyllini, Choeronycterini, Lonchophyllini, Hsunycterini, Sturnirini, and Stenodermatini), and nine subtribes (Brachyphyllina, Phyllonycterina, Anourina, Choeronycterina, Vampyressina, Enchisthenina, Ectophyllina, Artibeina, and Stenodermatina). The proposed arrangement avoids non-monophyletic associations, only keeping those detected based on analyses of DNA sequence data. We propose that a classification based on the strengths of the most complete morphological and genetic data sets will provide the most robust classification for multiple uses by science and society.

Key words: Phyllostomidae, higher-level classification, DNA sequence data

INTRODUCTION

The family Phyllostomidae (New World leaf-nosed bats) comprises more than 200 species in 60 genera (see Solari and Martínez-Arias, 2014; Hurtado and Pacheco, 2014), and is the second most speciose chiropteran family (Simmons, 2005). The family has undergone a radiation unparalleled in other mammalian families in terms of ecological and morphological diversity (Freeman, 2000; Dumont *et al*., 2012). Phyllostomidae encompasses a range of dietary diversity larger than that seen in any other monophyletic mammal family, including omnivorous, insectivorous, carnivorous, nectarivorous, frugivorous and even hematophagous species (Gardner, 1977*a*; Ferrarezzi and Gimenez, 1996; Dumont *et al*., 2012). Ecological variation in diets is associated with extensive morphological diversity that involves skeletal, muscle, digestive, kidney, sensory systems, and behavior (Phillips, 2000; Wetterer *et al*., 2000; Dumont, 2004; Monteiro and Nogueira, 2011; Baker *et al*., 2012; Dumont *et al*., 2012; Dávalos *et al*., 2014). Because this ecomorphological diversity has fascinated scientists for over a century, Phyllostomidae is one of the best-known and well-studied chiropteran groups (Jones *et al*., 2002). Although comparative studies abound in the literature, remarkably different systematic and phylogenetic analyses have been proposed based on different data sets and analysis methods (see reviews in Wetterer *et al*., 2000, and Baker *et al*., 2003). Until recently, there has been little agreement regarding the deep branching patterns and relationships in this remarkable radiation, leading to considerable instability in classifications (Simmons, 2005; Baker *et al*., 2012; Dávalos *et al*., 2012, 2014). Because of their diversity, abundance, and ubiquity across the Neotropics, phyllostomid bats are the main focus of a number of research efforts; therefore, a well-supported and stable classification is highly desirable to communicate information among those studying this family as well as those in other fields who appreciate the biodiversity within this complex. The categories of phyllostomid bats showing the least

uniformity in regard to their composition and classification have been the subfamilies and tribes (see Table 2 in Baker *et al*., 2003).

Our focus in this contribution – the first of a pair of companion papers on phyllostomid classification – is to produce a classification of Phyllostomidae that reflects the strongest evidence of monophyletic groups and relationship of clades based on comprehensive phylogenetic analyses of DNA sequence data (e.g., Wetterer *et al*., 2000; Baker *et al*., 2003; Datzmann *et al*., 2010; Rojas *et al*., 2011; Dumont *et al*., 2012; Botero-Castro *et al*., 2013; Dávalos *et al*., 2014). As part of this effort, we validate previously proposed names that have not met the restrictions and requirements of the International Code of Zoological nomenclature (hereafter referred to as the Code and in the literature cited as ICZN, 1999). In the first of these two companion papers, this effort is achieved by employing primarily DNA sequence data to validate and define each taxon name within the family. The second paper further defines and diagnoses each of these taxa with the remarkable morphology present in this radiation.

Taxonomic Background

The most taxonomically comprehensive studies based on direct analyses of morphology are those of Wetterer *et al*. (2000) and Dávalos *et al*. (2014). For DNA sequence data comprehensive studies include those of Baker *et al*. (2003), Rojas *et al*. (2011), Dumont *et al*. (2012), and Dávalos *et al*. (2014). Wetterer *et al*. (2000) used a primarily morphological data set including characters from numerous anatomical systems. Their analyses recovered a tree topology (Fig. 1; = figure 49 of Wetterer *et al*., 2000) that was quite similar to that of previous traditional classifications in recognizing feeding guilds as monophyletic (e.g., Miller, 1907; Simpson, 1945; Koopman, 1993; Simmons, 2005). In proposing a revised classification of the family based on their phylogenetic analyses, Wetterer *et al*. (2000) introduced both ranked (Ectophyllina) and unranked names (Hirsutaglossa, Nullicauda), and redefined other taxa (mostly lower level clades) so as to make them monophyletic.

The classification of Wetterer *et al*. (2000) was subsequently contested by molecular studies that recovered phylogenetic trees in which feeding guilds are not necessarily monophyletic. Baker *et al*. (2003) sequenced a 2.6 kb fragment of mtDNA (including 12SrRNA + RNA^{val}, 16SrRNA) and the nuclear RAG2 gene, and using Bayesian analyses found that nectar-feeding evolved at least twice in phyllostomids, and that primarily insectivorous genera clustered independently in a number of separate monophyletic clades in distant parts of the tree (Fig. 2; = figure 5b of Baker *et al*., 2003).

The monophyletic lineages recovered by Baker *et al*. (2003) were the basis for a revised classification of phyllostomids (Table 1), in which those

TABLE 1. Linnaean classification for the family Phyllostomidae proposed in this paper

Phyllostomidae	
Macrotinae	*Musonycteris*
Macrotus	*Lichonycteris*
Micronycterinae	*Scleronycteris*
Micronycteris	Lonchophyllinae
Lampronycteris	Lonchophyllini
Desmodontinae	*Lionycteris*
Diphyllini	*Lonchophylla*
Diphylla	*Platalina*
Desmodontini	*Xeronycteris*
Desmodus	Hsunycterini
Diaemus	*Hsunycteris*
Lonchorhininae	Carolliinae
Lonchorhina	*Carollia*
Phyllostominae	Glyphonycterinae
Macrophyllini	*Glyphonycteris*
Macrophyllum	*Trinycteris*
Trachops	*Neonycteris*
Phyllostomini	Rhinophyllinae
Gardnerycteris	*Rhinophylla*
Lophostoma	Stenodermatinae
Tonatia	Sturnirini
Phylloderma	*Sturnira*
Phyllostomus	Stenodermatini
Vampyrini	Vampyressina
Chrotopterus	*Chiroderma*
Mimon	*Vampyriscus*
Vampyrum	*Uroderma*
Glossophaginae	*Vampyressa*
Glossophagini	*Mesophylla*
Monophyllus	*Vampyrodes*
Glossophaga	*Platyrrhinus*
Leptonycteris	Enchisthenina
Brachyphyllini	*Enchisthenes*
Brachyphyllina	Ectophyllina
Brachyphylla	*Ectophylla*
Phyllonycterina	Artibeina
Phyllonycteris	*Artibeus*
Erophylla	Stenodermatina
Choeronycterini	*Ariteus*
Anourina	*Ardops*
Anoura	*Stenoderma*
Choeronycterina	*Centurio*
Hylonycteris	*Pygoderma*
Choeroniscus	*Sphaeronycteris*
Choeronycteris	*Ametrida*
Dryadonycteris	*Phyllops*

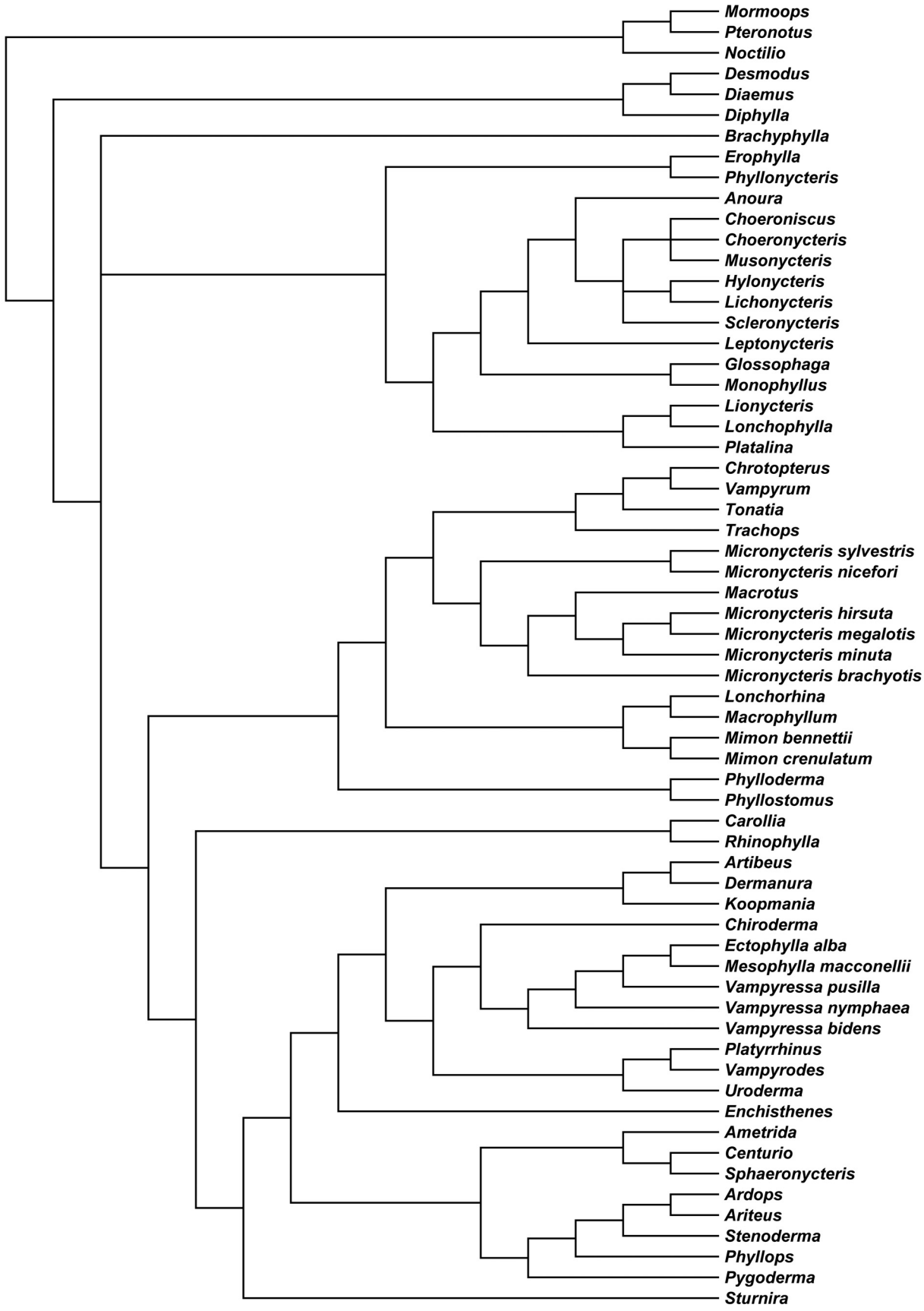

FIG. 1. Strict consensus tree from 18 most parsimonious trees (613 steps) resulting from a heuristic search of 150 morphological characters for 63 phyllostomid taxa (original data matrix modified from figure 49 from Wetterer *et al*., 2000)

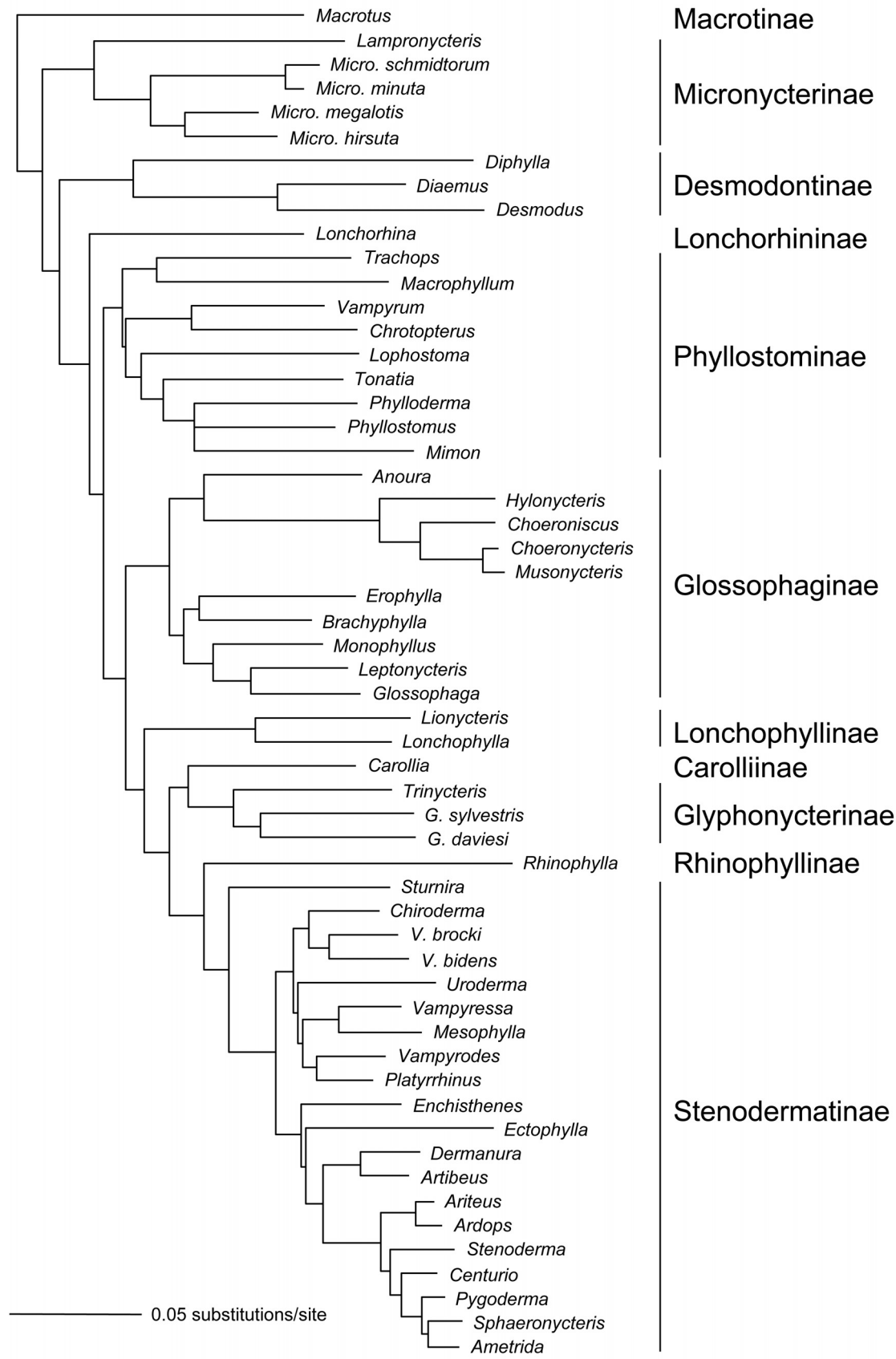

FIG. 2. Tree resulting from a Bayesian analysis of concatenated mtDNA and RAG2 data. Branch lengths depict percent sequence divergence among Phyllostomid species since their last common ancestor. Proposed subfamily classification is shown at the right. Modified from figure 5b from Baker *et al*. (2003)

authors proposed several new family-group names, redefined the content of established family-level names (e.g., Vampyressatini — Owen, 1987), and introduced new unranked taxa (Karyovarians, Victivarians, Phyllovarians, Dulcivarians, Carpovarians, Mesostenodermatini). The difference between branching order at the base of the molecular tree of Baker *et al*. (2000, 2003) and the tree generated in previous studies, including Wetterer *et al*. (2000) and Jones *et al*. (2002), were so different that analyses based on additional genes were appropriate to test monophyly of the proposed groups and their phylogenetic relationships. Several such tests have now been published (Datzmann *et al*., 2010; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014). These analyses, based on larger gene samples, have produced additional support for many of the clades detected by Baker *et al*. (2003). A study by Datzmann *et al*. (2010), which sampled more than 10 kb of nuclear DNA from multiple coding genes (vWF, RAG2, and exon 11 of *brca*-1), noncoding nuclear loci, and mitochondrial loci in species representing 29 phyllostomid genera, produced a tree largely concordant with Baker *et al*. (2003). Maximum likelihood analysis of these sequences produced support values for most nodes that were above 75%. Similar results have been found by Rojas *et al*. (2011; mitochondrial genes, including cytochrome *b*) and Dumont *et al*. (2012; mitochondrial genes, including COI and cytochrome *b*). These studies were also generally supportive of the branching order reported by Baker *et al*. (2003). Finally, a combined analysis of molecular and morphological data, with likelihood-based adjustments to reduce conflict between datasets (Dávalos *et al*., 2014), recovered most of the clades obtained by Baker *et al*. (2003). The two major areas of disagreement among these analyses concern the relationships of Lonchorhininae and the shared common ancestor of nectar feeders; these are discussed in our proposed classification under taxa affected by these incongruences. We conclude that the agreement among these hypotheses provides evidence that the molecular classification proposed in Baker *et al*. (2003), as slightly modified herein, have a reasonable probability of remaining stable.

Botero-Castro *et al*. (2013) assessed the phylogenetic contribution of entire mitochondrial genomes to phyllostomid relationships, including 11 species from seven of the subfamilies recognized by Baker *et al*. (2003). Although four lineages (Macrotinae, Lonchorhininae, Lonchophyllinae, and Glyphonycterinae) were missing in their analyses, they came out with a high congruence to the relationships recovered by the concatenation of individual mitochondrial and nuclear markers as in Baker *et al*. (2003) and subsequent authors.

At the time of its publication, Baker *et al*.'s (2003) classification was the only study based entirely on genetic data (karyotypes and mitochondrial plus nuclear gene sequences) with over 95% of all identified clades with strong statistical support. Although this classification has been often discussed (e.g., Gardner, 2008) it has not been followed by many subsequent authors (e.g., Simmons, 2005). A recognized problem with acceptance of the taxonomic proposals of Baker *et al*. (2003) was that they did not meet all the requirements of the ICZN (see below), making new names unavailable. Baker *et al*. (2003: 15) indicated that shared derived characters in the mtDNA and RAG2 sequences as identified in a Bayesian analysis made up the diagnoses, and therefore the availability, for each of the new taxon-names in that work, but the authors provided no details. Similar names had been proposed by other authors (e.g., Van Den Bussche, 1992), but these were not proposed or revised with regard to the specifications of the 3rd edition of the Code (ICZN, 1985) to verify their availability. Although the molecular sequence data of Baker *et al*. (2003) provided great phylogenetic (taxonomic) resolution, those authors did not aim to identify individual diagnostic characters. Those sequences were deposited in GenBank by these authors, but variation in alignment schemes prevents unambiguous identification of supporting diagnostic characters by subsequent researchers. Tools such as TreeBASE (www.treebase.org) are indispensable in deposition of character/taxon matrix as well as trees, allowing to unambiguously setting positional homology to identify diagnostic character-states in the context of a particular phylogeny. These tools allow identification of molecular synapomorphies that can serve to differentiate taxa and act as diagnostic traits for nomenclatural purposes.

The current Code (ICZN, 1999) is unambiguous about what is required for a name to be available. In addition to requirements for publication of nomenclatural acts (e.g., Art. 16.1 requests explicit indication of intention to propose a new name), the Code mandates the following regarding a family-group name, which includes subfamilies and tribes: 1. It must be a noun in the nominative plural formed from the stem of an available generic name (Arts. 11.7.1 and 13.2) or the whole genus name (Art. 29.1), which has to be cited in the description (Art.

16.2); 2. It must end with an appropriate family-group name suffix (Arts. 11.7.1.3 and 29.2); 3. It must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (Art. 13.1.1) or a bibliographic reference to such a statement (Art. 13.1.2). It may include a diagnosis to differentiate it from related and similar groups (Recomm. 13A); 4. The family-group includes all the taxa below superfamily and above genus, with as many ranks as may be desired or needed (Art. 35.1). Each family-group name must make a direct reference to a type genus (Art. 35.3). All names in the family-group follow these rules no matter their specific rank (Art. 35.2).

Translating a Phylogeny into a Classification

To produce a robust and stable classification of Phyllostomidae while retaining as much continuity as possible with historical uses of names, we propose a somewhat revised classification of the family with an emphasis on ensuring that all family-group names are available, clearly defined, and comprehensively diagnosed. Only well-supported monophyletic lineages are formally recognized, and new names are not coined if at least one available name exists for a particular clade. Names previously proposed but unavailable at this time need to be properly formulated, making them compliant with the Code, so they can be used as originally intended (e.g., in Wetterer *et al*., 2000, and Baker *et al*., 2003). Only the most commonly use is provided for these names, since complete taxonomic histories can be found in other sources (e.g., McKenna and Bell, 1997; Wetterer *et al*., 2000), but we do provide comments for each family-level name whether they are restricted from their original or most recent meaning or were not properly introduced in the relevant literature. Although we appreciate the arguments of Pauly *et al*. (2009) concerning the need for concordance between classifications and phylogenies, at present we chose not to establish or validate other non-Linnaean names, especially when these are above the genus level. Finally, we discuss the importance of formal definitions in a phylogenetic classification as complex as the one present in this family.

Materials and Methods

Using Genetic Data to Meet the Mandates of the ICZN Code

The advent of molecular biology and biochemistry including histology, protein electrophoresis, nucleotide sequencing, and cytogenetics have provided new insights into characters that can be used in systematics and phylogenetic studies of mammals (Baker, 1984; reviewed in Baker and Bradley, 2006). DNA sequencing and molecular biology have not only deepened our understanding of evolutionary relationships, in many cases these data provided powerful resolution of evolutionary relationships that were difficult to resolve with morphological data. This has resulted in major revisions in our understanding of the relationships and biodiversity of mammals (e.g., Honacki *et al*., 1982; Wilson and Reeder, 1993, 2005; Meredith *et al*., 2011; O'Leary *et al*., 2013) including bats (e.g., Hoofer and Van Den Bussche, 2003; Van Den Bussche and Hoofer, 2004; Simmons, 2005; Teeling *et al*., 2005; Miller-Butterworth *et al*., 2007). This is also true for subfamilies of phyllostomid bats (compare Baker *et al*., 1989 to Baker *et al*., 2003; Datzmann *et al*., 2010; Dumont *et al*., 2012; and Dávalos *et al*., 2014).

The classification that is described below for phyllostomid bats is quite different from that proposed previously by Miller (1907), Baker *et al*. (1989), Koopman (1994), McKenna and Bell (1997), Wetterer *et al*. (2000), Jones *et al*. (2002), and Simmons (2005). The major differences between our classification and the previous classifications listed above are primarily a product of the greater resolution provided by the DNA sequence data and the supporting computational methodologies in defining relationships among clades, especially in deep branches within bats, and in providing strong support for monophyletic assemblages.

Although there is an overlap in the genetic information that was used to recover the monophyletic assemblages that we recognize or describe as new (e.g., Rojas *et al*., 2011; Dumont *et al*., 2012; and Dávalos *et al*., 2014; each used the original mitochondrial ribosomal data set compiled by Baker *et al*., 2000, 2003), the computational methods used in each of the studies were different and the total content of genetic information and alignment varied among most studies. Nevertheless, these studies generally reached the same conclusions regarding major clades of phyllostomid bats. We interpret this as evidence that DNA sequence data have an important and significant phylogenetic signal, and include robust character states for the recognition of the content and context of the classification proposed herein for this family. However, as other analyses recover distinct and unique synapomorphies (meaning, shared changes of specific nucleotides in the sequence) this has hampered the use of them as standard characters equivalent to the morphological characters typically used for diagnoses of new taxa. An exception is Van Den Bussche (1992), who identified sets of specific changes in restriction-endonuclease sites in the ribosomal DNA in several clades within Phyllostomidae (his Table 1 and Figs. 1 and 2), which he then used to diagnose those taxa.

In the following classification, we describe or define new taxa using DNA sequence data as the characters that differentiate each taxon (Art. 13.1.1 — ICZN, 1999). The characters that we use for this purpose are drawn from the specifically aligned sequences of the genes that were analyzed to produce the phylogenetic trees shown in Baker *et al*. (2003), using algorithms and software packages (see below) to generate the tree and support values for clades associated with each name. GenBank accession numbers of the employed genes or motifs are used to provide the original sequence data employed in the alignment. The aligned data matrix in TreeBASE (TB2:S15071) provides the final source of these analyses and thus is the only reference for the analysis that resulted in our diagnoses. Additionally, other genetic data (such as karyotypes, allozymes, and restriction

sites) are used as diagnostic characters to define some specific groups. In the companion paper, Cirranello *et al.* (2016) describe and provide diagnostic characters using morphology for the same groups (= clades) that we recognize here.

Phylogenetic Analyses

Sequence data generated for previous studies (see Baker *et al*., 2000, 2003) and deposited in GenBank provided the data that we employed to define and diagnose taxa. Multiple sequence alignment was performed in Sequencher 4.9 software (Gene Codes Corporation, Ann Arbor, Michigan). The combined aligned matrix of RAG2 and mtDNA was submitted to TreeBASE (www.treebase.org; http://purl.org/phylo/treebase/phylows/study/TB2:S15071), and has 3315 characters, of which nucleotides 1–1363 correspond to the nuclear RAG2 gene, and nucleotides 1364–3315, to the mitochondrial genes 12S rRNA (1364–2152), $tRNA^{Val}$ (2153–2196), and 16S rRNA (2197–3315). jModelTest (Posada, 2008) was used to estimate the best-fit model of nucleotide substitution, using the Akaike information criteria (AIC); the estimated model of evolution was GTR+G+I for the concatenated dataset. This dataset included 61 operational taxonomic units (55 phyllostomids and six outgroups), with all subfamilies and tribes of Baker *et al*. (2000, 2003) represented. Bayesian hypotheses were generated with MrBayes 3.2 (Ronquist *et al*., 2012); all MrBayes analyses consisted of 10×10^6 generations with a sampling frequency of 5,000. The resulting tree (-lnL = 27045.6281) is available in the TreeBASE website. We traced character evolution by mapping specific substitutions in mitochondrial and nuclear DNA regions as obtained from the phylogenetic analyses of the molecular matrix deposited in TreeBASE (3315 bp). Lists of apomorphies were obtained through the reconstruction of ancestral states using parsimony, as implemented in Mesquite v. 2.75 (Maddison and Maddison, 2011).

Results

Family Phyllostomidae Gray 1825

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*, *Sturnira*, and *Stenoderma*.

Comments

Monophyly of Phyllostomidae to the exclusion of all other families is supported in Baker *et al*. (2003), Datzmann *et al*. (2010), Rojas *et al*. (2011), Dumont *et al*. (2012), and Dávalos *et al*. (2014). Variable restriction endonuclease-sites in the rRNA (Van Den Bussche, 1992) as well as morphological synapomorphies (Wetterer *et al*., 2000; Cirranello *et al*., 2016) provide additional support for the monophyly of Phyllostomidae.

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, *Chrotopterus* Peters 1865, *Gardnerycteris* Hurtado and Pacheco 2014, *Lophostoma* d'Orbigny 1836, *Macrophyllum* Gray 1838, *Mimon* Gray 1847 (does not include *Anthorhina* — see Gardner and Ferrell, 1990), *Trachops* Gray 1847, *Tonatia* Gray 1827 (sensu Lee *et al*., 2002), *Phylloderma* Peters 1865, *Phyllostomus* Lacépède 1799, *Vampyrum* Rafinesque 1815, *Lonchorhina* Tomes 1863, *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, *Scleronycteris* Thomas 1912, *Hsunycteris* Parlos, Timm, Swier, Zeballos and Baker 2014, *Lionycteris* Thomas 1913, *Lonchophylla* Thomas 1903, *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.

Lower level classification

The genera listed are best classified into 11 monophyletic subfamilies as outlined below. Of these taxa, five correspond to groups not traditionally recognized and therefore requiring a reorganization of the included genera (e.g., Phyllostominae as traditionally recognized is a non-monophyletic taxon

with at least five distinct lineages, each recognized here as a separate subfamily). For further reference see our Fig. 2 and Table 1. Several of these subfamily names are either newly proposed or formally defined and diagnosed for the first time here.

1. 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 *M. californicus.* This is the basal clade within Phyllostomidae, characterized by a proposed ancestral karyotype for the family (2n = 40 and 46, FN = 60 — Patton and Baker, 1978; Baker, 1979).

Genetic diagnosis

Support for Macrotinae is provided by 63 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Macrotinae	63 unique substitutions (apomorphies)
24 synapomorphies in the nDNA sequence	106 T→G; 132 T→C; 144 G→C; 159 T→C; 201 G→A; 231 T→C; 258 T→C; 270 T→C; 282 T→C; 315 T→C; 319 G→A; 382 G→A; 400 A→G; 502 A→G; 522 T→C; 593 C→A; 606 G→A; 660 T→C; 737 G→A; 868 G→A; 966 A→G; 1042 A→G; 1296 G→A; 1336 G→A
39 synapomorphies in the mtDNA sequences	1366 T→A; 1378 C→A; 1428 C→G; 1516 T→C; 1557 T→C; 1585 T→C; 1596 A→G; 1608 A→G; 1609 G→A; 1613 T→A; 1710 A→G; 1757 A→G; 1852 A→C; 1932 T→C; 1961 T→C; 1965 G→A; 1996 T→C; 2001 A→G; 2006 C→A; 2201 T→A; 2344 A→G; 2406 G→A; 2469 T→C; 2502 T→A; 2546 A→C; 2557 T→A; 2578 T→C; 2670 A→G; 2726 T→C; 2875 G→A; 2889 T→A; 2917 A→G; 2964 A→C; 3013 T→C; 3025 T→C; 3030 A→C; 3032 C→A; 3290 A→G; 3312 A→C

Reference sequences

GenBank AF316461 for the RAG2 gene, and AF263229 for the mtDNA sequence of *Macrotus waterhousii*.

Phylogenetic notes

Monophyly of Macrotinae is strongly supported in the concatenated gene tree (posterior probability = 1.0 — Baker *et al*., 2003) as well as under different sequence data arrangements and analytical methods performed by independent research groups (see Datzmann *et al*., 2010; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014). Macrotinae appears to be the basal lineage in the family after ancestral phyllostomids diverged from other bat families (see Fig. 2).

Macrotinae can be distinguished from all other bats by a karyotype considered to represent most of the ancestral character states for all phyllostomids (Baker *et al*., 2012; C. G. Sotero-Caio, unpublished data). This G-banded karyotype with homologous pairs identified and labeled is shown as figure 1 of Baker (1979). The hypothesis that this represents the primitive karyotype for the family derives from a global parsimony analysis using Mormoopidae (*Pteronotus* and *Mormoops*) and Noctilionidae as outgroups, which concluded that this karyotype (present in the extant populations of *M. waterhousii* with one chromosome exception, see Patton and Baker, 1978; Volleth *et al*., 1999) is like that present in the ancestor of all phyllostomids. No other subfamily has species with this proposed primitive karyotype. Other diagnostic molecular characters (restriction sites of the rDNA complex) were presented and discussed by Van Den Bussche (1992).

Comments

In his analysis of restriction-sites, Van Den Bussche (1992) introduced the name Macrotinae indicating that *Macrotus* (and Desmodontinae) possessed the restriction-site map proposed as primitive for Phyllostomidae. However, *Macrotus* was distinguished by immunological and chromosomal data (see Baker *et al*., 1989, who listed it as incertae sedis), and because vampires were already treated as a distinct subfamily, Van Den Bussche (1992) proposed the same status for *Macrotus*. A type genus was not explicitly identified, although *Macrotus* was the only genus included; therefore, following the regulations of the previous edition of the Code (ICZN, 1985 — Art. 11[f] Family-group names and Art. 29[a]) this taxon-name is considered as available from its original publication.

Included extant genera (and species)

Macrotus Gray 1843 (2 spp., includes *Otopterus* Lydekker 1891).

2. 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*.

Genetic diagnosis

Support for Micronycterinae is provided by 18 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Micronycterinae	18 unique substitutions (apomorphies)
2 synapomorphies in the nDNA sequence	576 C→T; 948 T→C
16 synapomorphies in the mtDNA sequences	1449 A→G; 1473 A→G; 1484 C→T; 1555 G→A; 1598 C→T; 1675 T→G; 1707 A→G; 1742 T→C; 1866 T→C; 2372 T→C; 2413 T→C; 2538 T→C; 2916 T→C; 2962 C→A; 3168 C→T; 3308 T→A

Reference sequences

GenBank AF316463, AF316465, AF316467, AF316468, and AF316470 for the RAG2 gene, and AF 411536, AY395819, AY395821, AY395823, and AF411535 for the mtDNA sequence of *Lampronycteris brachyotis*, *Micronycteris hirsuta*, *M. megalotis*, *M. minuta* and *M. schmidtorum*, respectively.

Phylogenetic notes

Monophyly of Micronycterinae was strongly supported in the concatenated gene tree (posterior probability = 1.0 — Baker *et al*., 2003) as well as under different sequence data arrangements and analytical methods performed by independent research groups (see Datzmann *et al*., 2010; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014).

The published karyotypes for members of Micronycterinae range from 2n = 25 and 26, FN = 32 (Ribas *et al*., 2013), 2n = 28, FN = 32 (Baker, 1973; Baker *et al*., 1973) and 2n = 30, FN = 32 (Baker *et al*., 1973) for *M. hirsuta*, 2n = 28, FN = 50 for *M. minuta* (Baker, 1973; Patton, 1976), and 2n = 38, FN = 66 for *M. schmidtorum* (Baker, 1973), to 2n = 40, FN = 68 for *M. megalotis* (Baker, 1967; Hsu *et al*., 1968; Patton, 1976). Additional diagnostic molecular characters (restriction sites of the rDNA complex) were presented and discussed by Van Den Bussche (1992).

Comments

The genera included in Micronycterinae have been variously classified as part of a more inclusive *Micronycteris* (sensu Sanborn, 1949) by Jones *et al*. (2002), or grouped within Phyllostominae (e.g., Wetterer *et al*., 2000) in recent classifications. Van Den Bussche (1992) introduced the name Micronycterinae for *Micronycteris* (sensu lato) alone, supporting its distinction based only on restriction-site data. He used the same criteria as for the name Macrotinae (see above), and these were sufficient for proposal of a new name under the previous edition of the Code (ICZN, 1985 — Art. 11[f] Family-group names). Therefore, this taxon name is available. However, Van Den Bussche (1992) only examined *M. minuta* but considered the genus to include all the species of *Micronycteris* (sensu Sanborn, 1949). Although Simmons and Voss (1998) divided the genus by raising the former subgenera to generic status, Wetterer *et al*. (2000) considered all these genera as closely related, as reflected by their use of the name Micronycterini (for *Macrotus*, *Micronycteris*, *Lampronycteris*, *Glyphonycteris*, *Trinycteris*, and *Neonycteris*) as a tribe of Phyllostominae. Baker *et al*. (2003), restricted Micronycterinae to *Micronycteris* (sensu stricto) and *Lampronycteris*. We herein maintain this arrangement.

This clade diverged from the remainder of Phyllostomidae after Macrotinae and before the divergence of the vampires (Desmodontinae). Rojas *et al*. (2011) and Dumont *et al*. (2012) also recovered this branching order in the phylogenetic tree of phyllostomids, as well as finding significant statistical support for the monophyly of the subfamily as defined herein. However, Dávalos *et al*. (2014) found Micronycterinae diverging from the remainder of Phyllostomidae after Desmodontinae. The most complete molecular datasets for species delimitation in these studies is that presented by Porter *et al*. (2007), Dumont *et al*. (2012), and Dávalos *et al*. (2014) which recover a monotypic *Lampronycteris* and several species of *Micronycteris*.

Included extant genera (and species)

Lampronycteris Sanborn 1949 (1 sp.), and *Micronycteris* Gray 1866 (11 spp., includes

Xenoctenes Miller 1907, *Leuconycteris* Porter *et al*. 2007, *Schizonycteris* Porter *et al*. 2007; *homezorum* [not *homezi* — see Solari, 2008] is a synonym of *M. minuta* — see Ochoa and Sanchez, 2005; Larsen *et al*., 2011; Siles *et al*., 2013).

3. Subfamily Desmodontinae J. A. Wagner, 1840: 375

Type genus

Desmodus Wied-Neuwied 1826.

Definition

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

Genetic diagnosis

Support for Desmodontinae is provided by 24 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Desmodontinae	24 unique substitutions (apomorphies)
5 synapomorphies in the nDNA sequence	84 C→A; 270 T→C; 774 T→C; 1176 A→G; 1260 A→G
19 synapomorphies in the mtDNA sequences	1366 T→C; 1394 T→C; 1602 A→G; 1625 C→T; 1816 T→C; 1818 T→C; 1824 T→C; 1887 T→C; 1961 T→C; 2018 T→A; 2050 T→C; 2345 C→G; 2430 A→C; 2464 A→C; 2470 T→C; 2557 T→A; 2565 A→G; 2736 G→A; 3243 T→C

Reference sequences

GenBank AF316444, AF316445, and AF316447 for the RAG2 gene, and AF263228, AF411534, and AF411533 for the mtDNA sequence of *Desmodus rotundus*, *Diaemus youngii*, and *Diphylla ecaudata*, respectively.

Phylogenetic notes

Diploid and fundamental numbers are 2n = 32, FN = 60 for *Diphylla*, 2n = 32, FN = 60 for *Diaemus* and 2n = 28, FN = 52 for *Desmodus* (Cadena and Baker, 1976; Baker *et al*., 1988). Karyotypic data that also provide shared derived character states diagnostic for this clade were described by Sotero-Caio *et al*. (2011), who used in situ hybridizations with chromosome paints derived from *Phyllostomus hastatus* and *Carollia brevicauda* (Pieczarka *et al*., 2005). They identified nine syntenic chromosome assemblages that were shared among all three genera and three of these (vampire chromosomal pairs 1, 3, and 4) as well as three inversions (4qi, 13i, and 15i) that were unique to the subfamily and are therefore diagnostic (Sotero-Caio *et al*., 2011; Pieczarka *et al*., 2013).

Comments

The only issue for this name stems from the use of 'Bonaparte 1845' as the author and date for the proposal of the name (e.g., Miller, 1907; McKenna and Bell, 1997; Simmons, 2005). We here recognize Wagner's earlier use of the name, which was proposed as the Sippe (tribe) Desmodina, within the family Istiophora (see Wetterer *et al*., 2000: 10). Composition of this taxon has not changed through the years, with all authors in the last 100 years agreeing that it includes the three species of vampire bats, represented by monotypic genera.

The clade and branching order of species that comprise the subfamily Desmodontinae (Fig. 2) has been present in all of the gene trees (Baker *et al*., 2000, 2003; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014), and the branching order is the same as found in analyses of morphological data (Fig. 1 of Wetterer *et al*., 2000). Although Datzmann *et al*. (2010) did not include *Diaemus* in their gene tree, the phylogenetic position of the vampire clade as diverging after Macrotinae and Micronycterinae but before the remainder of Phyllostomidae has been recovered in all the phylogenetic trees based on DNA sequence data cited above, except by that of Dávalos *et al*. (2014), although that branching has posterior probabilities below 0.9. This position differs from that of phylogenies based on morphology alone (see Wetterer *et al*., 2000), and documents the origin of vampires as an intrafamilial radiation within phyllostomid bats rather than basal to them.

Included extant genera (and species)

Diphylla Spix 1823 (1 sp.), *Desmodus* Wied-Neuwied 1826 (1 sp.), and *Diaemus* Miller 1906 (1 sp.).

4. Subfamily Phyllostominae Gray, 1825: 242

Type genus

Phyllostomus Lacépède 1799.

Definition

The clade arising from the last common ancestor of *Trachops*, *Macrophyllum*, *Vampyrum*, *Gardnerycteris*, and *Phyllostomus*.

Genetic diagnosis

Support for Phyllostominae is provided by six molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Phyllostominae	6 unique substitutions (apomorphies)
1 synapomorphy in the nDNA sequence	576 T→C
5 synapomorphies in the mtDNA sequences	2152 C→A; 2480 A→C; 2502 T→G; 2541 A→C; 3168 C→T

Reference sequences

GenBank AF316442, AF316458, AF316472, AF316479, AF316480, AF316489, AF316490, AF316495, and AF442085 for the RAG2 gene, and AF411530, AF411537–AF411544 for the mtDNA sequence of *Chrotopterus auritus*, *Gardnerycteris crenulatum*, *Lophostoma brasiliense*, *Macrophyllum macrophyllum*, *Phylloderma stenops*, *Phyllostomus hastatus* (and *P. elongatus*), *Tonatia saurophila*, *Trachops cirrhosus*, and *Vampyrum spectrum*, respectively.

Phylogenetic notes

The diploid numbers for this subfamily vary from 2n = 16 to 2n = 34 and most species have a karyotype comprised entirely of biarmed chromosomes; the fundamental number ranges from 20 to 60 (Baker, 1979). Chromosomal polymorphism has been described for *Gardnerycteris crenulatum*, in which two autosomal pairs vary between three different centromere positions. This polymorphism is geographically widespread and has been proposed as providing a selective advantage to heterozygotes, facilitating a balanced polymorphism (Baker *et al*., 1972). Gomes *et al*. (2012) analyzed this polymorphism by using G-bands and found that two pairs can have inversion heterozygous in Brazilian specimens. Sotero-Caio *et al*. (2015) have confirmed two inversions in different chromosome pairs using in situ hybridizations with *M. californicus* chromosome paints.

Comments

Although the original name was proposed for the family, as Phyllostomidae, its use as an infrafamiliar group comes from Gray (1866), who used the name Phyllostomina for a tribe that originally included *Tonatia* (as *Tylostoma*), *Phylloderma* (as *Guandira*), *Phyllostomus* (as *Phyllostoma* and *Alectops*), *Carollia* (also as *Rhinops*), *Micronycteris* (as *Schizostoma*), and *Rhinophylla*. It was further restricted by Miller (1907) to exclude *Carollia* and *Rhinophylla*, making it more consistent with a natural composition. Baker *et al*. (1989) expanded Phyllostominae to include a large assemblage of primitive omnivores (Phyllostomini), nectarivores (Glossophagini), and frugivores (Stenodermatini), to the exclusion of *Macrotus*, *Micronycteris* (sensu lato), Desmodontinae, and Vampyrinae. Subsequently Baker *et al*. (2003) took a different approach and greatly restricted Phyllostominae to remove taxa that we here recognize as representing several other subfamilies, in so doing rendering Phyllostominae sensu stricto monophyletic (see also Hoffmann *et al*., 2008).

Phyllostominae as recognized here is comprised of 10 genera (*Chrotopterus*, *Gardnerycteris*, *Lophostoma*, *Macrophyllum*, *Mimon*, *Phylloderma*, *Phyllostomus*, *Trachops*, *Tonatia*, and *Vampyrum*) which form a clade that diverged after Macrotinae, Micronycterinae, and Desmodontinae, but before the nectar-feeders and the remainder of Phyllostomidae. In all gene trees (Baker *et al*., 2003; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014), Lonchorhininae either diverges before or after Phyllostominae, but is never a member of the monophyletic group herein recognized as the subfamily Phyllostominae. The genera *Macrotus*, *Micronycteris*, *Lampronycteris*, *Lonchorhina*, *Trinycteris* and *Glyphonycteris* are removed and classified in four other subfamilies. This classification results in the smallest number of genera included in Phyllostominae ever proposed in any classification of the family (see Wetterer *et al*., 2000 for a review).

Included extant genera (and species)

Chrotopterus Peters 1865 (1 sp.), *Gardnerycteris* Hurtado and Pacheco 2014 (2 spp.), *Lophostoma* d'Orbigny 1836 (8 spp.), *Macrophyllum* Gray 1838 (1 sp.), *Mimon* Gray 1847 (2 spp., does not include *Anthorhina*), *Tonatia* Gray 1827 (2 spp. — sensu Lee *et al*., 2002), *Trachops* Gray 1847 (1 sp.), *Phylloderma* Peters 1865 (1 sp.), *Phyllostomus* Lacépède 1799 (4 spp.), and *Vampyrum* Rafinesque 1815 (1 sp.).

5. Subfamily Glossophaginae Bonaparte, 1845: 5

Type genus

Glossophaga E. Geoffroy, 1818.

Definition

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

Genetic diagnosis

Support for Glossophaginae is provided by eight molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Glossophaginae	8 unique substitutions (apomorphies)
4 synapomorphies in the nDNA sequence	51 T→C; 181 G→A; 203 A→G; 292 T→C
4 synapomorphies in the mtDNA sequences	1400 G→A; 1605 C→A; 2513 G→A; 3032 C→A

Reference sequences

GenBank AF316431, AF316436, AF316440, AF316441, AF316450, AF316452–AF316454, AF316473, and AF316475 for the RAG2 gene, and AY395806, AY395808, AY395809, AY395813, AY395814, AY395824, AY395835, AY395839, AY395840, and AY395844 for the mtDNA sequence of *Anoura geoffroyi* (and *A. caudifer*), *Brachyphylla cavernarum*, *Choeroniscus godmani* (and *C. minor*), *Choeronycteris mexicana*, *Erophylla sezekorni*, *Glossophaga soricina*, *Hylonycteris underwoodi*, *Leptonycteris curasoae*, *Monophyllus redmani* and *Musonycteris harrisoni*, respectively.

Phylogenetic notes

The karyotypic data available for Glossophaginae provides confirmation of the presence of four major clades of glossophagines in the gene trees of Baker *et al*. (2000, 2003), Datzmann *et al*. (2010), and Rojas *et al*. (2011); these clades (tribes in our classification) are defined below. The last common ancestor for members of Glossophaginae is the clade that unites the remaining five subfamilies of Phyllostomidae (Baker *et al*., 2003; Fig 2).

Comments

The complex of nectar feeding bats that comprises Glossophaginae has proven to be a remarkably complicated problem for the many taxonomists that have attempted to untangle relationships among these forms. This exploitation of the nectar feeding niche produced considerable convergence which has made it difficult to reconstruct their actual pattern of evolution. Morphological characters have proven misleading (see review and discussion in Dávalos *et al*., 2012), and non-differentially stained karyotypes have been interpreted in ways that suggested monophyly of groups that were subsequently refuted (e.g., the conclusion that *Carollia* and *Choeroniscus* had shared derived karyotypes — Baker, 1967).

One of the first divisions of this group was suggested by H. Allen (1898*a*), who listed three "alliances": the glossophagine, the choernycterine and the phyllonycterine. Under H. Allen's view, the genus *Phyllonycteris* represented a connection to *Brachyphylla* and, by extension, to the Brachyphyllina. With few exceptions, the composition of Glossophaginae did not suffer major changes until the recognition of Brachyphyllina by Gray (1866), Phyllonycterinae by Miller (1907) and later, Lonchophyllinae by Griffiths (1982). These three names have been used as subfamilies or tribes by previous authors; that suprageneric use is discussed in the corresponding sections below. Solmsen (1998) recognized four tribes within the original meaning of Glossophaginae (sensu lato).

Included extant genera (and species)

Anoura Gray 1838 (10 spp.), *Brachyphylla* Gray 1833 (2 spp.), *Choeroniscus* Thomas 1928 (3 spp.), *Choeronycteris* Tschudi 1844 (1 sp.), *Dryadonycteris* Nogueira, Lima, Peracchi, and Simmons 2012 (1 sp.), *Erophylla* Miller 1906 (2 spp.), *Glossophaga* E. Geoffroy 1818 (5 spp.), *Hylonycteris* Thomas 1903 (1 sp.), *Leptonycteris* Lydekker 1891 (3 spp.), *Lichonycteris* Thomas 1895 (2 spp., see Gardner 2008), *Monophyllus* Leach 1821 (2 spp.), *Musonycteris* Schaldach and McLaughlin 1960 (1 sp.), *Phyllonycteris* Gundlach 1860 (3 spp.), and *Scleronycteris* Thomas 1912 (1 sp.).

6. 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*.

Molecular diagnosis

Support for Lonchorhininae is provided by 57 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Lonchorhininae	57 unique substitutions (apomorphies)
18 synapomorphies in the nDNA sequence	33 T→C; 34 G→A; 141 G→A; 216 T→C; 258 T→C; 306 G→A; 342 A→G; 375 T→C; 477 T→C; 507 T→C; 666 A→G; 721 G→A; 918 T→C; 1026 A→C; 1134 T→C; 1143 G→A; 1152 A→G; 1340 →C
39 synapomorphies in the mtDNA sequences	1380 A→G; 1396 G→A; 1404 A→G; 1492 A→G; 1550 T→C; 1585 T→C; 1600 T→G, 1671 A→C; 1772 T→A; 1866 T→C; 1971 A→G; 2046 T→C; 2062 C→A; 2102 G→A; 2127 G→A; 2201 T→A; 2219 T→C; 2344 A→G; 2369 T→C; 2372 T→C; 2417 A→G; 2494 A→G; 2502 T→A; 2503 A→G; 2512 A→G; 2525 T→C; 2580 A→G; 2657 A→C; 2696 A→G; 2704 A→G; 2705 G→A; 2728 A→G; 2906 T→A; 2915 T→C; 2962 C→A; 3027 T→C; 3043 T→A; 3049 T→A; 3243 T→C

Reference sequences

GenBank AF316457 for the RAG2 gene, and AY395843 for the mtDNA sequence of *Lonchorhina aurita*.

Phylogenetic notes

Monophyly of Lonchorhininae is strongly supported in the concatenated gene tree (posterior probability = 1.0 — Baker *et al*., 2003) as well as under different sequence data arrangements and analytical methods performed by independent research groups (Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014). All members of this subfamily that have been karyotyped to date have a diploid number of 2n = 32, FN = 60 (Baker, 1973, 1979; Baker and Hsu, 1970; Baker *et al*., 1981; Barros *et al*., 2009). G- and C-bands for *L. aurita* were described by Barros *et al*. (2009) in a comparison with *Trachops* (Phyllostominae). These authors identified several G-banded chromosomes that *Lonchorhina* apparently shares with *Macrotus*, but they also identified six unique chromosomes pairs that with the use of chromosomal paints can be expected to resolve Lonchorhininae and define this subfamily.

Comments

The name Lonchorhinina was first proposed by Gray (1866) as a tribe name for *Lonchorhina*, which was distinguished by presence of a front plate of the nose-leaf with an elevated edge and a central process in front. Subsequent authors included this group within Phyllostominae (e.g., Smith, 1976; Griffiths, 1982; Baker *et al*., 1989). The content of Lonchorhinini was changed by Wetterer *et al*. (2000), who used it for the clade including *Lonchorhina*, *Macrophyllum*, and *Mimon*. Baker *et al*. (2003) restricted the name to its original content (*Lonchorhina* only), and elevated it to a subfamily level.

Various studies (e.g., Baker *et al*., 2003; Datzmann *et al*., 2010; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014) have placed *Lonchorhina* in different places within the phyllostomid tree and its true position remains unclear. Based on mitochondrial and nuclear genes, Baker *et al*. (2003) placed *Lonchorhina* as an independent clade diverging after Macrotinae, Micronycterinae and Desmodontinae, but before the remaining subfamilies. In the RAG2 gene tree *Lonchorhina* appears as sister to Lonchophyllinae, but this relationship is not strongly supported. The gene trees of Rojas *et al*. (2011), Dumont *et al*. (2012), and Dávalos *et al*. (2014) placed *Lonchorhina* as an independent lineage that diverged after all other Phyllostominae (sensu this paper) but before the origin of Glossophaginae and the remainder of Phyllostomidae. In the phylogeny obtained in this paper, Lonchorhininae comes out after Phyllostominae and Glossophaginae but before Lonchophyllinae (Fig. 3). Despite uncertainty regarding its positon in the phyllostomid tree, recovery of *Lonchorhina* as a statistically supported branch, distinct from all other subfamilies and genera (e.g., Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014) supports our decision to recognize the taxon as its own subfamily.

Included extant genera (and species)

Lonchorhina Tomes 1863 (5 spp.).

7. 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*.

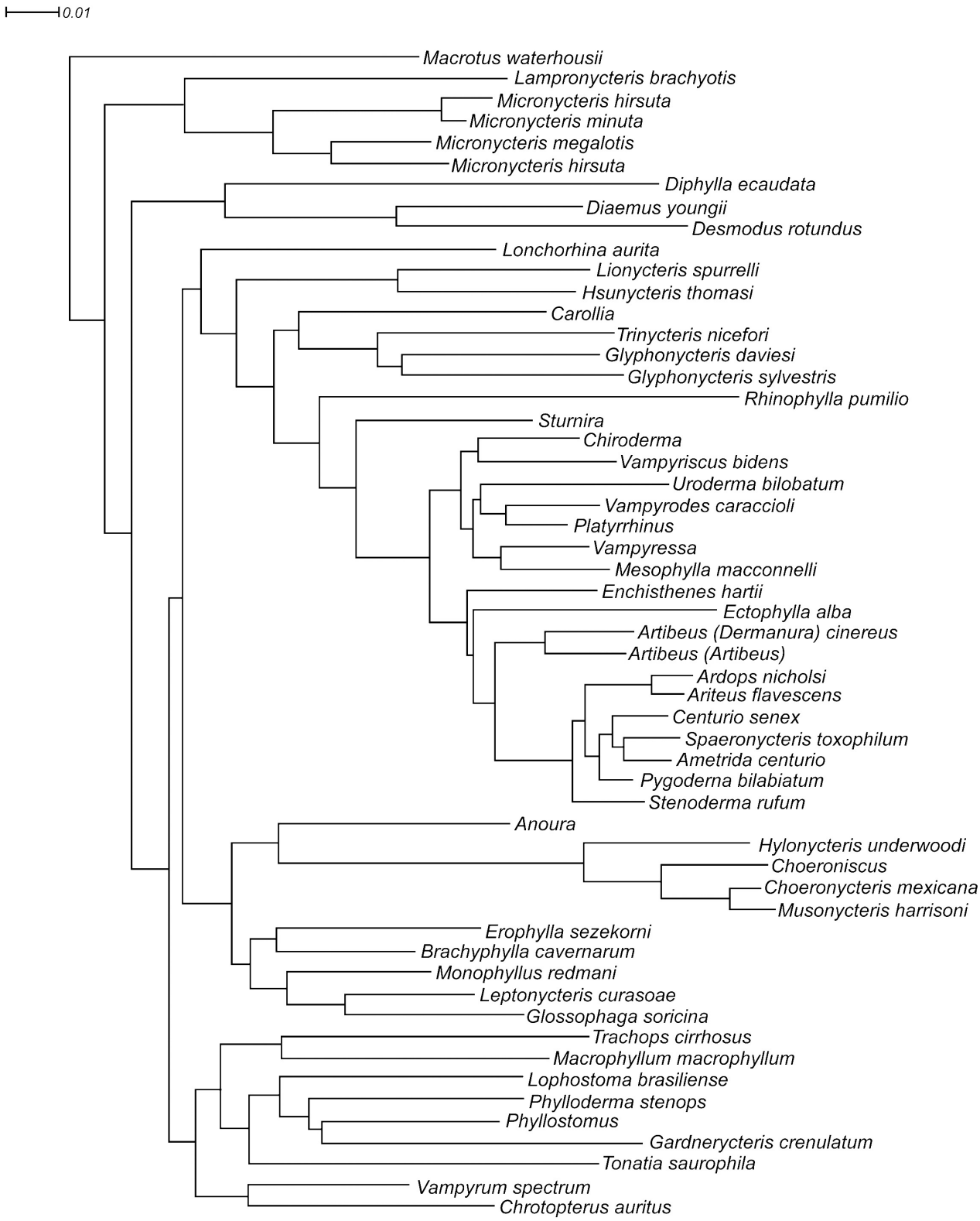

FIG. 3. Tree resulting from a Bayesian analysis of concatenated mtDNA and RAG2 data stored at TreeBASE, and used for identification of molecular synapomorphies. Branch lengths depict percent sequence divergence among taxa since their last common ancestor

Molecular diagnosis

Support for Lonchophyllinae is provided by 33 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Lonchophyllinae	33 unique substitutions (apomorphies)
10 synapomorphies in the nDNA sequence	111 G→C; 292 T→C; 465 G→A; 566 G→A; 576 T→C; 693 T→A; 720 C→T; 742 A→G; 1095 C→T; 1329 A→G
23 synapomorphies in the mtDNA sequences	1503 A→C; 1666 C→T; 1704 G→A; 1711 C→T; 1745 C→T; 1873 A→G; 1874 C→T; 1933 C→T; 1966 G→A; 1967 T→C; 2458 G→A; 2472 T→C; 2540 A→G; 2611 C→T; 2659 G→A; 2660 T→C; 2673 A→G; 2818 C→T; 2941 C→T; 2958 G→A; 3121 C→A; 3296 G→A; 3312 A→C

Reference sequences

GenBank AF316455 and AF316456 for the RAG2 gene, and AY395842 and AY395815 for the mtDNA sequence of *Hsunycteris thomasi* and *Lionycteris spurrelli*, respectively.

Phylogenetic notes

The genera *Platalina*, *Lionycteris*, and *Lonchophylla* have similar non-differentially stained karyotypes with 2n = 28, FN = 50 (Gardner, 1977*b*; Baker, 1979; Haiduk and Baker, 1982; Ribeiro *et al*., 2003; Parlos *et al*., 2014). This is probably the primitive karyotype for Lonchophyllinae (Parlos *et al*., 2014). Within *Hsunycteris*, the diploid number varies (2n = 30, 32 and 36) together with the fundamental number (34, 38, 40, 48 and 50) (Parlos *et al*., 2014). It is significant that none of the 2n/FN combinations present in Lonchophyllinae occurs in Glossophaginae, although the karyotype of *Xeronycteris* has not been described. Additional diagnostic molecular characters (restriction sites of the rDNA complex) were presented and discussed by Van Den Bussche (1992).

Comments

Only three genera were recognized when this subfamily was originally proposed, but two additional genera have been described since (*Xeronycteris* Gregorin and Ditchfield 2005, and *Hsunycteris* Parlos *et al*., 2014). Solmsen (1998) suggested that *Platalina genovensium* was only a large species in *Lonchophylla*. Lonchophyllinae were included as a tribe within Glossophaginae by Koopman (1993) and McKenna and Bell (1997). Recognition of this group as a different subfamily indicates at least two independent evolutionary origins of nectar-feeding from the basal phyllostomids (Baker *et al*., 2012; Dávalos *et al*., 2014).

The number of papers that have been published on the origin of nectar-feeding in phyllostomid bats has been extensive and involved considerable controversy (Baker, 1967; Griffiths, 1982; Warner, 1983; Smith and Hood, 1984; Wetterer *et al*., 2000; Carstens *et al*., 2002; Baker *et al*., 2003, 2012; Datzmann *et al*., 2010; Dávalos *et al*., 2014). Griffiths (1982) was the first to propose that nectar-feeding evolved twice in phyllostomids, noting that tongue morphology was different in lonchophyllines as opposed to glossophagines, whereas M. Tschapka and T. P. González-Terrazas (in litt.) notice differences in drinking behavior (lapping vs. pumping). Baker *et al*. (2003, 2012) proposed that the common ancestor of the two independent nectar-feeding lineages was primarily an insectivore taking some fruit, similar in morphology and life history strategy to *Glyphonycteris*, *Macrotus*, and *Micronycteris*. If this scenario is accurate, then nectar-feeding evolved at least twice in phyllostomids.

Lonchophyllinae is recovered as a monophyletic group to the exclusion of Glossophaginae in most gene trees (Baker *et al*., 2000, 2003; Datzmann *et al*., 2010; Rojas *et al*., 2011; Dávalos *et al*., 2014), except by the maximum likelihood and Bayesian trees of Dávalos *et al*. (2012), although with moderate to low support. Lonchophyllinae is recovered in the concatenated mtDNA+RAG2 tree with strong statistical support (Baker *et al*., 2003), whereas in another (Baker *et al*., 2000) Lonchophyllinae was sister to the Rhinophyllinae but with low support. In our phylogenetic tree (Fig. 3), Lonchophyllinae diverged from the remainder of the phyllostomids after Macrotinae, Micronycterinae, Desmodontinae, Phyllostominae, Glossophaginae, and Lonchorhininae, and before Carolliinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae. We suggest that Lonchophyllinae merits recognition as a subfamily based on the genetic data as well as the muscular and other morphological and nectar feeding differences (see Griffiths, 1982; Cirranello *et al*., 2016).

Included extant genera (and species)

Hsunycteris Parlos, Timm, Swier, Zeballos, and Baker 2014 (4 spp.), *Lionycteris* Thomas 1913

(1 sp.), *Lonchophylla* Thomas 1903 (11 spp.), *Platalina* Thomas 1928 (1 sp.), and *Xeronycteris* Gregorin and Ditchfield 2005 (1 sp.).

8. Subfamily Glyphonycterinae, new subfamily

Type genus

Glyphonycteris Thomas 1896

Definition

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

Molecular diagnosis

Support for Glyphonycterinae is provided by 11 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Glyphonycterinae	11 unique substitutions (apomorphies)
7 synapomorphies in the nDNA sequence	6 A→G; 273 T→C; 378 T→C; 876 A→G; 1008 T→C; 1293 T→C; 1340 T→C
4 synapomorphies in the mtDNA sequences	1503 A→C; 1665 C→A; 2673 A→G; 3113 A→T

Reference sequences

GenBank AF316464, AF316471 and AF316469 for the RAG2 gene, and AY395812, AY395841, and AY395830 for the mtDNA sequence of *Glyphonycteris daviesi*, *G. sylvestris* and *Trinycteris nicefori*, respectively.

Phylogenetic notes

Monophyly of Glyphonycterinae is strongly supported in the concatenated gene tree (posterior probability = 0.97 — Baker *et al*., 2003) as well as under several independent analyses (Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014).

Trinycteris nicefori and *Glyphonycteris daviesi* are the only two members of this subfamily that have been karyotyped and both have 2n = 28 and FN = 52 (Baker and Hsu, 1970; Patton, 1976; Honeycutt *et al*., 1980). Using non-differentially-stained karyotypes, these two species are not easily distinguished from several other phyllostomid bats, including some members of Micronycterinae and Lonchophyllinae (Baker, 1979; Honeycutt *et al*., 1980).

Comments

Trinycteris and *Glyphonycteris* have been classified as part of a more inclusive *Micronycteris* (sensu Sanborn, 1949) in the supertree analyses of Jones *et al*. (2002). These genera were also included within the tribe Micronycterini of Phyllostominae (sensu Wetterer *et al*., 2000), where these genera appeared as sister taxa, and this relationship was the basis for Simmons (2005) classification. The closest genus in the DNA sequence-based gene tree is *Carollia* (Carolliinae, sensu stricto), but given the morphological distinctiveness of these genera, and their separate taxonomic histories, Baker *et al*. (2003) chose to keep them in independent subfamilies. Additional genetic data and/or chromosomal painting data are needed to resolve relationships within the monophyletic group including the genera *Carollia*, *Glyphonycteris*, *Trinycteris*, and *Neonycteris*.

Included extant genera (and species)

Glyphonycteris Thomas 1896 (3 spp.; includes *Barticonycteris* Hill 1964), *Neonycteris* Sanborn 1949 (1 sp.), *Trinycteris* Sanborn 1949 (1 sp.). The inclusion of *Neonycteris* within this subfamily is based on the total evidence analyses by Wetterer *et al*. (2000) as this taxon, known only from two specimens collected over 70 years ago, has not been included in any genetic study.

9. Subfamily Carolliinae Miller, 1924: 53

Type genus

Carollia Gray 1838.

Definition

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

Molecular diagnosis

Support for Carolliinae is provided by 44 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Reference sequences

GenBank AF316437 for the RAG2 gene, and AY395836 for the mtDNA sequence of *Carollia brevicauda* (and *C. perspicillata*).

Phylogenetic notes

Monophyly of the genus *Carollia*, and therefore the Carolliinae is strongly supported in previous

Carolliinae	44 unique substitutions (apomorphies)
15 synapomorphies in the nDNA sequence	95 T→A; 270 T→C; 330 G→A; 738 C→A; 792 G→A; 861 T→C; 870 T→G; 882 A→G; 906 T→C; 933 G→A; 1044 T→C; 1120 A→G; 1191 T→C; 1255 A→C; 1341 A→G
29 synapomorphies in the mtDNA sequences	1452 T→C; 1492 A→G; 1518 A→G; 1531 A→G; 1649 T→C; 1650 A→C; 1684 T→C; 1686 A→G; 1710 A→G; 1772 T→A; 1939 A→G; 1996 A→G; 2003 G→C; 2009 A→C; 2199 T→C; 2369 T→C; 2375 G→A; 2413 T→C; 2470 T→C; 2506 G→A; 2546 A→C; 2940 T→C; 2961 A→G; 2965 T→C; 2995 T→C; 3043 T→A; 3075 G→A; 3119 T→C; 3121 C→A

analyses (Hoffmann and Baker, 2003; Wright *et al*., 1999). In the concatenated gene tree of Baker *et al*. (2003), Carolliinae formed a strongly supported clade with Glyphonycterinae (posterior probability = 0.99). In our phylogenetic tree (Fig. 3) it shares a common ancestry with Glyphonycterinae, Rhinophyllinae, and Stenodermatinae. The same branching order and the association of *Glyphonycteris* and *Trinycteris* as a monophyletic group that is sister to *Carollia* was recovered by gene trees of Baker *et al*. (2000, 2003), Rojas *et al*. (2011), Dumont *et al*. (2012), and Dávalos *et al*. (2014). The fact that *Glyphonycteris* and *Trinycteris* are sister to *Carollia*, and that *Rhinophylla* is not a member of either clade, is interpreted as justification for recognizing three subfamilies: Glyphonycterinae, Carolliinae, and Rhinophyllinae.

The karyotype of *Carollia* is comprised of 14 autosomal pairs that are unique among phyllostomid bats (pairs 7 and 9 are conserved in other species, see Pieczarka *et al*., 2005; Sotero-Caio *et al*., 2011; Ribas *et al*., 2015). There is a pair of large submetacentric chromosomes that are more than twice as large as the other autosomes, and two large subtelocentric pairs that are nearly twice as large as the remaining six pairs of autosomes. Some species are characterized by a multiple sex determination system in which males have one more chromosome (2n = 21) than the females (Hsu *et al*., 1968). In *C. benkeithi*, *C. brevicauda*, *C. perspicillata* and *C. sowelli*, there is an autosome translocated to the X that is larger than the original X. In all of these species, the homolog of the autosomal translocation is never translocated to the original Y. In some populations of *C. castanea* there is no autosome translocated to the X chromosome (Hsu *et al*., 1968; Baker and Bleier, 1971; Patton and Gardner, 1971; Stock, 1975; Parish *et al*., 2002). Chromosomal paints made from *Carollia* and *Phyllostomus* revealed that the karyotype of *Carollia* was so different from those of other phyllostomids that it was difficult to identify the rearrangements that shaped their extant chromosomes when compared to the proposed primitive karyotype for the family (Pieczarka *et al*., 2005). This highly-rearranged karyotype makes it distinguishable from other subfamilies, and validates subfamily status for this clade. Support for a karyotypic affinity between Carolliinae and Glyphonycterinae should be established through chromosomal painting; however, analysis of non-differentially stained karyotypes suggests that *Glyphonycteris* appears to have a more typical karyotype, with the observed diploid and fundamental numbers characteristic of other phyllostomid bats.

Comments

This group was originally proposed as Hemiderminae by Miller (1907), to contain the genera *Hemiderma* (=*Carollia*) and *Rhinophylla* and so exclude them from Phyllostominae. Although Carolliinae has been used consistently for these taxa for several decades, McKenna and Bell (1997) recognized it as a tribe within Stenodermatinae rather than at the subfamily level. Baker *et al*. (2000, 2003) subsequently concluded that Carolliinae was not monophyletic, with *Carollia* being sister to a clade including *Glyphonycteris* and *Trinycteris* whereas *Rhinophylla* was more closely related to Stenodermatinae. This finding has been confirmed in many other analyses (e.g., Baker *et al*., 2003; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014). We here formally recognize these relationships by restricting Carolliinae to *Carollia* only, and naming a new subfamily for *Rhinophylla* (see below).

Included extant genera (and species)

Carollia Gray 1838 (9 spp., see Solari and Baker, 2006; Zurc and Velazco, 2010).

10. Subfamily Rhinophyllinae, new subfamily

Type genus

Rhinophylla Peters 1865

Definition

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

Molecular diagnosis

Support for Rhinophyllinae is provided by 73 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Rhinophyllinae	73 unique substitutions (apomorphies)
17 synapomorphies in the nDNA sequence	363 G→A; 399 C→G; 400 A→G; 402 T→A; 498 T→C; 502 A→G; 504 T→G; 654 A→G; 696 A→G; 802 A→C; 882 A→G; 924 T→C; 1062 T→C; 1134 G→A; 1152 A→C; 1318 T→C; 1335 A→G
56 synapomorphies in the mtDNA sequences	1366 T→A; 1428 T→A; 1437 A→G; 1451 G→A; 1457 A→G; 1472 T→A; 1473 A→G; 1528 A→G; 1531 A→G; 1566 T→C; 1600 T→C; 1609 G→A; 1624 A→G; 1636 G→A; 1695 T→C; 1708 A→G; 1739 G→A; 1741 T→C; 1824 T→C; 1852 A→C; 1887 T→A; 1965 G→A; 1990 T→C; 1995 G→A; 1996 A→G; 2003 G→A; 2033 A→G; 2173 T→C; 2204 T→C; 2243 C→A; 2246 T→A; 2304 T→G; 2346 A→C; 2371 A→G; 2374 A→G; 2375 G→A; 2385 A→G; 2412 T→C; 2470 T→C; 2472 T→A; 2479 A→G; 2502 T→C; 2512 A→G; 2515 A→G; 2525 T→C; 2617 T→C; 2621 A→G; 2640 T→C; 2661 G→A; 2906 T→A; 2934 T→C; 3004 A→C; 3027 T→C; 3049 T→A; 3050 A→G; 3180 A→C

Reference sequences

GenBank AF316484 for the RAG2 gene, and AY395827 for the mtDNA sequence of *Rhinophylla pumilio*.

Phylogenetic notes

In all gene trees published to date (e.g., Baker *et al*., 2003; Rojas *et al*., 2011; Dumont *et al*., 2012; Dávalos *et al*., 2014), Rhinophyllinae appears as the sister group of the subfamily Stenodermatinae. Although three species are included in *Rhinophylla*, all phylogenetic studies (except by Dávalos *et al*., 2014) have included just one species. There is no significant statistical support for shared ancestry of Rhinophyllinae with any other subfamily within Phyllostomidae. Genetic divergence among members of Rhinophyllinae, for the cytochrome-*b* gene, is also distinctive, with Kimura 2-paramenters values always being greater than 0.16 and as high as 0.19 (Wright *et al*., 1999). Distance values within congeneric species in other genera of the family Phyllostomidae are never as great as 0.16 for cyt-*b* data.

A possible alternative to naming a new subfamily for *Rhinophylla* would be to include this clade in Stenodermatinae. However, as reported in the genetic characters that distinguish Stenodermatinae (see below), there are unique karyotypic characteristics including a chromosomal translocation of a small autosome to the X that diagnose that subfamily. This autosomal translocation to the X is absent in *Rhinophylla*. Furthermore, morphologically *Rhinophylla* is well distinguished from the diversity within Stenodermatinae (see Cirranello *et al*., 2016). Finally, there is a long history of use of Stenodermatinae for a clade excluding *Rhinophylla*, hence adding it to that group at this late date could cause confusion in the literature. Therefore, we conclude that *Rhinophylla* is best treated as distinct from both Carolliinae and Stenodermatinae at the subfamily level.

Species of *Rhinophylla* can be distinguished from members of Carolliinae by diploid and fundamental numbers and karyotypic characteristics. Baker and Bleier (1971), based on karyotypes, suggested that *Rhinophylla* does not form a clade with *Carollia*, a finding subsequently confirmed with sequence data. Diploid numbers in all *Rhinophylla* species range from 32 to 36 and fundamental numbers range from 46 to 62 (Baker, 1979; Gomes *et al*., 2012; and unpublished data for *R. alethina*), whereas in Carolliinae the diploid numbers range from 20 to 22 and the fundamental number ranges from 36 to 38. Autosomes for species in Rhinophyllinae form a gradated series with the largest autosome being slightly larger than the X and the smallest autosomes approaching dot size with no distinctive chromosomal arms. The number of acrocentric autosomes is never greater than 7 or fewer than three pairs. In the karyotype of *Carollia* there is an exceptionally large submetacentric pair as well as two large pairs of subtelocentric autosomes; the remaining autosomes are distinctly smaller. The largest number of acrocentric autosomes thus far recorded for Carolliinae is 2.

Comments

The phylogenetic analyses of Baker *et al*. (2003) placed *Rhinophylla* as sister to Stenodermatinae, and these authors noted that *Rhinophylla* could be included in the subfamily Stenodermatinae as a tribe. No formal diagnosis of the subfamily clade was provided, and therefore the proposed name was not available under the current Code (ICZN, 1999).

A diagnosis is presented above making this subfamily name available.

Included genera (and species)

Rhinophylla Peters 1865 (3 spp.).

11. 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*.

Molecular diagnosis

Support for Stenodermatinae is provided by 14 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Stenodermatinae	14 unique substitutions (apomorphies)
7 synapomorphies in the nDNA sequence	144 G→A; 279 C→A; 579 C→T; 592 G→T; 636 T→C; 834 T→C; 932 A→C
7 synapomorphies in the mtDNA sequences	1816 T→C; 1823 T→C; 2222 A→T; 2368 C→T; 2523 T→C; 2557 T→G; 2614 T→C

Reference sequences

GenBank AF316430, AF316433–AF316435, AF316438, AF316439, AF316442, AF316443, AF316448, AF316449, A316481, AF316483, AF316486–AF316488, and AF316491–AF316494 for RAG2, and AY395802–AY395804, AF263225, AF263227, AY395807, AY395810, AY395811, AY395818, AY395825, AY395828, AY395829, AY395831–AY395833, AY395838, AY395845, AY395846, and AY395862 for the mtDNA sequences of *Ametrida centurio*, *Ardops nicholsi*, *Ariteus flavescens*, *Artibeus hirsutus* (and *A. jamaicensis*), *Centurio senex*, *Chiroderma villosum* (and *C. trinitatum*), *Artibeus cinereus*, *Ectophylla alba*, *Enchisthenes hartii*, *Mesophylla macconnelli*, *Platyrrhinus helleri* (and *P. brachycephalus*), *Pygoderma bilabiatum*, *Sphaeronycteris toxophyllum*, *Stenoderma rufum*, *Sturnira lilium* (and *S. magna*), *Uroderma bilobatum*, *Vampyressa pusilla* (and *V. thyone*), *Vampyriscus bidens*, and *Vampyrodes caraccioli*, respectively.

Phylogenetic notes

There are shared derived features within the karyotype of stenodermatines. First, there has been a translocation of an autosome to the long arm of the X chromosome, which is unique to Stenodermatinae. This translocated autosome is between 10–20% of the total size of the X. In studies using chromosome paints derived from *Phyllostomus* and *Carollia*, Noronha *et al*. (2010) found that the translocated autosome corresponded to chromosome 15 in the karyotype of *Phyllostomus hastatus*. These authors also documented that the translocated chromosome to the X in *Carollia* is not the same chromosome that was translocated in Stenodermatinae.

Comments

This taxon has been consistently recognized for decades based on morphology as a clade grouping the fruit-eating species of phyllostomids. *Sturnira*, apparently the basal lineage in this clade, has been placed in a distinct subfamily of its own by some authors (Sturnirinae — Miller 1907) but most current authors follow Baker (1967) in placing *Sturnira* within Stenodermatinae, recognizing its basal position by treating it as a distinct tribe or subtribe (e.g., McKenna and Bell, 1997).

Karyotypes are variable within Stenodermatinae. *Sturnira*, *Artibeus*, *Ardops*, *Ectophylla*, and *Platyrrhinus* are characterized by a diploid number of 2n = 30 or 31 and a FN = 56, 10 pairs of metacentric autosomes and four pairs of subtelocentric autosomes and a subtelocentric X, and either two Y chromosomes (one the original Y, the other being the homologous autosome that was translocated to the long arm of the X) or a biarmed Y composed of the two Ys (Greenbaum *et al*., 1975; Tucker, 1986). This karyotype has been proposed to be primitive for Stenodermatinae (Baker *et al*., 1979) and has apparently been conserved throughout their exceptional morphological diversification to exploit fruit and plant material. There are a number of highly rearranged karyotypes within Stenodermatinae: *Mesophylla* (2n = 21/22, FN = 20), *Vampyressa thyone* (2n = 23/24, FN = 22; 2n = 22/23, FN = 22; 2n = 18, FN = 20), and *Vampyressa melissa* (2n = 14, FN = 24), *Centurio* (2n = 28, FN = 52), but these all are thought to have been derived from the above mentioned primitive karyotype (2n = 30/31, FN = 56) with the autosome translocated to the X

chromosome (Greenbaum *et al*., 1975; Gardner, 1977*b*; Baker *et al*., 1979, 1982).

Included genera (and species)

Ametrida Gray 1847 (1 sp.), *Ardops* Miller 1906 (1 sp.), *Ariteus* Gray 1838 (1 sp.), *Artibeus* Leach 1821 (23 spp., see Larsen *et al*., 2010 and Solari *et al*., 2009), *Centurio* Gray 1842 (1 sp.), *Chiroderma* Peters 1860 (5 spp.), *Ectophylla* H. Allen 1892 (1 sp.), *Enchisthenes* K. Andersen 1906 (1 sp.), *Mesophylla* Thomas 1901 (1 sp.), *Phyllops* Peters 1865 (1 sp.), *Platyrrhinus* Saussure 1860 (21 spp., see Velazco *et al*., 2010; Velazco and Lim, 2014), *Pygoderma* Peters 1863 (1 sp.), *Sphaeronycteris* Peters 1882 (1 sp.), *Stenoderma* E. Geoffroy 1818 (1 sp.), *Sturnira* Gray 1842 (23 spp., see Velazco and Patterson, 2013, 2014), *Uroderma* Peters 1866 (5 spp. — see Mantilla-Meluk, 2014), *Vampyressa* Thomas 1900 (5 spp. — see Tavares *et al*., 2014), *Vampyriscus* Thomas 1900 (3 spp.), *Vampyrodes* Thomas 1900 (2 spp., see Velazco and Simmons, 2011).

Names Available and/or Proposed for Tribes

A number of tribal-group names have been proposed for subdivisions of the more diverse phyllostomid subfamilies. We discuss below those names that we consider to be appropriate (i.e., those associated with monophyletic groups) and useful for recognizing groups within subfamilies.

1. 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*.

Molecular diagnosis

Support for Desmodontini is provided by 32 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Desmodontini	32 unique substitutions (apomorphies)
9 synapomorphies in the nDNA sequence	108 A→G; 177 T→C; 273 T→C; 502 A→G; 504 T→C; 792 G→A; 940 T→A, 1299 T→C; 1348 A→G
23 synapomorphies in the mtDNA sequences	1380 A→G; 1388 T→C; 1399 A→G; 1404 A→G; 1436 A→G; 1466 A→T; 1531 A→G; 1778 T→G; 1823 C→A; 1971 A→G; 2286 A→C; 2304 T→C; 2347 A→G; 2629 T→C; 2906 T→C; 2961 A→T; 2966 A→G; 2968 T→C; 3121 C→A; 3283 A→G; 3284 A→G; 3302 T→C; 3304 T→C

Phylogenetic notes

The association between *Desmodus* and *Diaemus* has been recovered in all the phylogenetic analyses (see above) and is recognized by use of this name at the tribe level. The inclusion of *Diaemus* and *Desmodus* in this tribe is justified by the closer relationship shown in the gene, allozyme, and albumin data trees (Baker *et al*., 1988, 2000, 2003) and by the genetic distance these two genera are from *Diphylla*. See additional comments in the subfamily rank account.

Comments

Koopman (1993) recognized this close association by listing *Diaemus* as a junior synonymy of *Desmodus*.

Included genera (and species)

Desmodus (1 sp.), *Diaemus* (1 sp.).

2. Tribe Diphyllini, new tribe

Type genus

Diphylla Spix 1823.

Definition

The clade arising from the last common ancestor of all populations of *Diphylla*, and the basal one within the subfamily Desmodontinae, highly divergent from the clade of *Desmodus* and *Diaemus*.

Molecular diagnosis

Support for Diphyllini is provided by 62 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Phylogenetic notes

Diphylla has the same diploid and fundamental number as *Diaemus*, however it is distinguished by four chromosomal pairs that do not share the same order of syntenic gene associations with other vampire species (Cadena and Baker, 1976; Sotero-Caio *et al*., 2011). Additional diagnostic molecular

Diphyllini	62 unique substitutions (apomorphies)
9 synapomorphies in the nDNA sequence	165 T→C; 206 A→G; 303 G→A; 606 G→A; 1134 T→C; 1239 G→A; 1311 A→G; 1340 T→C; 1352 A→G
53 synapomorphies in the mtDNA sequences	1364 C→G; 1384 T→C; 1386 T→C; 1406 C→A; 1423 C→A; 1428 C→A; 1480 T→C; 1600 T→A; 1604 T→C; 1609 G→A; 1610 A→G; 1629 T→C; 1630 T→C; 1645 T→C; 1647 G→A; 1694 A→C; 1695 G→C; 1760 T→C; 1772 T→C; 1964 G→A; 1966 G→A; 2003 G→A; 2033 A→G; 2053 T→C; 2329 G→A; 2378 A→C; 2385 A→C; 2471 T→C; 2472 T→C; 2482 T→A; 2483 T→C; 2500 G→A; 2541 A→C; 2550 T→C; 2553 T→C; 2577 A→G; 2614 T→A; 2619 A→G; 2703 G→A; 2705 G→A; 2738 G→A; 2797 C→A; 2901 G→A; 2919 T→C; 2962 C→G; 3031 A→G; 3049 T→A; 3132 T→C; 3165 T→C; 3174 T→C; 3289 A→G; 3296 G→C; 3308 T→C

characters (rDNA restriction sites) were presented and discussed by Van Den Bussche (1992).

Comments

Because of the distinction of Desmodontini (see above), Baker *et al*. (2003) proposed this new name for the *Diphylla* lineage. Genetic data indicated a deep genealogical divergence, comparable to those separating other subfamilies in the molecular tree of Baker *et al*. (2003, 2012). However, this taxon was not identified as new, a type genus was not indicated, and thus the name was not available under the Code. These deficiencies are addressed above to make the name available.

The genus *Diphylla* has been an independent clade for at least 21mya, since it diverged from the other vampire bats (Baker *et al*., 2012). This is longer than most subfamilies have been independent clades within Phyllostomidae. Biochemical analyses of both allozymes and albumins are compatible with the hypothesis that the *Diphylla* clade has existed for a substantial geological time relative to the last common ancestor for *Desmodus* and *Diaemus* (Baker *et al*., 1988).

Included genera (and species)

Diphylla (1 sp.).

3. Tribe Macrophyllini Gray, 1866: 113

Type genus

Macrophyllum Gray 1838.

Definition

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

Molecular diagnosis

Support for Macrophyllini is provided by 18 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Macrophyllini	18 unique substitutions (apomorphies)
3 synapomorphies in the nDNA sequence	606 G→A; 612 G→A; 1056 C→T
15 synapomorphies in the mtDNA sequences	1428 C→T; 1476 G→A; 1886 C→T; 1933 C→T; 2006 C→T; 2151 C→T; 2373 G→A; 2428 C→A; 2436 C→T; 2517 G→T; 2574 C→T; 3034 C→T; 3040 G→A; 3052 C→T; 3178 G→A

Phylogenetic notes

These two genera have the same fundamental number (FN = 56) but are distinguished from each other by differences in diploid numbers, with *Trachops* having a 2n = 30 karyotype (Baker, 1967) and *Macrophyllum*, a 2n = 32 karyotype (Baker *et al*., 1982) with two additional acrocentric autosomes. *Trachops* has an acrocentric X whereas the centromere position of the X has not been distinguished in *Macrophyllum*.

Comments

This taxon was originally proposed for *Macrophyllum* only, to distinguish it from *Lonchorhina* by its truncated (as opposite to a conical) interfemoral membrane. Baker *et al*. (2003) also included *Trachops* in Macrophyllini a relationship not previously proposed or suggested. The association of *Macrophyllum* and *Trachops* to the exclusion of all other genera was recovered in both mitochondrial and RAG2 gene trees (Baker *et al*., 2000, 2003), as well as the gene tree of Rojas *et al*. (2011) and Dávalos *et al*. (2014).

Included genera (and species)

Macrophyllum (1 sp.) and *Trachops* (1 sp.).

4. Tribe Phyllostomini Gray, 1825: 242

Type genus

Phyllostomus Lacépède 1799.

Definition

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

Molecular diagnosis

Support for Phyllostomini is provided by four molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Phyllostomini	4 unique substitutions (apomorphies)
3 synapomorphies in the nDNA sequence	126 G→A; 336 A→G; 918 T→A
1 synapomorphies in the mtDNA sequences	1364 C→T

Phylogenetic notes

The diploid number ranges from 16 to 34 in Phyllostomini, and the fundamental number, from 20 to 60 (Patton, 1976; Baker, 1979). There have been extensive chromosomal rearrangements in this tribe, as noticed by Baker and Bickham (1980) when describing karyotypic megaevolution.

Comments

Baker *et al*. (1989) first used Phyllostomini as a tribe name, but its content was even more restricted in their most recent classification (Baker *et al*., 2003), including only five genera (*Lophostoma*, *Tonatia*, *Mimon*, *Phylloderma*, and *Phyllostomus*). Wetterer *et al*. (2000) further restricted Phyllostomini to *Phyllostomus* and *Phylloderma* only, a change that we reject based on more recent phylogenetic analyses based nuclear and combined mitochondrial and nuclear data (Baker *et al*., 2000, 2003; Rojas *et al*., 2011; Dávalos *et al*., 2014). Recent analyses on chromosomal data using chromosome painting and in situ hybridizations provide independent support for this taxonomic arrangement (Ribas *et al*., 2015; Sotero-Caio *et al*., 2015).

Gardnerycteris crenulatum shows a geographically widely distributed polymorphism in two pairs of chromosomes that involves at least two chromosomal morphs, including submetacentric + subtelocentric and acrocentric + submetacentric forms (Gomes *et al*., 2012). This chromosomal polymorphism was proposed to confer a selective advantage to explain its wide geographic range (Baker *et al*., 1972). Obviously this complex of bats has a very dynamic chromosomal evolutionary history. The gene trees also suggest some generic assemblages (e.g., *Mimon* as traditionally recognized — Dávalos *et al*., 2012, 2014; Hurtado and Pacheco, 2014) may not be monophyletic.

Included genera (and species)

Lophostoma (8 spp.), *Tonatia* (2 spp.), *Gardnerycteris* (2 spp.), *Phylloderma* (1 sp.), and *Phyllostomus* (4 spp.).

5. Tribe Vampyrini Bonaparte, 1837: 8

Type genus

Vampyrum Rafinesque 1815.

Definition

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

Molecular diagnosis

Support for Vampyrini is provided by 14 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Vampyrini	14 unique substitutions (apomorphies)
2 synapomorphies in the nDNA sequence	21 C→A; 915 C→T
12 synapomorphies in the mtDNA sequences	1472 T→A; 1473 A→G; 1492 A→G; 1799 A→G; 2009 G→A; 2274 T→C; 2345 C→T; 2540 A→G; 2907 A→T; 2961 A→G; 3121 C→A; 3189 C→G

Phylogenetic notes

These two genera have distinct diploid and fundamental numbers (2n = 28 and 30 and FN = 52 and 56). Both genera have biarmed autosomes and X chromosomes, as well as an acrocentric Y. The difference in fundamental numbers is achieved by a relative reduction in the number of biarmed chromosomes by one pair, which would require at least two chromosomal rearrangements (Baker, 1979).

Comments

A close relationship between *Vampyrum* and *Chrotopterus* has been presumed for decades, and was recovered in the morphological analyses of Wetterer *et al*. (2000) as well as in the genetic based

trees of Baker *et al*. (2000, 2003) and Rojas *et al*. (2011), as well the combined analyses in Dávalos *et al*. (2012, 2014). However, the generic composition of Vampyrini was more inclusive in previous studies, including Baker *et al*. (1989; who included *Trachops*) and Wetterer *et al*. (2000; who included *Tonatia* sensu lato and *Trachops*). Evidence from DNA sequence data put those genera in other clades that we recognized as different tribes (see above).

Included extant genera (and species)

Vampyrum (1 sp.) and *Chrotopterus* (1 sp.). Analyses by Dávalos *et al.* (2014) and Rojas *et al.* (In press) suggest that *Mimon* (sensu stricto) belongs into this tribe. Although we did not include this genus in this analysis, and therefore cannot test that relationship, we chose to consider it as part of this tribe.

6. Tribe Choeronycterini Solmsen, 1998: 97

Type genus

Choeronycteris Tschudi 1844.

Definition

The clade arising from the last common ancestor of the genera *Anoura*, *Hylonycteris* and *Musonycteris.*

Molecular diagnosis

Support for Choeronycterini is provided by 14 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Choeronycterini	14 unique substitutions (apomorphies)
3 synapomorphies in the nDNA sequence	465 G→A; 916 G→A; 1170 A→G
11 synapomorphies in the mtDNA sequences	1405 A→C; 1406 C→T; 1428 C→T; 1476 G→A; 1613 T→C; 1874 C→T; 2004 C→T; 2254 A→T; 2393 G→A; 2941 C→T; 3112 C→T

Phylogenetic notes

DNA sequence data support monophyly of two major clades within Glossophaginae: Choeronycterini, and a larger clade comprising the tribes Glossophagini, Brachyphyllini and Phyllonycterini (Baker *et al*., 2003, 2012; Rojas *et al*., 2011; Dávalos *et al*., 2014). Karyotypic data (Haiduk and Baker, 1982) and restriction sites of the rDNA complex (Van Den Bussche, 1992) grouped *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris*, to the exclusion of *Anoura*. Based on genetic distances, the rate of molecular evolution in Choeronycterini appears to be among the fastest within Phyllostomidae (Baker *et al*., 2003).

Comments

The name choeronycterini was applied by H. Allen (1898*a*, as the choernycterine) in his review of the Glossophaginae, for a group that included *Choeronycteris* (as *Choernycteris*) and *Anoura* (listed as *Anura* and *Lonchoglossa*). That proposal fulfills the requirements of Art. 11.7.1 but not those of Art. 11.7.2 (ICZN, 1999), about latinization and use, and therefore we referred the name Choeronycterini to Solmsen (1998), whom used it as the name for a group that included *Choeronycteris*, *Choeronyscus*, (*Musonycteris* as a subgenus), and *Hylonycteris*, but not *Anoura*. Based on molecular data published later by Baker *et al*. (2003), this tribe name was used by Carstens *et al*. (2002), who included seven genera characterized by incomplete zygomatic arches and absence of lower incisors: *Anoura*, *Choeroniscus*, *Choeronycteris*, *Musonycteris*, *Hylonycteris*, *Lichonycteris*, and *Scleronycteris*.

Included extant genera (and species)

Anoura (10 spp.), *Choeroniscus* (3 spp.), *Choeronycteris* (1 sp.), *Dryadonycteris* (1 sp.), *Musonycteris* (1 sp.), *Hylonycteris* (1 sp.), *Lichonycteris* (2 spp.), and *Scleronycteris* (1 sp.).

7. Tribe Glossophagini Bonaparte, 1845:5

Type genus

Glossophaga E. Geoffroy 1818.

Definition

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

Molecular diagnosis

Support for Glossophagini is provided by six molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Glossophagini	6 unique substitutions (apomorphies)
2 synapomorphies in the nDNA sequence	318 T→C; 1161 A→G
4 synapomorphies in the mtDNA sequences	2005 C→T; 2254 A→C; 2600 A→C; 3168 C→T

Phylogenetic notes

The smallest definition of this tribe reflects the closest karyotypic affinities among these three genera, as provided by Baker and Lopez (1970). However, in that same work they identified that *Erophylla* and *Brachyphylla* (members of the current Brachyphyllini) have the same diploid number of 2n = 32 and FN = 60, with the X being about 5% of the genome and the Y just a small acrocentric. This karyotype is essentially the same for all species within this clade, as has been confirmed by G-band analyses (Baker and Bass, 1979; Baker *et al*., 1982; Haiduk and Baker, 1982). The karyotypic uniformity shown by these genera is compatible with the theory that these genera have undergone morphological diversification with a common karyotype that has been maintained by stabilizing selection (Baker and Bass, 1979; Haiduk and Baker, 1982). In other words, chromosomal rearrangements are not a viable mechanism to explain the origin of the morphological diversity in *Brachyphylla*, *Erophylla*, *Phyllonycteris*, *Glossophaga*, *Leptonycteris* and *Monophyllus*, even though these genera have been recognized as members of four different subfamilies in many past classifications.

Comments

Carstens *et al*. (2002) and Baker *et al*. (2003) recognized the complex relationships among species of Glossophaginae in the form of 4 tribes; the first tribe included *Glossophaga*, *Leptonycteris*, and *Monophyllus*. Wetterer *et al*. (2000) used Glossophagini in a wider sense, also including all genera herein recognized as part of Choeronycterini in addition to the genera traditionally included in Glossophagini.

Included extant genera (and species)

Glossophaga (5 spp.), *Leptonycteris* (3 spp.) and *Monophyllus* (2 spp.).

8. Tribe Brachyphyllini Gray, 1866: 115.

Type genus

Brachyphylla Gray 1833.

Definition

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

Molecular diagnosis

Support for Brachyphyllini is provided by seven molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Brachyphyllini	7 unique substitutions (apomorphies)
7 synapomorphies in the mtDNA sequences	1760 T→C; 2148 T→C; 2612 C→T; 2995 T→C; 3025 T→C; 3048 T→C; 3181 G→A

Phylogenetic notes

The three genera comprising Brachyphillini share a diploid number of 2n = 32 and a fundamental number of FN = 60 (Baker and Lopez, 1970). The G-banded karyotype of *Brachyphylla* is indistinguishable from that of *Phyllonycteris* and *Erophylla*, as well from as all members of Glossophagini, but is unique from the karyotypes of all other phyllostomid bats studied thus far (Baker and Bass, 1979). This is compatible with the hypothesis that *Brachyphylla*, *Erophylla* and *Phyllonycteris* shared a common ancestry with Glossophagini as recognized here (see above). The relationship between Glossophagini and Brachyphyllini is confirmed in the phylogenetic tree (Fig. 3) based on DNA sequence variation. Additional diagnostic molecular characters (restriction sites of the rDNA complex) for Brachyphyllini were presented and discussed by Van Den Bussche (1992).

Comments

The name Brachyphyllini has been accorded subfamily rank in many previous classifications (e.g., McKenna and Bell, 1997; Wetterer *et al*., 2000), typically including a single genus, *Brachyphylla*, which has a distinctive morphology (see Miller, 1907) that validates its separation from Glossophagini. *Brachyphylla* was included within Stenodermatinae by H. Allen (1898*b*) and Miller (1907), but was soon removed to its own taxon due to morphological differences. The morphological diversity seen among the three genera we include in Brachyphyllini (*Brachyphylla*, *Erophylla*, and *Phyllonycteris*) was used to justify recognition of two subfamilies for these taxa (Brachyphyllinae and

Phyllonycterinae; Miller, 1907; Koopman, 1993). However, the presence of synapomorphies in the DNA sequence data that robustly supports the tribes Glossophagini and Brachyphyllini as monophyletic to the exclusion of the rest of Glossophaginae and other subfamilies (Baker *et al*., 2003; Rojas *et al*., 2011) is compelling. Baker *et al*. (2003) considered the Brachyphyllini as represented by *Brachyphylla* only, but consideration of the morphological evidence suggests a closer (recent) relationship to *Phyllonycteris* and *Erophylla*.

Included extant genera (and species)

Brachyphylla (2 spp.), *Phyllonycteris* (3 spp.), and *Erophylla* (2 spp.).

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

Type genus

Hsunycteris Timm, Swier, Zeballos, and Baker 2014.

Definition

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

Molecular diagnosis

Support for Hsunycterini is provided by 27 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Hsunycterini	27 unique substitutions (apomorphies)
7 synapomorphies in the nDNA sequence	324 C→T; 382 G→C; 948 T→C; 1158 T→C; 1164 T→G; 1318 T→C; 1359 A→G
20 synapomorphies in the mtDNA sequences	1398 A→G; 1634 A→G; 1686 A→G; 1778 T→A; 1842 A→G; 2126 C→T; 2141 G→A; 2151 C→T; 2158 T→C; 2202 A→G; 2273 A→C; 2309 A→C; 2381 C→T; 2406 G→A; 2493 G→A; 2543 T→C; 3034 C→A; 3037 T→C; 3187 A→G; 3282 T→C

Phylogenetic notes

The karyotype of *Hsunycteris* is characterized by a 2n = 32–38; all karyotypes of Hsunycterini species have multiple acrocentric autosomes (Gardner, 1977*b*; Baker *et al*., 1982; Ribeiro *et al*., 2003; Parlos *et al*., 2014). Parlos *et al*. (2014) discussed additional morphological and molecular characters, including two nuclear genes (Fgb-I7 and TSHB-I2).

Comments

This taxon was recently proposed to distinguish the karyotypic singularity of species in the genus *Lonchophylla* (sensu lato), which was recognized as a paraphyletic taxon. Three small species, plus one unnamed form, in the former genus were listed under the new genus *Hsunycteris* and listed as a distinct tribe based on phylogenetic analyses of molecular data (Parlos *et al*., 2014). According to a recent phylogenetic analysis by Rojas *et al*. (In press), *Lonchophylla mordax* would be closer to the genus *Hsunycteris* than to *Lonchophylla* (sensu stricto), as predicted by Parlos *et al*. (2014), following Woodman and Timm (2006) and Woodman (2007).

Included extant genera (and species)

Hsunycteris (4 spp.).

10. 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*.

Molecular diagnosis

Support for Lonchophyllini is provided by 33 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Lonchophyllini	33 unique substitutions (apomorphies)
16 synapomorphies in the nDNA sequence	93 A→G; 333 A→G; 363 G→A; 381 A→C; 408 G→A; 502 A→G; 586 A→G; 587 G→C; 723 C→T; 864 A→G; 867 G→A; 874 T→G; 963 A→G; 1008 T→C; 1038 T→C; 1320 G→A
17 synapomorphies in the mtDNA sequences	1398 A→T; 1452 T→C; 1462 A→G; 1465 T→C; 1654 T→C; 1778 T→G; 1852 A→C; 1862 A→T; 1954 T→C; 2287 T→C; 2359 G→A; 2422 A→T; 2441 C→T; 2598 A→G; 3118 T→C; 3283 A→G; 3310 G→A

Phylogenetic notes

The genera *Platalina*, *Lionycteris*, and *Lonchophylla* (sensu stricto) have similar non-differentially stained karyotypes with 2n = 28, FN = 50 (Gardner, 1977*b*; Baker, 1979; Haiduk and Baker, 1982; Ribeiro *et al*., 2003; Parlos *et al.*, 2014; Almeida *et al.*, 2016). The karyotype of *Xeronycteris* has not been described. Additional diagnostic molecular characters (restriction sites of the rDNA complex) were presented and discussed by Van Den Bussche (1992).

Comments

Recognition of these taxa as a different tribe is supported by their divergent position in recent independent phylogenetic analyses (Dávalos *et al*., 2014; Parlos *et al*., 2014), and the distinction in diploid number and presence of acrocentric chromosomes, according to the karyotypes known thus far (Parlos *et al*., 2014). These groups stay the same (in composition, not specific branching order) in the recent topology of Rojas *et al*. (In press).

Included extant genera (and species)

Lionycteris Thomas 1913 (1 sp.), *Lonchophylla* Thomas 1903 (11 spp.), *Platalina* Thomas 1928 (1 sp.), and *Xeronycteris* Gregorin and Ditchfield 2005 (1 sp.).

11. Tribe Sturnirini Miller, 1907: 38

Type genus

Sturnira Gray 1842.

Definition

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

Molecular diagnosis

Support for Sturnirini is provided by 37 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Phylogenetic notes

The karyotype of Sturnirini is characterized by a 2n = 30 and a FN = 56, with 10 pairs of metacentric autosomes, four pairs of subtelocentric autosomes, and a subtelocentric X and a submetacentric Y (Baker *et al*., 1979; Tucker, 1986). Additional diagnostic molecular characters were discussed by Van Den Bussche (1992; restriction sites of the rDNA complex).

Sturnirini	37 unique substitutions (apomorphies)
17 synapomorphies in the nDNA sequence	153 A→C; 165 T→C; 249 A→G; 462 T→C; 468 A→G; 474 T→C; 651 A→G; 666 A→G; 744 G→C; 864 A→G; 1086 G→A; 1128 T→C; 1164 T→G; 1242 A→G; 1251 A→G; 1345 T→C; 1347 A→G20
20 synapomorphies in the mtDNA sequences	1428 T→C; 1684 T→C; 1818 T→C; 1846 T→C; 1873 A→G; 1887 T→C; 1967 T→C; 2009 A→G; 2046 T→C; 2107 T→C; 2254 A→C; 2326 A→G; 2372 T→C; 2502 T→A; 2612 T→C; 2629 T→C; 2965 T→A; 2968 T→C; 2995 T→C; 3049 T→C

Comments

This taxon was originally proposed as a subfamily to include *Sturnira* only. The basis for its distinction was related to the "aberrant and highly specialized" tooth structure (Miller, 1907). Subsequent authors have noted the close relationships of *Sturnira* to stenodermatines, and treated it as a tribe or subtribe of Stenodermatinae, or simply as a junior synonym (e.g., Koopman, 1993; McKenna and Bell, 1998).

Included extant genera (and species)

Sturnira (23 spp.).

12. Tribe Stenodermatini Gervais, 1856: 32n

Type genus

Stenoderma E. Geoffroy 1818.

Definition

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

Molecular diagnosis

Support for Stenodermatini is provided by 13 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Stenodermatini	13 unique substitutions (apomorphies)
2 synapomorphies in the nDNA sequence	366 A→G; 1260 G→A
11 synapomorphies in the mtDNA sequences	1799 A→G; 1918 C→T; 1923 G→A; 2278 T→C; 2624 A→G; 2628 A→C; 2917 A→T; 3025 C→T; 3064 C→T; 3065 T→A; 3308 T→A

Phylogenetic notes

The karyotype of most species within this clade is characterized by a 2n = 30–31 and a FN = 56, with 10 pairs of metacentric autosomes, four pairs of subtelocentric autosomes, and a subtelocentric X and a submetacentric Y (Greenbaum *et al*., 1975; Baker *et al*., 1979; Tucker, 1986). However, a particular set of karyotypic variants occur within the subtribe Vampyressina (see Gardner, 1977*b* and discussion below).

Comments

This name was restricted to the 'short-faced' fruit bats by H. Allen (1898*b*; Stenodermini) based on the presence of a round hard palate; later, Owen (1987) validated the distinction of this clade in a morphological analysis. Morphological (e.g., Wetterer *et al*., 2000) and molecular (e.g., Baker *et al*., 2000) data agree that Stenodermatini is monophyletic, although with different arrangements for the included genera (see below).

Included genera (and species)

Ametrida (1 sp.), *Ardops* (1 sp.), *Ariteus* (1 sp.), *Artibeus* (23 spp.), *Centurio* (1 sp.), *Chiroderma* (5 spp.), *Ectophylla* (1 sp.), *Enchisthenes* (1 sp.), *Mesophylla* (1 sp.), *Phyllops* (1 sp.), *Platyrrhinus* (21 spp.), *Pygoderma* (1 sp.), *Sphaeronycteris* (1 sp.), *Stenoderma* (1 sp.), *Uroderma* (5 spp.), *Vampyressa* (5 spp.), *Vampyriscus* (3 spp.), *Vampyrodes* (2 spp.).

Names Available and/or Proposed for Subtribes

1. Subtribe Anourina, new subtribe

Type genus

Anoura Gray 1838.

Definition

The clade arising from the last common ancestor of all species of *Anoura*, a highly divergent clade within Choeronycterini.

Molecular diagnosis

Support for Anourina is provided by 33 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Anourina	33 unique substitutions (apomorphies)
8 synapomorphies in the nDNA sequence	291 G→A; 477 T→C; 504 T→C; 972 A→G; 1032 T→C; 1251 A→G; 1317 A→G; 1318 T→C
25 synapomorphies in the mtDNA sequences	1393 G→A; 1394 T→C; 1600 T→A; 1602 A→G, 1604 T→C; 1852 A→C; 2008 T→C; 2017 G→A; 2159 A→G; 2201 T→C; 2274 T→A; 2286 A→C; 2379 A→C; 2501 A→G; 2502 T→A; 2506 G→A; 2514 G→A; 2527 T→C; 2655 A→G; 2706 T→C; 2719 A→C; 2875 A→G; 3043 T→A; 3186 T→C; 3308 T→A

Phylogenetic notes

Members of Anourina share a diploid number of 30 and a fundamental number of 56; the largest autosomal pair is metacentric, there are five pairs of autosomes with subtelomeric centromere placement, the sex determining system XX/XY, and Y chromosome is dot sized (Gardner, 1977*b*; Haiduk and Baker, 1982). This invariant karyotype distinguishes Anourina from all other species of phyllostomids that have been karyotyped thus far (Haiduk and Baker, 1982). The most obvious diagnostic feature is the largest autosomal pair, which is almost twice as large as the largest of the remaining autosomes and is comprised of linked segments from six different chromosomal pairs (12, 4, 16, 9, 17, and 14) present in *Macrotus californicus* identified using in situ hybridizations of chromosome paints (Sotero-Caio *et al*., 2013).

Comments

Baker *et al*. (2003: 24) proposed this subtribe to include only *Anoura* based on its large genetic divergence with respect to the remaining Choeronycterini. Although a new name, it was not mentioned as such in the original publication and the type genus was not mentioned, hence the name was not compliant with the Code (ICZN, 1999). This is corrected here to make the name available.

Included extant genera (and species)

Anoura (10 spp.).

2. Subtribe Choeronycterina Solmsen, 1998: 97

Type genus

Choeronycteris Tschudi 1844.

Definition

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

Molecular diagnosis

Support for Choeronycterina is provided by 61 molecular synapomorphies (below) in the aligned

dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Choeronycterina	61 unique substitutions (apomorphies)
44 synapomorphies in the nDNA sequence	126 A→G; 319 G→A; 327 A→G; 381 A→C; 384 T→C; 400 A→G; 414 T→C; 444 T→C; 456 T→C; 538 A→G; 555 A→G; 598 A→G; 639 A→G; 663 T→C; 732 T→G; 783 A→C; 825 A→G; 834 T→C; 843 T→G; 852 A→C; 855 A→G; 876 A→G; 881 C→T; 882 A→G; 896 T→C; 901 A→C; 902 A→G; 903 A→G; 923 A→G; 924 T→C; 948 T→C; 963 A→G; 966 A→C; 999 A→G; 1017 T→C; 1071 T→C; 1134 T→C; 1158 T→C; 1197 T→G; 1260 A→G; 1267 A→G; 1345 T→G; 1347 A→G; 1359 A→C
17 synapomorphies in the mtDNA sequences	1396 G→A; 1685 G→A; 1695 T→C; 1966 G→A; 2152 C→T; 2378 A→C; 2430 A→C; 2472 T→C; 2486 G→A; 2495 C→T; 2507 T→C; 2509 T→C, 2517 G→T; 2528 A→G; 2964 A→T; 3048 T→C; 3075 G→A

Phylogenetic notes

This group has undergone a reduction of diploid and fundamental number so that karyotypes range from 2n = 20 to 2n = 16 and FN = 36 to 24. To achieve these numbers requires several karyotypic rearrangements that are uncommon in most karyotypic evolutionary scenarios (Haiduk and Baker, 1982). Additional diagnostic molecular characters (rDNA restriction sites) were presented and discussed by Van Den Bussche (1992).

Comments

This name applies to the clade comprising the core of Choeronycterini of Baker *et al*. (2003) to the exclusion of *Anoura*. This name was coined according to the third edition of the Code (ICZN, 1985), so although it was not explicitly proposed, Solmsen (1998) gave it a clear taxonomic rank (Art. 11, I, 1), and accompanied it with a description of the characters that differentiate the taxon. Thus, these four genera were characterized in the allometric space by an elongated palate relative to total skull length. The addition of *Lichonycteris*, *Scleronycteris*, and *Dryadonycteris* to this group was based on the findings of Wetterer *et al*. (2000), Carstens *et al*. (2002), and Nogueira *et al*. (2012) using morphological data.

Included extant genera (and species)

Choeroniscus (3 spp.), *Choeronycteris* (1 sp.), *Dryadonycteris* (1 sp.), *Musonycteris* (1 sp.), *Hylonycteris* (1 sp.), *Lichonycteris* (2 spp.), and *Scleronycteris* (1 sp.).

3. Subtribe Brachyphyllina Gray, 1866: 115

Type genus

Brachyphylla Gray 1833.

Definition

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

Molecular Diagnosis

Support for Brachyphyllina is provided by 22 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Brachyphyllina	22 unique substitutions (apomorphies)
5 synapomorphies in the nDNA sequence	194 T→C; 273 T→G; 599 A→G; 803 T→C; 1263 G→C
17 synapomorphies in the mtDNA sequences	1516 T→C; 1685 G→A; 1759 T→C; 1824 T→C; 2173 T→C; 2189 A→G; 2200 G→A; 2274 T→A; 2315 T→C; 2345 C→G; 2347 A→C; 2378 A→C; 2500 G→A; 2501 A→G; 2506 G→A; 2637 A→G; 3290 A→G

Phylogenetic notes

As noted earlier, no karyotypic traits diagnose this taxon.

Comments

This genus has been accorded subfamily rank in previous classifications (e.g., McKenna and Bell, 1997; Koopman, 1993; Wetterer *et al*., 2000), mostly because of its distinctive morphology (see Miller, 1907). *Brachyphylla* was included within Stenodermatinae by H. Allen (1898*b*) and Miller (1907).

Included extant genera (and species)

Brachyphylla (2 spp.).

4. Subtribe Phyllonycterina Miller, 1907: 171

Type genus

Phyllonycteris Gundlach 1860.

Definition

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

Molecular Diagnosis

Support for Phyllonycterina is provided by 42 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Phyllonycterina	42 unique substitutions (apomorphies)
9 synapomorphies in the nDNA sequence	276 T→C; 363 G→A; 411 G→A; 459 G→A; 566 G→A; 721 G→A; 737 G→A; 847 A→G; 1340 T→C
33 synapomorphies in the mtDNA sequences	1431 A→G; 1504 A→G; 1600 T→C; 1613 T→C; 1643 T→C; 1649 T→C; 1763 T→C; 1784 A→C; 1799 A→G; 1842 A→G; 2002 A→G; 2157 G→A; 2158 T→C; 2199 T→C; 2202 A→G; 2346 A→C; 2369 T→C; 2372 T→C; 2373 G→A; 2417 A→G; 2422 A→C; 2483 T→C; 2498 A→G; 2502 T→G; 2525 T→A; 2580 A→G; 2691 A→G; 2692 A→G; 2881 T→A; 2906 T→C; 3027 T→C; 3049 T→C; 3311 A→C

Phylogenetic notes

The G-banded karyotype of *Phyllonycteris* and *Erophylla* is indistinguishable from that of *Brachyphylla*, as well as from all members of Glossophagini. The relationships are confirmed in the phylogenetic tree (Fig. 3) based on DNA sequence variation. Additional diagnostic molecular characters (restriction sites of the rDNA complex) were presented and discussed by Van Den Bussche (1992).

Comments

Before being recognized as representing an independent group, *Phyllonycteris* was associated with *Brachyphylla* by H. Allen (1898*a*); the original designation of Phyllonycterina by Miller (1907) also included *Erophylla*. Phyllonycterina has been accorded subfamily (Koopman 1993) or tribal (McKenna and Bell 1997) rank in previous classifications, mostly because of their distinctive morphology (see Miller, 1907).

Included extant genera (and species)

Erophylla (2 spp.) and *Phyllonycteris* (3 spp.).

5. Subtribe Vampyressina, new subtribe

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*.

Molecular diagnosis

Support for Vampyressina is provided by 8 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Vampyressina	8 unique substitutions (apomorphies)
4 synapomorphies in the nDNA sequence	168 C→T; 286 G→A; 391 C→T; 1149 A→T
4 synapomorphies in the mtDNA sequences	1758 A→G; 2510 A→G; 3168 C→T; 3189 T→G

Phylogenetic notes

This clade includes genera and species characterized by highly rearranged karyotypes if compared to the proposed stenodermatine ancestral condition (2n = 30 — Baker, 1973, 1979). Only *Platyrrhinus* and *Vampyrodes* in Vampyressina have retained the primitive karyotype for Stenodermatinae, whereas all other genera (*Chiroderma*, *Uroderma*, *Mesophylla*, *Vampyressa*, and *Vampyriscus*) have highly derived karyotypes that require multiple chromosomal rearrangements to explain the karyotypes of extant species (Baker, 1979). In fact, most species have karyotypes that are unique for all bats and that not only involve typical euchromatic rearrangements, but also unique sex chromosome conditions. In *Mesophylla*, for example, the Y chromosome has either been deleted or translocated to an autosome pair (Baker, 1973; Greenbaum *et al*., 1975). Of all Stenodermatinae the greatest amount of chromosomal evolution is present in this subtribe. The karyotype within species of *Vampyressa* and *Vampyriscus* is diagnostic because of low diploid and fundamental numbers (Gardner, 1977*b*; Baker, 1979).

Comments

This name was originally proposed as Vampyressatini by Owen (1987: 62), for *Vampyressa* only (*V. pusilla*, *V. brocki*, and *V. bidens*), but the same author (p. 33) recommended this nomenclatural arrangement should not be adopted. It was also used by Ferrarezi and Gimenez (1996) and Wetterer *et al*. (2000), but with an expanded content, usually by adding *Mesophylla* and *Ectophylla*. Its content was modified by Baker *et al*. (2003: 25) but the requirements to make the name available (ICZN, 1999) were not met. These deficiencies are addressed in this account.

Included extant genera (and species)

Chiroderma (5 spp.), *Mesophylla* (1 sp.), *Platyrrhinus* (21 spp.), *Uroderma* (5 spp.), *Vampyressa* (5 spp.), *Vampyriscus* (3 spp.), and *Vampyrodes* (2 spp.).

6. Subtribe Enchisthenina, new subtribe

Type genus

Enchisthenes K. Andersen 1906.

Definition

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

Molecular diagnosis

Support for Enchisthenina is provided by 20 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Enchisthenina	20 unique substitutions (apomorphies)
6 synapomorphies in the nDNA sequence	126 A→G; 477 T→C; 519 G→C; 743 A→C; 825 A→G; 940 T→C
14 synapomorphies in the mtDNA sequences	1747 C→A; 2232 A→C; 2252 G→A; 2254 A→G; 2274 T→A; 2612 T→C; 2696 A→G; 2705 G→A; 2902 G→A; 2958 G→A; 3121 C→A; 3165 T→C; 3189 T→C; 3284 G→A

Phylogenetic notes

The karyotype of *Enchisthenes hartii* has a 2n = 30/31, FN = 56. This karyotype is unique and diagnostic among stenodermatine bats by having two fewer pairs of metacentrics and two additional pairs of subtelocentrics (Baker, 1967; Hsu *et al*., 1968). Enchisthenina is the basal clade within a larger group including *Ectophylla*, *Artibeus* plus *Dermanura*, and the short-faced bats (Fig. 3). *Enchisthenes* does not share the heterochromatic repeat unit that identifies *Artibeus* and *Dermanura*, and the data generated on Southern blot analysis, in situ hybridization, and mitochondrial DNA sequences indicate that *Enchisthenes* is not closely related to either *Dermanura* or *Artibeus* (Van Den Bussche *et al*., 1993). Additional diagnostic molecular characters (rDNA restriction sites) were presented and discussed by Van Den Bussche (1992).

Comments

This name was originally proposed as Enchistheneini by Owen (1987: 61) to include *Enchisthenes* only. As with other names in that work, it was listed in an Appendix with an indication that they were new names plus a list of the included genera and species. However, this name was not used consistently within that publication. The taxon-name *Enchisthenes* was used as the type genus for Enchistheneini (by monotypy) on page 61, but the author recommended not adopting these nomenclatural arrangements several pages earlier (p. 33) and in another appendix *Enchisthenes* was included under *Dermanura* (p. 65). Baker *et al*. (2003: 26) used Enchisthenina in the same way as Owen (1987: 61) but did not include information required by the Code (ICZN, 1999) to make it an available name. These deficiencies are addressed in this account.

Included extant genera (and species)

Enchisthenes (1 sp.).

7. Subtribe Ectophyllina, new subtribe

Type genus

Ectophylla H. Allen 1892.

Definition

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

Molecular diagnosis

Support for Ectophyllina is provided by 46 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Ectophyllina	46 unique substitutions (apomorphies)
14 synapomorphies in the nDNA sequence	216 T→G; 219 T→A; 285 T→C; 468 A→C; 486 T→C; 502 A→G; 555 A→C; 600 T→C; 627 T→C; 814 G→A; 923 A→G; 930 A→G; 1102 T→G; 1179 T→A
32 synapomorphies in the mtDNA sequences	1423 C→A; 1428 T→C; 1472 T→C; 1476 G→A; 1612 C→A; 1624 A→G; 1625 C→A; 1644 T→A; 1654 T→C; 1694 A→G; 1757 G→A; 1758 A→G; 1818 T→C; 1933 C→A; 2046 T→A; 2065 G→A; 2148 T→C; 2200 G→A; 2241 G→A; 2315 T→C; 2344 A→G; 2372 T→C; 2422 A→G: 2557 G→A; 2591 C→A; 2627 A→C; 2637 A→G; 2659 G→A; 2670 A→C; 2880 T→C; 3112 C→A; 3178 G→A

Phylogenetic notes

Ectophylla and *Mesophylla* have sometimes been regarded as forming a monophyletic group, perhaps even congeneric (e.g., Wetterer *et al*., 2000). However in the molecular trees of Baker *et al*. (2000, 2003) and Hoofer and Baker (2006), *Ectophylla* stands as a well-defined independent lineage, separate from the remainder of the small fruit-eating bats including *Mesophylla*.

Comments

This taxon was originally proposed by Wetterer *et al*. (2000: 140) to describe a large clade including the genera *Artibeus*, *Chiroderma*, *Dermanura*, *Ectophylla*, *Enchisthenes*, *Koopmania*, *Mesophylla*, *Platyrrhinus*, *Uroderma*, *Vampyressa*, and *Vampyrodes*. As originally proposed by Wetterer *et al*. (2000) it was an unavailable taxon name, lacking indication of a type genus and a clear statement of its distinction from other similarly ranked taxa. In the restricted sense of Baker *et al*. (2003), this subtribe only includes *Ectophylla*, with the other genera split in three subtribes: Artibeina, Enchisthenina, and Vampyressina. However, Baker *et al*. (2003) also did not include information required by the Code (ICZN, 1999) to make it an available name. These deficiencies are addressed in this account.

Included extant genera (and species)

Ectophylla (1 sp.).

8. Subtribe Artibeina H. Allen, 1898: 269

Type genus

Artibeus Leach 1821.

Definition

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

Molecular diagnosis

Support for Artibeina is provided by 14 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Artibeina	14 unique substitutions (apomorphies)
4 synapomorphies in the nDNA sequence	33 T→G; 435 A→G; 469 T→G; 1161 A→C
10 synapomorphies in the mtDNA sequences	1644 T→C; 1666 C→T; 1710 A→G; 1936 A→G; 2199 T→C; 2368 T→C; 2418 A→G; 2491 T→C; 2506 T→A; 2964 A→C

Phylogenetic notes

Species of *Artibeus* and *Dermanura* have five pairs of biarmed chromosomes that are homologous with pairs found in *Macrotus* (Baker *et al*., 1979). These biarmed homologous pairs are thought to be primitive for the family (Patton, 1976).

Comments

H. Allen (1898*b*) definition of Artibeini listed *Artibeus*, *Dermanura*, *Sturnira*, and *Uroderma* (p. 269), but the last genus is not ever mentioned again in the text. Owen (1987:62) used Artibeina as a tribe to include *Vampyressa*, *Mesophylla*, *Chiroderma*, *Vampyrodes*, *Vampyrops* (= *Platyrrhinus*), and the nominotypical subtribe [p. 63] Artibeini, including *Artibeus*, *Ectophylla*, and *Uroderma*. As with other names proposed by Owen (1987) in Appendix IV, the same author (p. 33) recommended not following the recommendations in that appendix. Our definition is more restricted and includes only one genera with two subgenera (Simmons, 2005), sometimes considered distinct and valid genera (Hoofer *et al*., 2008; Solari *et al*., 2009).

Included extant genera (and species)

Artibeus (23 spp.; the subgenus *Dermanura* includes 11 spp.).

9. Subtribe Stenodermatina Gervais, 1856: 32n

Type genus

Stenoderma E. Geoffroy 1818.

Definition

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

Molecular diagnosis

Support for Stenodermatina is provided by 20 molecular synapomorphies (below) in the aligned dataset (TreeBASE project TB2:S15071) of the nuclear RAG2 gene, as well as the mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes.

Stenodermatina	20 unique substitutions (apomorphies)
6 synapomorphies in the nDNA sequence	72 T→C; 279 A→G; 400 A→G; 813 A→G; 835 A→G; 1203 A→C
14 synapomorphies in the mtDNA sequences	1397 C→T; 1542 T→C; 1886 C→A; 2107 T→C; 2314 T→C; 2488 C→T; 2493 G→A; 2494 A→G; 2510 A→G; 2526 T→C; 2540 A→C; 2666 T→C; 2680 A→G; 3075 G→A

Phylogenetic notes

Two genera (*Centurio* and *Sphaeronycteris*) share a karyotype with 2n = 30 and FN = 56 that is thought to be primitive for the subfamily, whereas the other five genera (*Ametrida*, *Ardops*, *Ariteus*, *Phyllops* and *Stenoderma*) have one fewer pair of autosomes and show 2n = 28 and FN = 52 (Greenbaum *et al*., 1975; Gardner, 1977*b*). Additional diagnostic molecular characters (rDNA restriction sites) were presented and discussed by Van Den Bussche (1992).

Comments

Wetterer *et al*. (2000: 140) indicated they were proposing a new subtribe when using Stenodermatina, but this name just represented a new rank for the original name and hence was equivalent to subtribe Stenodermatini as used by Owen (1987). Regardless, the name dates to Gervais (1856). Genera listed by Wetterer *et al*. (2000) as belonging to this group were *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Phyllops*, *Pygoderma*, *Sphaeronycteris*, and *Stenoderma*, which is much like the definition of short-faced bats proposed by other authors including Owen (1987) and Lim (1993). Baker *et al*. (2003) kept the same content, although *Phyllops* was not included in their phylogenetic analyses.

Included genera (and species)

Ametrida (1 sp.), *Ardops* (1 sp.), *Ariteus* (1 sp.), *Centurio* (1 sp.), *Phyllops* (1 sp.), *Pygoderma* (1 sp.), *Sphaeronycteris* (1 sp.), and *Stenoderma* (1 sp.).

Discussion

This contribution and its companion (Cirranello *et al*., 2016) are designed to provide a revised Linnaean classification for the nearly 60 genera in the family Phyllostomidae to serve scientists and others interested in proper communication about the biology, biodiversity, and significance to society of members of this diverse family. Building such a classification sounds deceptively simple; unfortunately, taxonomy of long-studied groups is often more complicated than it seems. Considering that several subfamily, tribe and subtribe taxon-names proposed by us and others were not available due to failure to meet the criteria of the code of the ICZN (1985, 1999), and that some disagreement about phylogenetic relationships still remains, it became obvious that creating a Linnaean classification is not a simple task. Hopefully we have addressed issues so that all names in our proposed classification describe well-supported, demonstrably monophyletic groups that are also fully code compliant.

Genetic data, especially DNA and RNA sequences, have proven to be a powerful tool for documenting monophyletic groups and phylogenetic relatedness. While these data can provide a diagnosis, currently such a diagnosis is code-compliant for a Linnaean classification only when it is clearly documented as we have done above. Although data sets from different species and specimens and using different alignment and computational methods can produce different alignments and trees resulting in potentially different synapomorphies, tools (such as TreeBASE) now exist that help document original alignments, trees, and thus, synapomorphies. However, as next-generation sequencing produces datasets comprising several billion base pairs, SNPs, or other motifs per taxon, describing diagnostic data using text descriptions may prove difficult or impossible. If bioinformatic descriptions of datasets typical of current next-generation sequencing methods (which cannot be understood without the aid of computer algorithms) are to be used in description and definition of Linnaean taxa (Fischman, 1996; Grace, 1997; Baker *et al*., 1998), some code rule changes will be necessary. In the meantime, the descriptions of diagnostic sequence traits that we provide here attempt to accommodate this problem.

In our proposed classification of subfamilies, we recognize eleven clades as subfamilies defined by genetic data which, by large, are also supported by karyotypic (this paper) and/or morphological data (Cirranello *et al*., 2016). This classification provides

a framework for interpretation of the exceptional morphological and ecological diversity within this family, and hence to better understand the mode and tempo of evolution that resulted in this unique biodiversity (Baker *et al*., 2012; Dávalos *et al*., 2012; Rojas *et al*., In press). Although each has their own limitations, a synthesis of the strengths of the morphological, karyotypic, and genetic data validates our proposed classification for future studies. Viewed in the context of monophyletic assemblages, the origin and divergence of species traits (be they anatomical, behavioral, biochemical, genetic, or physiological) related to nectarivory or sanguivory, sensory systems, or social systems can be better understood (Datzmann *et al*., 2010; Rojas *et al*., 2011; Baker *et al*., 2012; Dumont *et al*., 2012; Dávalos *et al*., 2014). The exceptional genetic biodiversity in this family and the rapidly developing field of genomics holds considerable promise to understand the genetics basis for evolution of adaptive radiation. For example, Phillips and Baker (2015) leveraged knowledge of phyllostomid phylogeny to understand evolution of vampire bat salivary glands.

An additional aspect of this work was the extent of applications of karyotypic data to identify synapomorphies for several proposed taxa. Cytogenetic data have been used in *Drosophila* to define taxa and relatedness (Lemeunier and Ashburner, 1976; Carson and Yoon, 1982) and "the cytological criterion as the primary factor in determining phylogenetic relationships indeed has led to changes in the classification of some species in some taxa" (Wasserman, 1982: 65). The power of karyology in *Drosophila* is greatly enhanced by the unique polythene chromosomal maps that permit determination of homology across distant taxa (Carson *et al*., 1992). It is possible today to show homology across all mammalian families and even orders (Telenius *et al*., 1992; Ferguson-Smith and Trifonov 2007). However, no such resolution of homology for chromosomes across distant taxa was possible until the development of techniques such as chromosome painting (Sotero-Caio *et al*., 2015). We conclude that the use of chromosome paints and in situ hybridizations will prove to be a powerful tool to identify unique chromosome rearrangements associated with diversification events at various places in a complicated phylogenetic tree, such as the one presented in Fig. 2 for phyllostomid bats.

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