REVISIONARY SYSTEMATICS AND PHYLOGENY OF VAMPYRESSA AND STENODERMATINAE (CHIROPTERA: PHYLLOSTOMIDAE)

by

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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ABSTRACT

REVISIONARY SYSTEMATICS AND PHYLOGENY OF VAMPYRESSA AND STENODERMATINAE (CHIROPTERA: PHYLLOSTOMIDAE)

by

Valéria da Cunha Tavares

Advisor: Dr. Nancy B. Simmons, Ph.D.

Vampyressa are delicate yellow-eared fruit bats widely distributed in the Neotropical region but rare locally. This dissertation contains a comprehensive phylogenetic reappraisal of this genus, in light of a robust hypothesis of evolutionary relationships for Stenodermatinae (Chiroptera: Phyllostomidae) - one of the most morphologically diverse subfamily of Neotropical frugivorous bats. Data from diverse morphological systems, a nuclear (RAG 2) and a mitochondrial (cytochrome b) gene were gathered for at least one species of each genus of Stenodermatinae to provide a robust total evidence analysis of the subfamily. Data generated were used to test alternative hypotheses of ingroup relationships within stenodermatines and generic rearrangements for Vampyressa s.l. and related genera.

The morphological character set included 181 new out of 300 characters and encompassed data from the pelage, vibrissae and papillae, patagium, skull morphology, postcranial morphology, hyoid apparatus, tongue, digestive and reproductive tract. Detailed descriptions were provided to each character, with demarcation of different states observed and ordering hypotheses for multistate characters, when applied. A total of 2083 characters in combination were analyzed with cladistic parsimony methods. Subsets of data were also examined separately, as follows: craniodental data; all morphology; Cytochrome b; RAG2; Cytochrome b plus RAG 2 combined.

Analyses of all characters resulted in a clearly paraphyletic Vampyressa s.l., which was divided into two clades: one encompassing Vampyressa bidens, V. brocki and V. nymphaea + Chiroderma and the other consisting of Vampyressa melissa, V. pusilla, and V. thyone. A clade consisting of Vampyressa bidens, V. brocki, and V. nymphaea was well supported, and a clade comprising V. brocki and V. nymphaea received strong support.

Analyses of separated sets of characters generally did not contradict the all-characters trees overall with the exception of relationships between Mesophylla and Ectophylla that formed a clade according to the morphological data. Morphology disagreed with the total evidence analysis concerning to the relationships between those taxa and Vampyressa, but were generally concordant concerning to other relationships.

A complete diagnosis is provided for taxa split from Vampyressa (s.l.), namely Metavampyressa and Vampyriscus, on the basis of shared ancestry and unique characters. Ectophylla and Mesophylla were considered full distinct genera as each of these two genera had a set of unique combinations of characters justifying the retention of generic status. The designation of tribes to reflect the principal clades recovered within stenodermatines is suggested.

[flor]

To my mother, “coauthor”, and dearest friend, Ízide.

To my daughter and dearest inspiration, Sofia.

^v^

***El sueño de la razón produce monstros*.**

Goya

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This is the most important part of this work.

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restricted to the proximal spear (character 62), the swollen region around eyes (character 86), and the outgrowth behind the noseleaf (character 87). Picture is a courtesy of Jesus Molinari; (B) Ametrida centurio, from Rio Madeira, AM, Brazil, showing the fur in the internal ear pinna (character 12), the three vibrissae surrounding the noseleaf (character 38) and their respective vibrissal papilla forming flesh skin flaps (character 40), the hairless lip region (character 3), the white spots in the neck (character 14), the shallow folds separating the edges of the spear from the central rib of the noseleaf (character 62), the virtually unicolored noseleaf (character 65), and the roughly regularly toothed lateral edge of the tragus (character 55). Picture is a courtesy of Paulo Bobrowieck; (C) Mesophylla macconnelli, from Rio Madeira, AM, Brazil, showing the rudimentary white spots in its face (character 5), the pale body coloration overall (character 16), the bright uniformly yellow-colored ear pinna and noseleaf (characters 47, 65 and 66). Picture is a courtesy of Paulo E. D. Bobrowieck; (D) Chiroderma villosum, from Porto Trombetas, PA, northern Brazil, showing the broad-ovate shape of the noseleaf lancet (character 61), the deep folds of the lateral edges of the spear separating them from the central rib (character 62), the noseleaf with indistinctive gradations of color (characters 65) but overall dull-colored (character 66). Picture by Valéria C. Tavares; (E, F) Vampyressa bidens (=Vampyriscus bidens) from eastern, Pará, Brazil, showing the pair of facial white stripes of similar breadth (character 6), bright white (character 7), dorsal facial white stripes that run all the way in parallel (character 8), the

Appendix

Introduction

Phyllostomidae is the largest family of Neotropical bats, with more than 140 species currently recognized (Koopman, 1993; Simmons, 2005). Phyllostomids are extraordinarily diverse, exhibiting the greatest diversity of feeding habits within the order Chiroptera. Evolutionary relationships of the family Phyllostomidae have been extensively discussed in the literature (e.g. Honeycutt and Sarich, 1987; Baker et al., 1989; Van Den Bussche, 1992; 1993; Van Den Bussche et al., 1993; 1998; Wetterer et al., 2000; Baker et al., 2000; 2003) but many relationships within subfamilies and at lower hierarchical levels remain unresolved and controversial. While a considerable number of studies have focused on the evolutionary interrelationships under a cladistic framework of certain subfamilies of phylostomids, such as of nectarivorous bats (e.g. Griffiths, 1982; Haiduk and Baker, 1982; Smith and Hood, 1984; Carstens et al., 2002; Dávalos and Jansa, 2004) others have been focus of fewer studies, such as the subfamily Stenodermatinae (e.g. Owen, 1987; Lim, 1993).

There have been few attempts in the literature at a phylogenetic analysis focusing at stenodermatine bats. Some proposed phylogenies previous to 1990's have used comparative approaches and described relationships not based explicitly on principles of shared ancestry of characters (e.g. Baker, 1973; Smith, 1976; Gardner, 1977a; Owen, 1987; Lim, 1993). Lim (1993) conducted the first strictly explicit phylogenetic analysis focused in the stenodermatines along with a critique of what he pointed out to be the "only (…) attempt at a phylogenetic analysis of all stenodermatine bats" (Lim, 1993: 147, referring to the work of

Owen, 1987). However, as discussed in Lim (1993), the methods used in Owen (1987) to identify a preferred tree were incompletely compatible with true cladistic methods as they incorporated analyses of continuous data (not at that time effectively implemented in phylogenetic algorithms), and used a compromise method (Adam's consensus) that may favor a choice of relationships not found in any of original trees.

After Lim's (1993) study, the most significant analysis including stenodermatines was the comprehensive morphological analysis of phyllostomid relationships by Wetterer et al. (2000). A series of molecular analyses including stenodermatines have been carried out in the last decade (e.g. Baker et al., 2000; 2003; Hoofer and Baker, 2006) allowing new tests of data robustness and support for particular resulting relationships. However none of these analyses included all genera of stenodermatines, which were not the focus of those studies.

Stenodermatines have traditionally been separated into two groups, one consisting of Sturnira and the other comprising the remaining genera, with Sturnira species considered to forming either a tribe (Sturnirini, e.g. in Koopman and Jones, 1970; Koopman, 1993; Wetterer et al., 2000) or a subtribe (McKenna and Bell, 1997). Historically a cohesive assemblage (e.g. Miller, 1907; Baker et al., 1989), "non-sturnirine stenodermatines" have been more finely split taxonomically into clades reflecting phylogenetic relationships only recently (e.g. Wetterer et al., 2000; Baker et al., 2003; Simmons, 2005).

The tribe Stenodermatini (non-sturnirine stenodermatines) was recently recognized and split into subtribes Ectophylina and Stenodermatina based on morphological and restriction site data by Wetterer et al., 2000, a change adopted by Simmons (2005). Stenodermatina species (sensu Wetterer et al., 2000, and Simmons, 2005: Ametrida, Ardops, Ariteus, Centurio, Phyllops, Pygoderma, Sphaeronycteris and Stenoderma) commonly known as “short-faced bats”, have long been identified as sharing many derived characters (e.g. de La Torre, 1961; Gardner, 1977a; Greenbaum et al., 1975; Lim, 1993; Wetterer et al., 2000; Tavares and Simmons, 2000; Baker et al., 2003; Dávalos, 2007) but the remaining stenodermatine bats formed a less well-supported group. This putative clade - the “long-faced” bats) - consists of a large assemblage of species with unclear evolutionary interrelationships.

“Long-faced stenodermatines” include Artibeus, Chiroderma, Ectophylla, Mesophylla, Metavampyressa, Platyrrhinus, Uroderma, Vampyressa, Vampyriscus, and Vampyrodes, a group found to be monophyletic by Wetterer et al. (2000), who named the subtribe Ectophyllina to accommodate them taxonomically. In an alternative taxonomic arrangement based on the results of molecular analyses (mtDNA 12s, rRNA, tRNAVal, 16s rRNA and RAG2), Baker et al. (2003) suggested the name Vampyressina to identify a clade with the genera Chiroderma, Vampyriscus, Uroderma, Vampyressa, Mesophylla, Vampyrodes and Platyrrhinus. In the analyses of Baker et al. (2003) the new name Mesostenodermatini was also suggested to accommodate several subtribes: Ectophylina (rearranged in relation to Wetterer’s et al. 2000 definition to contain only Ectophylla), Enchisthenina (exclusive for Enchisthenes), and Artibeina (Artibeus and Dermanura).

Problems in the resolution of relationships among a few terminal taxa (e.g. Vampyressa, Mesophylla, Ectophylla, Enchisthenes) clearly affect the understanding of the evolutionary patterns in the broad context of stenodermatines. No analysis to date has combined a robust set of characters from diverse systems coded for all genera of stenodermatines. This has impaired the understanding of the evolutionary history of the clade because stenodermatines are so diverse anatomically that many characters become autapomorphic when taxonomic sampling is incomplete. Therefore, the analysis of subsets of taxa within stenodermatines apart from others may result in recovery of superficial relationships. Ectophylla, a taxon with many autapomorphic characters, seems the best example to illustrate this situation. Among stenodermatines, no relationships have been more obscure than those of Ectophylla, Mesophylla, and Vampyressa.

The monophyly of Vampyressa (sensu Simmons, 2005) and relationships with those two genera (Mesophylla and Ectophylla) has long been questioned based on karyotypic and morphological data (e.g. Thomas, 1909; Starret and Caseber, 1968; Baker, 1973; Owen, 1987). Only recently has the monophyly of Vampyressa been tested in an explicitly phylogenetic framework using morphological (Lim, 1993; Wetterer et al., 2000) or molecular data (Baker et al., 2003; Porter and Baker, 2004; Hoofer and Baker, 2006).

The first strong evidence from an explicit phylogenetic analysis to challenge the monophyly of Vampyressa came from the morphological study of Wetterer et al., (2000). However, this analysis examined the phylogenetic relationships of only three species, (Vampyressa bidens, V. nymphaea and V. pusilla) in the broad context of a study of phyllostomid relationships. No comprehensive morphological phylogenetic test of Vampyressa is available, and the conclusions on the evolution of this complex based on morphology were a by-product of broader analyses not focusing in the clades involving Vampyressa and allies, and hence lacked many fine-grained characters potentially relevant to interrelationships in this complex.

As in the case of the study of Wetterer et al. (2000) the analyses of Porter and Baker (2004) did not include all Vampyressa species, but it shed the first molecular light demonstrating paraphyly of the genus based on cytochrome-b data. Based on their data, Porter and Baker (2004) suggested the recognition of Vampyriscus (Vampyriscus bidens, V. brocki, and V. nymphaea) as a distinct genus apart from Vampyressa, a result later corroborated by the molecular analyses of Hoofer and Baker (2006), who examined all taxa included in "Vampyressa" (sensu Simmons, 2005).

In summary, the recent advances of molecular studies toward resolving interrelationships within Vampyressa (sensu Simmons, 2005) and its allies (e.g. Baker et al. 2000, Baker et al., 2003, Porter and Baker, 2004, Hoofer and Baker, 2006) were not tested under a comprehensive phylogeny of morphological characters and were never tested with the framework of a combined analysis. To accomplish this test is one of the main focuses of this contribution.

In this study, I perform separated and combined analyses (molecular and morphological data) of the phylogeny of stenodermatines with all extant genera currently known included and subgenera, in the case of Artibeus and Vampyressa (s.l.). For Vampyressa I included all currently recognized species. Data consisted of several sets of characters combined from molecular and morphological sources, attempting to reach a consensus about stenodermatine interrelationships based in robust evidence from different character systems.

Historical background: a summary for the Stenodermatinae

As Wetterer et al. (2000) already provided a complete history of proposed relationships of phyllostomid bats I will refrain to repeat it here. I however summarize here the most influential studies focusing on the history of stenodermatine relationships beginning with Miller's (1907) benchmark compendium on bat taxonomy.

Many suggestions about relationships within stenodermatines and other related taxa have arisen over the past century, including different ideas about the composition of the subfamily.

Miller (1907) included Brachyphilla along with the taxa now included in Stenoderminae, and placed Sturnira in Sturnirinae.

De la Torre (1961) suggested sister relationships of Chiroderma, Vampyriscus (= Vampyressa bidens) and Mesophylla. Peterson (1968) considered V. pusilla and V. melissa as distinct lines of evolution separate from that leading to V. brocki, V. nymphaea, and V. bidens, all of them related to Ectophylla. On the other hand, Starret and Caseber (1968) suggested a close relation between V. pusilla and M. macconnelli based on morphological characters.

Slaughter (1970) recognized a lineage consisting of Vampyrops (= Platyrrhinus), Chiroderma, and Ectophylla and another lineage composed of Uroderma, Stenoderma, Artibeus and Centurio within Stenodermatinae. Slaughter (1970) suggested a possible progressive line from the less derived (Platyrrhinus) to the “more derived” taxa (Ectophylla). Sturnira, along with

Brachyphylla (today placed into its own subfamily), were identified by Slaughter (1970) as the most dentally primitive stenodermatines.

Baker (1973) split stenodermatines into three groups based on morphology of the Y chromosome, and recognized four lineages within Stenodermatinae based on these data plus morphology: (1) Uroderma species; (2) short-faced Ametrida, Centurio, Stenoderma, and Sphaeronycteris (plus Ardops, Ariteus, Phyllops and Pygoderma based on morphological similarity); (3) Enchisthenes; (4) Chiroderma, Mesophylla, Vampyressa plus Ectophylla, the latter inferred based on morphological similarity.

Greenbaum et al. (1975) corroborated Baker's (1973) decision to include Ardops, Ariteus and Phyllops within a "short-faced" lineage based on his study of the karyotypes of those species, and suggested closer affinities between the Antillean species than between them and continental species of short-faced bats. On the other hand, contradicting Baker's (1973) predictions, Greenbaum et al. (1975) described the karyotype of Ectophylla, which was missing from Baker's (1973) study, and reported no support for the previously suggested associations between Mesophylla and Ectophylla. Greenbaum et al. (1975) also suggested associations of Chiroderma to Mesophylla and Vampyressa based on his karyological study.

Smith (1976), based on a somewhat idiosyncratic interpretation of previous studies and data sources, recognized a large clade consisting of Chiroderma, Ectophylla, Mesophylla, Sturnira, Uroderma, Vampyressa, Vampyrodes, and Platyrrhinus and another large clade composed of short-faced bat species Ardops, Ariteus, Phyllops, and Stenoderma, which in turn had a clade formed by Artibeus and Enchisthenes as its sister taxon. From the Smith's (1976) perspective therefore Artibeus and Enchisthenes were part of the "short-faced" group.

Gardner (1977a) discussed relationships of stenodermatines within a broader perspective of phyllostomid relationships, largely based on inferences from chromosomal data. Gardner (1977a) left the position of Sturnira and Uroderma unresolved. Chiroderma, Mesophylla, and Vampyressa (s.l.) formed a clade, and the latter two genera were sister taxa. Artibeus and Enchisthenes formed a clade that nested together in an unresolved politomy with Ectophylla, Vampyrodes, and Vampyrops. The short-faced stenodermatines Ametrida (continental), Ardops, Ariteus, and Phyllops (Antillean) formed a clade, and Centurio and Sphaeronycteris another one; Stenoderma and Pygoderma had uncertain position among the short-faced bats.

Owen (1987, see fig. 1A) incorporated analyses of continuous and discrete craniodental data, and used Adam's consensus techniques to reach conclusions regarding stenodermatine relationships. Among the most contentious conclusions of Owen (1987, see fig. 1A) were the suggestions that Mesophylla should be considered congeneric with Vampyressa and that Artibeus was not monophyletic, and should small Artibeus be placed in Dermanura.

Owen (1991, see fig. 1B) included species of Artibeus (Dermanura), Enchisthenes (= Dermanura hartii, Artibeus hartii) and all short-faced stenodermatines in a study designed to elucidate relationships among these taxa. Owen (1991, see fig. 1B) recommended recognizing Enchisthenes as a distinct genus, and named a new genus, Koopmania, for "Dermanura concolor" (= Artibeus concolor).

Lim (1993, see fig. 1C) revised the characters described by Owen (1987; 1991, see figs. A and B), included new characters, and reviewed with criticism the methods of analysis used and conclusions made by Owen (1987, see fig. 1). Overall Lim (1993, fig. 1C) recovered two large clades within stenodermatines, one encompassing all short-faced genera (subtribe Stenodermatina, Wetterer et al., 2000; Simmons, 2005) and the other with Sturnira and the remaining stenodermatines.

Van Den Bussche (1991, see fig. 2A) mapped restriction-site data from rDNA for phyllostomids on trees proposed in the studies of Smith (1976) and Baker et al. (1989) striving to better resolve relationships among genera. Restriction site information supported better the topological hypothesis of Baker et al. (1989) than Smith's (1976). Restriction-site data (Van Den Bussche, 1991, see fig. 2A) provided evidence for the monophyly of short-faced bats (subtribe Stenodermatina, Wetterer et al., 2000; Simmons, 2005) and supported a clade formed by Uroderma, Vampyrodes, and Platyrrhinus yet relationships within stenodermatines remained largely unresolved.

Van Den Bussche et al. (1993, see fig. 2B) specifically investigated relationships between stenodermatines using partial sequences of the cytochrome b gene and an EcoRI-defined nuclear satellite DNA repeat. According to Van Den Bussche et al.'s (1993, see fig. 2B) analysis, Artibeus, "Dermanura" (currently a subgenus of Artibeus, used to encompass the small-bodied forms of this genus) and Koopmania (= Artibeus concolor) were monophyletic, united by the presence of a DNA repeat satellite and cytochrome b data. On the other hand Enchisthenes, traditionally allied to Artibeus (lato sensu), appeared as sister to Centurio.

Van Den Bussche et al. (1998) conducted a phylogenetic analysis of a subset of stenodermatintes based on the entire cytochrome b gene of several species of Artibeus (s. l.), and found again support for the monophyly of Artibeus (s. l., Simmons, 2005), with Artibeus (Artibeus) and Artibeus (Dermanura) as sister taxa. The recognition of Enchisthenes as a distinct genus separated from Artibeus that had previously been detected by the nuclear DNA repeat (Van Den Bussche et al., 1993, and see fig. 2B) was also corroborated by the results of the cytochrome b analysis.

Gimenez (1993, fig. 1D) used lingual morphology in her analysis of intergeneric relationships among phylostomid bats, and found support for a clade composed of Mesophylla, Vampyressa, and Chiroderma. Three other clades were recovered in Gimenez's (1993) analysis, one with Ametrida and Pygoderma, another with Dermanura, Koopmania, Platyrrhinus, and the sister taxa Artibeus and Uroderma, and finally one with Chiroderma, Mesophylla and Vampyressa.

In their comprehensive study of phylogeny of the family Phyllostomidae, Wetterer et al. (2000, fig. 3A) recovered a monophyletic though poorly supported Stenodermatinae, support for which increased substantially if Sturnira was excluded. Among their noteworthy results, Wetterer et al. (2000, fig. 3A) found support for a clade formed by Mesophylla and Ectophylla, and suggested that these two taxa should be considered congeneric (Ectophylla the senior synonym). Short-faced bats were strongly supported as a clade and Wetterer et al. (2000) suggested that this group should be recognized as a subtribe (Stenodermatina).

Baker et al. (2000) presented a phylogeny based on an analysis of the nuclear RAG2 gene. There were several differences between their tree and Wetterer et al. (2000)'s mostly morphological tree with respect to stenodermatine phylogeny, notably relationships between Vampyressa (s.l.) Mesophylla and Ectophylla. Vampyressa pusilla (included V. thyone at that time) formed a clade with Mesophylla, whereas Ectophylla was shifted to a large clade with Artibeus (lato sensu), Enchisthenes and the short-faced bats (subtribe Stenodermatina). Positions of Ectophylla and Enchisthenes within this clade remained uncertain based on the RAG2 data.

Baker et al. (2003, fig. 3B) subsequently reanalyzed data for RAG 2 together with new data from the mtDNA gene (12S rRNA, tRNA^{Val}, and 16S rRNA) to resolve relationships of phyllostomids. Based on their phylogenetic results, Baker et al. (2003) proposed a novel taxonomic arrangment for the family. Among their main results and taxonomic proposals, Baker et al. (2003) found a clade consisting of Mesophylla, Vampyressa, Chiroderma, Uroderma, Platyrrhinus, and Vampyrodes, for which they proposed the name Vampyressina. Another large clade formed within stenodermatines had a series of successive sister taxa and clades: Enchisthenes, Ectophylla, a clade formed with Artibeus (Artibeus) and Artibeus (Dermanura), a clade formed by short-faced Antillean species Ardops and Ariteus, and then a succession of short-faced taxa.

Three subsequent publications with phylogenetic analyses of molecular data (Porter and Baker, 2003, Lim et al., 2004, and Hoffer and Baker, 2006) focused specifically in the relationships among the “vampyressine” bats as defined in Baker et al., (2003). Porter and Baker (2003) analyzed cyt-b data, and Hoffer and Baker (2006) analyzed ND3–ND4 and cytochrome b combined, and both studies recovered a paraphyletic Vampyressa s.l. suggesting the recognition of Vampyriscus to encompass V. bidens, V. brocki and V. nymphaea, while Vampyressa was restricted to Vampyressa melissa, V. pusilla, and V. thyone. Additionally, these studies as well as that of Lim et al. (2004) provided support for recognition of Vampyressa thyone as a distinct taxon separate from Vampyressa pusilla. However, these studies disagreed concerning the relationships among Vampyressa (s.l.), Ectophylla, and Mesophylla.

There remained several alternatives of studies to be undertaken to better resolve relationships among stenodermatines, particularly in the case of complex relationships such as of Vampyressa, Ectophylla and Mesophylla: (1) to include in a phylogenetic study of Stenodermatinae preferably representatives of all genera of stenodermatines (and subgenera as adequate) as to test monophyly of Ectophyllina/Vampyressina (s. Wetterer et al., 2000, and Baker et al., 2003); (2) to produce a robust set of morphological data with fine-grained characters focused in the description of stenodermatines; and (3) to testing the resolution provided by a robust set of combined molecular + morphology data. Those goals are summarized below:

Goals of this study

This study was designed with the following main goals:

(1) To accomplish a robust multi-system analysis of phylogenetic relationships within Stenodermatinae, including characters from the external morphology, skull, tooth, occlusal patterns, postcranium, soft tissues, hyoid apparatus, nuclear and mitochondrial DNA gene sequences;

(2) to test the monophyly of *Vampyressa* (s. l., Simmons, 2005) and provide a diagnosis of the genus (or the genera within it if paraphyly is demonstrated) and hypotheses of generic rearrangements for *“Vampyressa”* (sensu Simmons, 2005) and allied genera (*e.g.* *Mesophylla*);

(3) to test monophly of several stenodermatine clades previously recovered and named at higher hierarchical levels (*e.g.*, subtribes Ectophyllina as proposed in Wetterer *et al*., 2000; and Vampyressina as proposed in Baker *et al*., 2003.

Materials and Methods

Taxonomic Sampling and Character Scoring

To test the monophyly of proposed subtribes within Stenodermatinae and assess the ingroup relationships of clades within stenodermatine bats, I included one species representative of each currently recognized genus of Stenodermatinae, except in two cases of genera with historically questioned monophyly: Artibeus and Vampyressa (s.l. Simmons, 2005).

In the case of Artibeus, one species of each currently recognized subgenera were treated as separate exemplars. Those were represented by Artibeus (Artibeus) jamaicensis (s.l. Simmons, 2005), Artibeus (Dermanura) cinereus and Artibeus (Koopmania) concolor.

Some authors have suggested the recognition of Vampyriscus to include Vampyressa bidens, V. brocki, and V. nymphaea) apart from Vampyressa, based on recent results from the analysis of molecular data (e.g. Porter and Baker, 2004; Hoofer and Baker, 2006). As the genus limits and definition of Vampyressa are in state of flux (s.l. Simmons, 2005) based on the recent evidences of its paraphyletism (e.g. Wetterer et al., 2000; Porter and Baker, 2004; Hoofer and Baker, 2006), I included every currently recognized species as exemplars.

Finally, several authors have suggested and/or have treated Mesophylla as a junior synonymous of Ectophylla (e.g. Goodwin and Greenhall, 1962; Simmons and Voss, 1998; Wetterer et al., 2000). On the other hand, molecular data appear to support the recognition of Mesophylla and Ectophylla as separate genera (e.g. Baker et al., 2000; Baker et al., 2003; Hoofer and Baker, 2006). For practical purposes, I recognized a priori Mesophylla as a distinct genus from Ectophylla following Simmons (2005) whom considered relationships among those genera as still unclear.

I scored characters for the species selected at species level. The criteria for choice of exemplar species other than the cases for Artibeus and Vampyressa were (1) availability of the species in museum collections (of both preserved specimens and tissues) and (2) availability of RAG and cytochrome-b sequences and/or tissues and, as far as possible, (3) relatively unambiguous taxonomic status. The item (3) aimed to rule out taxa suspected of representing species complexes or undescribed/unrecognized taxa. However, many specimens of Vampyressa (s.l.) proved to be misidentified and/or representative of new, unrecognized taxa. All unrecognized taxa were left aside and will be properly listed and described elsewhere. Table 1 lists the terminal taxa used in this study.

Within limits of specimen availability, I examined from 20 to 300 individuals of each species included (see Appendix 1) totaling over 1599 specimens studied. I examined skins, skulls, skeletons, and alcohol preserved specimens both macroscopically and using a dissecting microscope. Whenever possible I took measurements of a minimum of five individuals per sex for all characters related to proportions although larger series were often studied as they were available. I usually made sketches and notes of my observations. Measurements were made with digital calipers to the nearest 0.01 mm. Characters were documented with a digital camera Nikon 4500 (4 megapixels), a microscope adapter and photo lenses (10x). No character based on proportions was documented using photographs: only discrete observations of specimens.

New characters are identified as such in the end of each character account, in the character descriptions list. In cases that I employed characters used by previous authors, citations are provided listing works in which those characters have been used since they were first framed, and any changes in descriptions, interpretations and/or scorings are discussed. Characters for which I have not added my own observations are also specified in the character descriptions.

Following conventions of most recent morphological studies, the symbol "- " was used in the matrix to indicate cases in which a particular character was not applicable to certain taxa due to the effects of evolution. Missing data (cases in which appropriate specimens or observations were not available) was coded "?" in the data matrix. Both cases (missing and inapplicable) are specified in the character descriptions when applied to particular characters and taxa. The complete data matrices are provided in Appendix 2.

Most of the cases involving polymorphisms were scored and analyzed as composites (e.g. 0/1) but not transformation series (see Mabee and Humphries, 1993; Wiens, 2000, and Simmons and Geisler, 2002 for discussions on how to treat polymorphisms). In few cases polymorphisms were treated as a single state; those are specified in the character descriptions. I ordered multistate characters (e.g. 0⇔1⇔2⇔3) whenever assumptions of homology between states could reflect hypothesis of evolutionary changes in progressive fashion suitable to be described in a series of logically intermediate steps. Ordered characters are specified individually in the character descriptions.

I included autapomorphies for the ingroup taxa as they might be useful in broader analysis as synapomorphies, and because they may serve to help with redefining some taxa that were part of the focus of this study (e.g. Ectophylla, Mesophylla, Artibeus).

Outgroup choice

Multiple outgroups improve the generality of an analysis, providing a test of ingroup monophyly (Nixon and Carpenter, 1993). I used two closely related taxa outside to the stenodermatine clade to provide a partial test of Stenodermatinae monophyly, and a more distantly related phyllostomine taxon to root the tree. Monophyly of the family Phyllostomidae has been agreed and corroborated with substantial evidence by many authors, as has monophyly of Stenodermatinae (e.g. Wetterer et al. 2000, Baker et al., 2000 and references cited therein). The outgroup taxa chosen were Carollia brevicauda and Rhinophylla pumillio, (Carolliinae) and Phyllostomus hastatus (Phyllostomidae). All analysis were run with unconstrained outgroup and ingroup, and therefore outgroup taxa served to testing ingroup monophyly.

My efforts were concentrated in characters focusing in the ingroup taxa, and there were no systematic attempts to resolve outgroup positions and relationships.

Morphological characters

The utilization of character congruence, i.e., various sources of data, may increase the robustness of phylogenetic analysis (e.g. Kluge and Wolf, 1993; De Queiroz, 1993; De Queiroz et al., 1995). I used data from the pelage, vibrissae and associated papillae, general external morphology, patagium, sexual dimorphism, skull morphology, skull ontogenesis, postcranial morphology and myology, hyoid myology, tongue, digestive and reproductive tract.

Molecular characters

The choice of sequence data for phylogenetic analysis is constrained by the pace of evolution of the gene (which should be neither too fast to be saturated with change, nor too slow to not offering phylogenetic information), and by other sources of “noise”, such as constraints related to functionality that may obscure the phylogenetic signal. Nuclear gene sequences are a very promising source of data for phylogenetic studies, particularly for resolving deep branch relationships, whereas mitochondrial genes have been proved to be highly informative for resolving relationships among closely related species (e.g. Irwin et al., 1991; Smith and Patton, 1991; Van Den Bussche et al., 1998). Nonetheless, nuclear genes have also been recently found to provide resolution at lower taxonomic levels for mammals (e.g. didelphid marsupials, Jansa and Voss, 2000). For the present study I have chosen sequence data of the Recombination-Activating Gene-2, (RAG2), and the mitochondrial cytochrome b. Cytochrome b has been chosen because (1) it appears to bear significant phylogenetic information for inferring lower level phylogenetic relationships within the subfamily Stenodermatine (e.g. Porter and Baker, 2004); (2) it has been relatively well-studied and several sequences for different species are available. The item (2) was the principal reason for choice of RAG2, which has been used to inferring phylogenetic relationships within phyllostomids (Baker et al., 2000; 2003). Both genes (cytb and RAG2) were never studied in combination with morphological data to study stenodermatine relationships.

DNA Sequences

DNA was isolated from liver tissue and was extracted using a Qiagen DNeasy Tissue Extraction Kit (Qiagen, Inc.) following the manufacturer's protocol. DNA extraction and amplification was conducted in three facilities: the Cullman Laboratory for Molecular Systematics, the Molecular Laboratory for invertebrate systematics (currently at the Sackler Institute for Comparative Genomics), both at the American Museum of Natural History (AMNH), New York, NY, and in the Laboratório de Biodiversidade e Evolução Molecular (LBEM) in the Federal University of Minas Gerais (UFMG), Brazil.

Extracted DNA was used as a template in PCR reactions with primers described by Dávalos and Jansa (2004) and Porter and Baker (2004), for cytochrome b; for RAG-2 amplification I overall followed the procedures described by Baker et al. (2000). Initial amplifications using genomic DNA as a template were performed as standard 25 or 35 L reactions using Hotstart Taq polymerase (Qiagen) and recommended concentrations of primers, unincorporated nucleotides, buffer, and MgCl2. Reactions were performed on a Perkin-Elmer 9700 Thermal Cycler using 37 cycles of the following conditions: denaturation at 95º for 20 sec; annealing at 50-55º for 15 sec; extension at 72º for 1 min. All amplifications were preceded by a 95º soak for 15 min and followed by a 7-min extension at 72º. Reamplifications were only performed on DNA extracted from liver tissue.

For reamplifications, PCR products were purified via electrophoresis through a 2% low melting-point agarose gel (NuSieve GTG, FMC). The appropriate size band was excised from the gel using a Pasteur pipette, and the gel plug was melted in 300 L sterile water at 73º for 20 min. The resulting gel-purified product was used as a template in 30 or 40 L reamplification reactions with Ampli-Taq polymerase (Promega). Reactions were subjected to 35 PCR cycles using annealing temperatures of 52-55º. PCR products were prepared for sequencing using a Qiagen BioRobot 3000 or manual cleaning, and were sequenced in both directions using amplification primers and dye-terminator chemistry (dRhodamine Ready Reaction Kit, Applied Biosystems, Inc.). Sequencing reactions were purified through an MgCl2-ethanol precipitation protocol and run on an ABI 3100 automated sequencer.

Sequence editing and matrix preparation

Sequences were edited using Sequencher 4.1 software (GeneCodes, Corp.). Base-calling ambiguities between strands were resolved by choosing the call on the cleanest strand.

A total of 33 new sequences of cytb, and 12 new sequences of RAG2 were generated as part of this study and will be deposited in GenBank. As far as possible, one complete sequence of each gene (RAG2 and cytb) was randomly chosen, when there was more than one sequence complete for a same terminal taxon) among those produced in the present study and that downloaded from genbank, to be incorporated in the matrix.

The list of selected sequences that entered the matrixes is given by their accession numbers (genbank) or tissue voucher numbers, in the table 2.

Phylogenetic Methods

Maximum Parsimony as implemented in PAUP* 4.0B10 (Swofford, 2002) was used to analyze both all characters combined (= total evidence analysis) and subsets. The analyses of partitions and of the entire matrix served to distinct objectives.

The analyses of separate data partitions and comparisons of resulting trees to look for congruent patterns have been called “taxonomic congruence”, a approach that was highly criticized in the early’s 1990 (e.g. Klugle and Wolf, 1993). Alternatively, “character congruence”, or “total evidence” is the combination of all available data in a single matrix, an approach deemed to produce more parsimonious explanation for the data, overcome noise, and be theoretically more robust (e.g. Myiamoto and Fitch, 1995, Kluge, 1989, but see Barret et al., 1991).

As argued by Wetterer et al. (2000), taxonomic congruence often involves an artificial division of data, particularly in the case of morphological systems. In agreement to these authors, I took the “total evidence” or “character congruence” approach as the best hypothesis about phylogenetic relationships, but nevertheless ran partitioned analyses to explore the phylogenetic signal and to analise patterns of convergence within subsets of the data.

In summary I partitioned data into subsets to be able to (1) determine how much disagreement may exist among subsets of characters (2) compare the present results with other formerly presented by authors that used similar datasets, and consequently facilitate comparisons with preceding studies (3) to evaluate the evolutionary responses provided through the analysis of particular systems in separate and the levels of resolution to stenodermatine phylogeny provided by them and (4) to observe if the greater resolution in certain parts of the trees of particular partitions may be verified in the trees resulting from more than one partition and principally in the total evidence tree.

Subsets of the total evidence matrix were therefore examined separately, as follows: (1) craniodental data only (2) all morphological data (3) Cytochrome b data only (4) RAG2 data only (5) Cytochrome b plus RAG 2 combined. The single subset of morphological characters analysed in separate - craniodental - was taken apart from the total of morphological characters to be compared with a recent hypothesis of phylogenetic relationships focusing in the same morphological systems (skull and tooth), which was the phylogeny of phyllostomids by Wetterer et al. (2000, see fig. 3A).

I conducted all Maximum Parsimony (MP) analyses using the heuristic search algorithm implemented in PAUP* 4.0B10 (Swofford, 2002). Each search was conducted with 1000 iterations of the heuristic search algorithm with random taxon addition and TBR branch swapping. I set PAUP commands for saving all the trees found in each random addition sequence replicate in one file, and then set for filtering for the best trees overall saving them in a separate file. All characters were equally weighted in all analyses. I used both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) to optimize characters.

I calculated Bremer support values (Bremer, 1988) for the total evidence tree using MacClade 4.08 (Maddison and Maddison, 2005) and PAUP* 4.0B10 (Swofford, 2002). I calculated Bootstrap values (Felsenstein, 1985) for each data partition and for the entire matrix with 1,000 pseudoreplicates using a heuristic search with 20 random additions, TBR branch swapping, and a maximum of 200 trees retained in each random addition replicate.

All analyses were performed with a priori unrooted trees and no outgroup designation and the trees were subsequently rooted after designation of outgroup as suggested in Nixon and Carpenter (1993).

Institutional Abreviations

The institutional abbreviations listed below are used in the text. **AMNH,** American Museum of Natural History, New York, New York, USA; **BMNH,** The Natural History Museum, London, United Kingdom; **DZSJRP**, Departamento de Zoologia e Botânica da Universidade Estadual Paulista, São José do Rio Preto, SP; **FMNH,** Field Museum, Chicago, Illinois, USA; **IAVH**, Instituto Alexander von Humboldt, Villa de Leyva, Colombia; **ICN**, Instituto de Ciencias Naturales, Bogotá, Colombia; **INPA**, Instituto de Pesquisas da Amazônia, Manaus, Amazonas, Brasil; **MUSM,** Museo de la Universidad San Marcos, Lima, Peru; **MVZ**, Museum of Vertebrate Zoology, Berkeley, California; **MZUSP**, Museu de Zoologia da Universidade de São Paulo; **RM**, Rijksmuseum van Natuurlikje Historie, Leiden, Holand; **ROM**, Royal Ontario Museum, Ontario, Canada; **UFMG**, Laboratório de Mastozoologia da Universidade Federal de Minas Gerais/UFMG, Belo Horizonte, MG; **MCN**, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais/PUC-MG, Belo Horizonte, MG; **MZ**, Museu de Zoologia, curso de Mestrado da Pontifícia Universidade Católica de Minas Gerais/PUC-MG, Belo Horizonte, MG; **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor, Michigan; **UNIVALLE**, Museo de la Universidad del Valle, Cali, Colombia; **USNM,** National Museum of Natural History (Smithsonian), Washington, DC, USA.

Character descriptions

The morphological characters and the character states used in this analysis are described below, split into broad categories (e.g. external morphology, tooth morphology) and smaller sets (e.g. respectively, pelage, premolars) for ease of presentation. As far as possible, characters are listed starting with those best observed in dorsal view, then in ventral view, and from anterior to posterior, rostral to caudad, from medial to lateral, and so on. I assumed that states occur symmetrically in both sides of the body axis hence describing characters in the singular mode unless otherwise indicated (e.g. "the narial opening").

This listing comprises 300 characters describing the morphology of stenodermatines, being 181 newly decribed characters, and several other modified from the descriptions of previous authors, in order to more finely fit to stenodermatines. After descriptions I added other relevant comments when appropriate: (1st) comments on the inapplicability of a characters for particular taxon/a, and/or report on polimorphisms, (2nd) explanations relative to ordering choice and scheme in the case of multistate characters, (3rd) use of the character in previous analyses or not.

Of 300 morphological characters, 91 were described through multistate hypotheses of character evolution, being 47 of those ordered. The 209 remaining characters were binary.

External morphology

Pelage

Character 1: Dorsal pelage differentiation.

Dorsal pelage differentiated into over and under hairs (0), or dorsal pelage uniform (1).

Phyllostomus hastatus, Sturnira lilium, Ardops and Ariteus have thin under hairs and thick dark over hairs. In contrast, the pelage covering the body of Rhinophylla pumilio, Carollia brevicauda, Artibeus cinereus, Ectophylla, and most stenodermatines (e.g. Chiroderma, Vampyressa) is not differentiated into thick and thin hairs.

Benedict (1957) originally described differentiations in texture of the body-covering pelage of bats. Straney (1980) first used it in a component analyzes, and Wetterer et al. (2000) first used it in a phylogenetic analysis. My character states are similar to those described by Wetterer et al. (2000: character 1) as well as is my scoring for the same species analyzed in this and that study, with the exception that I scored Ariteus with (0) while they did not find pelage differentiation in this species.

Character 2: Guard hairs.

Guard hairs absent (0), or long and fine pale hairs, more than three times longer than regular dorsal pelage present on head and dorsum (1).

Phyllostomus hastatus, Carollia brevicauda and most stenodermatines (e.g. Vampyressa thyone), independently of having differentiated dorsal pelage into thick and thin hairs (see character 1) do not have “guard hair” pelage.

"Guard-hairs" (as called in the present study) are very thin and long pale hairs distributed sparsely over the pelage of the head and dorsum of Rhinophylla pumilio and of some stenodermatines (e.g. Chiroderma villosum, Sphaeronycteris. see fig. 4).

Guard-hairs have been previously observed by Timm et al. (1999) for Chiroderma villosum and for C. villosum and Sphaeronycteris (see fig. 4) by J. Molinari (personal communication).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 3: Distribution of facial pelage.

Entire face covered with dense fur including upper and lower lip regions (0), or large areas of face naked in lower lip region (1), or face virtually naked in both, lower and upper lip regions (2), or face virtually naked from forehead to chin (3).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Mesophylla) have densely hairy faces. In contrast, Ariteus and Phyllops falcatus have bare areas in the lower lip region. A third condition occurs in some other stenodermatines (e.g. Ametrida and Pygoderma, and see fig. 4) that have large areas of virtually naked skin covering the upper and lower lip areas. The ventral bare area of these species extends to the base of the chin, and the superior bare area terminates at level of the ventral edge of the horseshoe. Finally, a fourth condition is observed in Centurio and Sphaeronycteris. These two species have large regions of naked skin on their faces encompassing the regions of the lower chin up to the forehead, and including part of the periorbital region (see fig. 4).

I interpreted the conditions seen in Ametrida, Ardops, Ariteus, Phyllops, Pygoderma, and Stenoderma as progressive intermediate forms, and ordered this character 0⇔1⇔2⇔3 to reflect this series of logically intermediate steps.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 4: Distribution of body pelage.

Body uniformly covered with fur (0), or axillary region and upper lateral chest scarcely haired (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Sturnira lilium, Artibeus concolor, and Vampyressa nymphaea), Rhinophylla pumilio, Carollia brevicauda, and Phyllostomus hastatus have their body uniformly covered with fur. In contrast, Ametrida and Pygoderma have scarcely haired skin in the axillary and upper lateral chest region.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 5: Facial stripes.

Facial pelage uniform (0), or facial pelage sometimes disrupted by rudimentary white spots or stripes either anterodorsal or ventromedial (1), or pale colored dorso-medial and ventro-lateral facial stripes always present (2).

The facial pelage is uniform in color and facial stripes are completely absent in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, Sturnira lilium, and Ectophylla. In contrast, in some stenodermatines (e.g. Mesophylla) a pale patch sometimes is present dorsal to the noseleaf and a short ventrolateral stripe is sometimes present, yet the rostrum appears often uniformly colored (fig. 4). A third condition is observed in many stenodermatines that always have well-defined dorso-medial and ventro-lateral facial stripes (e.g. Platyrrhinus helleri and Vampyressa bidens).

The presence of facial stripes in Artibeus concolor and Mesophylla has been subject of disagreement in the literature. Lim (1993) mentioned that live individuals of these species have faint white facial stripes, which is in disagreement with Wetterer et al. (2000). I observed that some individuals of both species, Artibeus concolor and Mesophylla, have their rostra sometimes subtly disrupted by white spots resembling rudimentary white lines (fig. 4) and created an intermediate state for this character. I also scored Chiroderma villosum with state 1, since the facial stripes are not constantly seen in this species and are faint when they appear.

I interpreted the conditions seen in Artibeus concolor, Mesophylla and Chiroderma villosum as intermediate and ordered this character 0⇔1⇔2 to reflect a series of logically intermediate steps in the appearance and development of facial stripes in stenodermatines.

Owen (1987: table 1 and appendix II, character 4) used this character for the first time in a phylogenetic analysis as part of a complex character with observations about pelage color and pattern. Owen (1991: 24, character 8) used facial stripes as a separate character, as did Lim (1993:162, character 1) and Wetterer et al. (2000: 49, character 6).

Character 6: Breadth of facial stripes.

Dorso-medial (= supraorbital) and ventro-lateral (= malar) facial stripes subequal in breadth (0), or dorso-medial facial stripes wider and more than ventro-lateral stripes (1).

Most stenodermatines with facial stripes (see character 5) have dorso-medial and ventro-lateral stripes that are subequal in breadth (e.g. Vampyressa bidens, see fig. 4). In contrast, in Vampyressa brocki, V. melissa and V. nymphaea the dorso-medial facial white stripe appears consistently wider than the ventro-lateral stripe.

Most specimens of V. bidens have subequal dorso-medial and ventro-lateral stripes, but some specimens preserved in fluid (e.g. ROM 521620) have ventro-lateral facial white stripes that are slightly wider than the dorso-medial facial white stripes. It is not clear if this is consistently true in live specimens or is an artifact, so V. bidens was scored with state (0) in this study.

I detected variation in this character for Vampyrodes and scored this taxa 0/1 in the data matrix.

Species lacking facial stripes were scored “-”.

In a phylogenetic analysis of the genus Platyrrhinus, Velazco (2005) erected a character to account for variation in the brightness between facial stripes (Velazco, 2005: 6, character 2). Velazco (2005) found that the majority of Platyrrhinus species had similarly brightened dorso-medial and ventro-lateral facial stripes with the exception of P. vittatus. The nature of the present character is like that of Velazco’s character 2 (2005: 6, character 2) but because of the variation I detected within Vampyressa species, I defined differences between the dorso-medial and ventro-lateral stripes relative to the width of the stripes to describe relative conspicuousness of the two stripes. Overall vividness of both facial stripes (anterodorsal and ventromedial) is treated in character 7.

Character 7: Brightness of facial stripes.

Facial stripes faint (0), or bright, strongly marked (1).

Facial stripes are faint in some stenodermatines (e.g. Vampyressa pusilla). In contrast, facial stripes are bright and conspicuous in several other stenodermatines (e.g. Vampyressa brocki, see fig. 4). I defined conspicuousness of facial stripes based on the vividness of white lines in relation to the background pelage color. In Vampyressa pusilla, for example, the lines tend to be faint and inconspicuous, a pattern that is reinforced since the white stripes by the lack of strong contrast with the generally pale beige pelage of this species. Alternatively, species such as Vampyressa bidens have vivid white stripes, which strongly contrast with their generally darker pelage, independent of differences of pelage tonalities among these species.

Species lacking facial stripes were scored “-”.

A similar character has been used by Velazco (Velazco, 2005: 6, character 2) with the difference that brightness of both dorso-medial and ventro-lateral stripes were treated together, as vividness of these two stripes seems to vary in concert in the taxa in my analysis.

Character 8: Direction of dorso-medial facial stripes.

Paired facial dorsal stripes run roughly parallel with no connection between the stripes at any point (0), or stripes converge anteriorlly to meet behind noseleaf (1).

The paired dorso-medial facial stripes of most stenodermatines with those stripes run roughly parallel and usually do not meet at any point (e.g. Uroderma bilobatum, and Vampyressa bidens, and see fig. 4). In contrast, the paired dorso-medial stripes usually meet at their anteriormost point in Vampyressa brocki and Vampyressa nymphaea (fig. 5).

Species lacking facial stripes were scored “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 9: Posterior end of dorso-medial facial stripe.

Dorso-medial white facial stripe relatively long, extends posteriorly to the level of the posterior insertion of the cone of pinna (0), or stripe relatively short, terminates at the level of antero-medial insertion of the pinna (1).

The posterior end of the dorso-medial facial stripe extends to a variable distance among stenodermatines. This stripe is relatively long and terminates adjacent to the posterior insertion of the cone of the ear pinna in some species (e.g. Platyrrhinus helleri, Vampyressa nymphaea) (see fig. 4). In contrast, the stripe is relatively short in other species, tapering or gradually vanishing at approximately at the level of anterior medial insertion of the pinna (e.g. Vampyressa pusilla).

Species lacking facial stripes were scored “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 10: Anterior tip of ventro-lateral facial stripe.

White ventro-lateral stripe well-defined from posterior end to a point at the level of anterior rim of orbit or posterior to it (0), or to a point anterior to the anterior rim of orbit, usually reaching the corner of the mouth (1).

The ventro-lateral stripe extends to the anterior face, often reaching the corner of the mouth, in many stenodermatines (e.g. Uroderma bilobatum, Vampyressa nymphaea). In contrast, in some stenodermatines the ventro-lateral stripe fades out at the level of anterior rim of orbit or even more posteriorly, and does not approach the corner of the mouth (e.g. Vampyrodes).

Species lacking facial stripes were scored “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 11: Hair in the external pinna.

External ear pinna densely hairy up to a half (0), or pinna with short and dense hair at base and dorsal anterior border of ear pinna (1), or hair restricted to base of pinna (2), or with scarce hairs, almost naked (3).

Some stenodermatines have dense hair covering over the proximal half of the pinna (e.g. Ardops, Vampyressa melissa). In contrast, Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and several stenodermatines (e.g. Vampyressa brocki) have short, dense hair at the base and anterior border of the external ear pinna. A third condition is found in some other species of stenodermatines (e.g. Ectophylla), which have hair restricted to the base of the external ear pinna. Finally, in other stenodermatines (e.g. Centurio) the pinna is virtually naked.

I interpreted the conditions seen in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and several stenodermatines (e.g. Ectophylla) as intermediate and ordered this character 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps in the distribution of hair in the external pinna of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 12: Hair in the internal pinna.

Hair macroscopically inconspicuous on inner surface of ear pinna, not dense, does not contrast with background color of skin of pinna (0), or hair conspicuous, dense, and paler than the background color of skin of pinna (1).

Carollia brevicauda, Rhinophylla pumilio and many stenodermatines (e.g. Vampyressa bidens) have inconspicuous hair in the internal pinna that does not contrast with the background skin color of the pinna. In contrast, in some stenodermatines (e.g. Chiroderma villosum, Vampyressa melissa) the hair on the surface of the internal ear pinna is denser and often of a paler, contrasting in color with the background skin color of the ear (see fig. 4).

In the skins and live individuals of Phyllostomus hastatus that I examined, the hair on the inner surface of the pinna was relatively short and moderately dense, and it was often paler than the background color provided by the skin of the inner pinna. However, this condition appears variable among species of Phyllostomus (e.g. P. latifolius appears to have contrasting hair, but P. discolor appears to have not). It also may vary depending on variation in pelage color of P. hastatus since there is a high spectrum of pelage tonalities in this species (e.g.

see Emmons, 1997). Since mapping this character in phyllostomine bats was beyond my goals in this study, I scored P. hastatus conservatively with (1) pending further examination of this apparently distinct condition.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 13: Shoulder spots in pelage.

Shoulder pelage uniform (0), or orange or brownish spot of hair pelage sometimes conspicuous in the shoulder (1), or white spot, formed by completely white fur, always present in each shoulder (2).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatine bats (e.g. Platyrrhinus helleri, and Vampyressa thyone), the pelage of the shoulder is of a uniform color and has no differently colored spots. In contrast, Sturnira lilium often has a tuft of orange or brownish hairs contrasting with the background shoulder pelage. These shoulder spots, often called “epaulletes,” seem to be formed by glandular secretions and are found only in adult individuals (Davis et al., 1964). Finally, “short-faced” bats (subtribe Stenodermatina, e.g. Ardops, Pygoderma) always have a tuft of completely white hairs in the shoulder.

I scored Ectophylla “-“ as did Wetterer et al. (2000) since this species has shoulders completely covered with white hairs.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Owen (1987: table 1 and appendix II, character 4, 1991: 24, character 9), Lim (1993: 162, character 2), and Wetterer et al. (2000: 51, character 8) used a similar but not identical character previously in phylogenetic analyses to describe the presence of white tufts of fur on the shoulders of short-faced bats (subtribe Stenodermatina). The difference between the present character and the description of shoulder pelage of stenodermatines given by these authors (Owen, 1991, Lim, 1993, Wetterer et al. 2000) is that I erected a separate state to describe the tufts of Sturnira lilium, which differ from those of short-faced bats in being darker in color than the surrounding fur, and in being apparently caused by glandular secretions rather than presence of fur that is intrinsically a radically different color than the surrounding pelage.

Character 14: Neck spots in pelage.

White neck spot absent (0), or sometimes or always present (1).

In most bats including Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and many stenodermatines (e.g. Artibeus jamaicensis), the pelage of the neck is of a uniform color and does not have white spots. In contrast, a white spot is sometimes present in the neck of some stenodermatines (e.g. Ametrida, and Centurio).

I scored Ectophylla "-" as did Wetterer et al. (2000) since this species has a neck completely covered with white hairs.

Wetterer et al. (2000: character 9) first used this character in a phylogenetic analysis. Although the neck spot appears to be always present in some species (e.g. Sphaeronycteris, see fig. 1) it is sometimes present in others (e.g. Ametrida, and Pygoderma). Given to the low number of specimens available in museums of some of these species (e.g. Sphaeronycteris) I decided to conservatively erect a single state accounting for presence lumping "always" with "sometimes" as suggested by Wetterer et al. (2000).

Character 15: Distribution of fur in the forearm.

Forearm virtually hairless in all of its extension (0), or most of dorsal forearm sparsely furred, but hair present and restricted to proximal forearm (1), or forearm partially covered with dense fur which extends distally up to less than one-half the length of the forearm (2), or fur extends distally from one half to two thirds the length of the forearm (3), or forearm mostly hairy, fur covers more than two thirds the length of the forearm (4).

There is scarce, short and fine hair in the forearm of Ectophylla alba, which is virtually hairless. In contrast, Phyllostomus hastatus and Carollia brevicauda have most of the length of their forearms scarcely hairy when compared to most stenodermatine bat species, and the hairs present are restricted to their proximal forearms. A third condition is found in Rhinophylla pumilio and some stenodermatines (e.g. Sturnira lilium), which have fur covering less than a half the length of the forearm, approximately one-third of its extension. A fourth condition, which is found in most stenodermatine bats, is a relatively hairy dorsal forearm with the hair covering approximately the proximal half of the forearm up to two thirds of its length (e.g. Artibeus concolor, Vampyressa bidens). Finally, a fifth condition appears in other stenodermatines, which have a forearm densely covered with hair along most of its length, covering up more than two thirds of its length (e.g. Vampyressa melissa).

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps as observed in the distribution of fur in the forearm of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 16: Overall dorsal fur coloration.

Dorsal pelage is dark brown or dark gray macroscopically (0), or medium brown to dark beige (1), or pale beige, gray or white (2).

Phyllostomus hastatus and Carollia brevicauda have a relatively darker dorsal pelage, either brownish or grayish. In contrast, many medium-sized stenodermatines have a medium brown to beige coloration (e.g. Vampyrodes, and Vampyressa bidens). A third condition may be observed in Rhinophylla pumilio and many stenodermatines that have a paler dorsal pelage beige, gray or completely white (e.g. Mesophylla, Vampyressa thyone, Ectophylla).

I am aware that individuals of Phyllostomus hastatus and Carollia brevicauda may have pelage variation including strong reddish-orange colorations (e.g. Reid, 1997, Emmons, 1997; Paulo E. Bobrowieck, personal communication; V. Tavares, personal observation) and this pattern is treated separately in character 16. I scored P. hastatus and C. brevicauda with (0).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 17: Color variation.

Color of pelage, both upper and underparts, with variants within populations (0), or uniform within populations (1).

Phyllostomus hastatus, Carollia brevicauda and Sturnira lilium populations have variants in terms of pelage, which may be grayish, reddish, yellow-brownish, or cinnamon to orangey. In contrast, most stenodermatines have uniform patterns of pelage across individuals within populations (e.g. Vampyressa brocki, Uroderma bilobatum, Chiroderma villosum).

Color variation within bat populations and the occurrence of molts in some species of molossids, mormoopids, and vespertilionids (respectively Chiroptera: Molossidae, Mormoopidae and Vespertilionidae) was early described by Constantine (1957, 1958), and more recently associated to migration patterns (Cryan et al., 2004). I am not aware of any studies on color variants of stenodermatines, carollines or phyllostomines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 18: Gradations of color in dorsal pelage.

Dorsal pelage color is uniform (0), or neck and the upper back are paler than the lower back (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and many stenodermatines have a dorsal pelage that is uniformily colored from the head to the pelvic region (e.g. Uroderma bilobatum). In contrast, in other species the neck and upper back are paler than the lower back, independent of the overall coloration of pelage (e.g. Ectophylla, which has a white upper back and grayish lower back, Vampyressa thyone, which has light beige, whitish upper back and a beige lower back).

From a macroscopic perspective, the back pelage of Ectophylla is thus alike with the condition I described for V. nymphaea and V. brocki. Platyrrhinus helleri and Uroderma bilobatum were both scored with (0) but some individuals (e.g. P. helleri from Mandinga, Panama, USNM 305376, and U. bilobatum from Jutiapa, Guatemala, AMNH 217405) had a pattern similar to that I described for species with macroscopical gradations of color.

Davis (1975) has first noticed the paler upper parts in females of Vampyressa bidens collected by him near Iquitos, Peru. I found both males and females with this bicolored pattern within my sample.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 19: Dorsal stripe.

Dorsal pelage lacking a white midline stripe (0), or white midline stripe present (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Vampyressa melissa) lack a white midline dorsal stripe. In contrast, a dorsal stripe of variable length and brightness is seen in other species of stenodermatines (e.g. Uroderma bilobatum, Platyrrhinus helleri, Vampyressa brocki).

Although all stenodermatines that have a white dorsal stripe also have facial stripes, the opposite is not true: therefore having a white dorsal stripe is an independent character. The dorsal midline stripe may vary in length and color intensity, and these variations are treated as separate characters below (see characters 20 and 21).

I scored Vampyressa brocki and V. nymphaea as having dorsal stripes although the stripes in these taxa are not as conspicuous as in other Vampyressa (s.l., and see character 20), and in some specimens seems to absent (e.g. USNM 579075, from Isla Popa, Panama) yet traces of it can be observed in all individuals examined for these species. Therefore V. brocki and V. nymphaea always have a white midline stripe in their dorsal pelage. I scored Chiroderma villosum 0/1 because it may present a faint stripe (see character 20) though in most cases it is lacking.

Finally, I scored Ectophylla as having no dorsal stripe. Although it may be argued that Ectophylla is mostly white-haired, it does have a lower back that is often grayish/brownish, which provides a contrasting substrate for a paler line. Additionally, although the dorsal line when present varies in length anteriorly (see character 21), it invariablly extends posteriorly to the pelvic region. Given the pelage pattern in Ectophylla, it seems like that it would show at least a trace of a white line on its lower back if one were present.

Several authors have previously used characters related to the presence/absence and other descriptive aspects of the white dorsal stripes of stenodermatines. Owen (1987) treated variations in facial stripes, patches of fur, and presence of dorsal stripes in a single character, and Wetterer et al. (2000) described those in separate characters.

Character 20: Conspicuousness of the dorsal stripe.

White dorsal stripe bright, contrasts strongly with the background color of pelage (0), or stripe faint, does not contrast strongly with background color of pelage (1).

When a middorsal stripe is present, in most stenodermatines it has a bright white color that contrasts sharply with the background color of the pelage in some stenodermatines (e.g. Platyrrhinus helleri and Uroderma bilobatum). In contrast, Vampyressa nymphaea and V. brocki have a faint dorsal stripe that does not contrast much with the background dorsal pelage. I scored Chiroderma villosum "1" because in the occasions when there appears a midline stripe in its dorsal pelage it is always quite faint.

Species lacking a dorsal stripe were scored "-".

Velazco (2005: 8, character 11) first described a character accounting for the variation in the brightness of the dorsal stripe in his study of Platyrrhinus phylogeny.

Character 21: Anterior extent of dorsal stripe.

Dorsal stripe extends anteriorly to top head, runs between the distal fourth or more of the paired facial dorso-medial stripes (0), or dorsal stripe terminates anteriorly at the base of the head or caudad, does not run between facial dorso-medial stripes or if it does, it is only in a small extension (1), or begins below the base of the neck (2).

In all stenodermatines that have a dorsal stripe it begins posteriorly over the pelvic region. However there are differences in the anterior extent of the dorsal stripe. In Platyrrhinus helleri and Vampyrodes the dorsal stripe extends anteriorly to the top head running parallel and medial to the dorso-medial facial stripes along at least one fourth of the length of the latter. In contrast, the dorsal midback stripe terminates anteriorly at the base of the head but does not extend between the facial stripes, or overlaps only with their posterior tips in Uroderma bilobatum and Vampyressa bidens. In V. bidens the dorsal stripe tends to terminate exactly where the facial stripes begin. Finally, V. brocki and V. nymphaea have the anterior tip of the dorsal stripe largely displaced caudad, located below the base of their neck, often at mid thoracic region. I scored Chiroderma villosum "-" because there is no consistent pattern in the extent of anterior tip of a midback stripe in this species, when it faintly appears.

I found one exception to the general pattern for Vampyressa nymphaea: the specimen UNIVALLE 3827, from the Colombian Chocó had the anterior tip of dorsal line, yet very faintly, terminating just below neck. I also found a skin of Vampyressa nymphaea (USNM 483723, from Rio Zaballetas, Valle del Cauca, Colombia), with a large white spot occupying the lateral right lower back that seemed to be an anomaly perhaps due to cicatrization process.

Species lacking dorsal stripes were scored "-".

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the anterior extent of the dorsal stripe in stenodermatines with dorsal stripes.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 22: Distribution of fur on dorsal propatagium and chiropatagium.

Dorsal propatagium and chiropatagium hairless or only sparsely haired (0), or propatagium and part of the dorsal chiropatagium (a strip adjacent to the body) hairy (1).

The dorsal propatagium and chiropatagium are sparsely haired or hairless in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, and some stenodermatines (e.g. Ectophylla). In contrast, the dorsal propatagium (= antebrachial membrane), and sometimes a stripe of the chiropatagium adjacent to the body are hairy in some stenodermatines (e.g. Vampyressa melissa, and Vampyressa sp. from Bocas del Toro, Panama).

This character may be observed in live individuals and in dry skins with open wings. Unfortunately, skins with open wings are much more rare in collections than skins with folded wings, making it difficult to observe this and other characters describing distribution of fur in the plagiopatagium (see characters below). More variation warranting description may result from the observation of a larger number of individuals and species of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 23: Distribution of fur on ventral propatagium.

Ventral propatagium (= antebrachial membrane) with sparse or inconspicuous fur (0), or with conspicuous, pale fur present (1).

Contrary to the apparently concerted distribution of fur in the dorsal propatagium and chiropatagium (described in character 22, above), the distribution of fur in the ventral propatagium (described in the present character) and in the ventral chiropatagium (described in character 24) seems to vary independently.

Phyllostomus hastatus, Carollia brevicauda and some stenodermatines (e.g. Sturnira lilium) have inconspicuous hair on the ventral propatagium. In contrast, Rhinophylla pumilio and many stenodermatines have a ventral propatagium that is covered with conspicuous pale fur (e.g. Uroderma bilobatum). The fur in part of the ventral plagiopatagium in those species is often dense and of a pale color contrasting against the darker patagium, which provides the impression that the bat with the wings open is larger than it actually is.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 24: Distribution of fur on ventral chiropatagium.

Ventral chiropatagium (= arm wing) with sparse fur (0), or with fur not much contrasting with ventral chiropatagium membrane and distributed in a stripe proximal to the body (1), or with conspicuous fur that is paler than chiropatagium and distributed in a large area of ventral chiropatagium, extending posteriorly up to the level of half of abdomen (2).

The chiropatagium (= arm wing) is the part of plagiopatagium (= wing membrane) enclosed between the lateral body and the fifth metacarpal. The ventral chiropatagium is sparsely furred in Carollia brevicauda, Sturnira lilium, and in some stenodermatines (e.g. Mesophylla). In contrast, the chiropatagium of Rhinophylla pumilio and many stenodermatines is moderately furred in its anterior part (proximal to the forearm) and along a stripe proximal to the body (e.g. Uroderma bilobatum), and the fur does not contrast much against the chiropatagium. A third condition is observed in some other stenodermatines, in which the ventral chiropatagium has paler, conspicuous fur distributed in a large area, extending posteriorly up to the level of a plane passing through half of the length of the abdomen (e.g. Chiroderma villosum) (see fig. 6).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected through the observation of the distribution of fur on ventral chiropatagium of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 25: Distribution of fur on the dorsal uropatagium.

Dorsal uropatagium (= interfemoral membrane) scarcely furred (0), or conspicuously hairy (1).

Phyllostomus hastatus, Carollia brevicauda and many species of stenodermatine bats (e.g. Vampyressa bidens) have a sparsely furred dorsal uropatagium. In contrast, Rhinophylla pumilio, Sturnira lilium and many other stenodermatines (e.g. Chiroderma, Vampyressa melissa) have a hairy dorsal uropatagium.

I have erected separate characters to describe the distribution (this character) and conspicuousness (character 26) of fur in the uropatagium, and the occurrence of a fringe in the trailing edge of uropatagium, which I describe in character 27.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 26: Color of fur on dorsal uropatagium relative to that of the skin of the dorsal uropatagium.

Hair on the dorsal surface of uropatagium contrasts with the color of the skin of the uropatagium (0), or has a similar color to skin of uropatagium, being inconspicuous macroscopically (1).

In Rhinophylla pumilio, Sturnira lilium and some stenodermatines with a hairy tail membrane, the fur is conspicuous and contrasts with the color of the skin of dorsal uropatagium (e.g. Vampyressa melissa). In contrast, in other stenodermatines with a hairy uropatagium (e.g. Platyrrhinus helleri and Vampyrodes) the fur is cryptic, i.e., it does not contrast with the tail membrane and is not conspicuous.

Phyllostomids (stenodermatines and outgroup species) with scarcely furred uropatagia were scored “-“.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 27: Fringe in the distal edge of uropatagium.

No fringe of hair on the distal (trailing) edge of uropatagium (0), or inconspicuous fringe in the medial part of distal edge of uropatagium, generally of the same color of hair distributed in the dorsal uropatagium (1), or distinctive fringe of pale hairs occupying most of the distal edge the uropatagium (2).

No distinctive fringe of hairs is observed in the trailing edge of tail membrane (= uropatagium) of Carollia brevicauda, Rhinophylla pumilio and several stenodermatines (e.g. Chiroderma villosum, Ectophylla, Vampyressa nymphaea). Short-faced bats and Sturnira have an inconspicuous fringe concentrated in the medial distal edge of uropatagium, generally cryptic with a color similar to the fur in the dorsal uropatagium. In contrast, a fringe of short, conspicuous, whitish hairs extends along most of the trailing edge of the tail membrane of Platyrrhinus helleri, Vampyrodes, and Vampyressa melissa).

Lim (1993) and Wetterer et al. (2000) used this character previously in phylogenetic analyses. Wetterer et al. (2000) found many other taxa with fringes in their uropatagium (e.g. Stenodermatina species). According to the present observations, Vampyressa melissa is the only stenodermatine that has both a hairy dorsal surface of uropatagium with conspicuous fur (see character 26) and a distinctive, dense fringe of hairs occupying most of the uropatagium posterior edge.

Character 28: Distribution of fur on the ventral uropatagium.

Ventral uropatagium sparsely furred throughout (0), or with fur concentrated in the medial part (1), or furred throughout (2).

The ventral surface of the uropatagium of Phyllostomus hastatus, Carollia brevicauda, and of many stenodermatines (e.g. Chiroderma villosum, Mesophylla) is only sparsely furred. In contrast, there is hair in the ventral uropatagium of Rhinophylla pumilio and some other stenodermatines concentrated in its medial part (e.g. Vampyressa brocki, V. nymphaea). A third condition is observed in some stenodermatines that have a large surface of the ventral uropatagium that is furred (e.g. Vampyressa melissa).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps perceived through the observation of variation in the distribution of fur in the ventral uropatagium of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 29: Distribution of fur on dorsal surface of foot.

Dorsal surface of foot sparsely furred (0), or covered with fur (1).

The dorsal surface of the foot of Phyllostomus hastatus, Carollia brevicauda and of many stenodermatines (e.g. Sphaeronycteris, Vampyressa brocki) is sparsely furred or naked. In contrast, the dorsal foot is hairy in Rhinophylla pumilio, Sturnira lilium and in several other stenodermatines (e.g. Enchisthenes, Vampyressa melissa).

Velazco (2005) has first used this character in his phylogenetic analysis of Platyrrhinus.

Character 30: Banding pattern of dorsal fur.

Dorsal fur unicolored (0), or dorsal fur at least partially bicolored, with pale base and brown tip, present minimally in the lower dorsum (1), or dorsal fur mostly tricolored, with dark base and tip and a pale medium band (2).

The dorsal fur is unicolor in Phyllostomus hastatus, which is generally independent of color variants within populations of this species (see character 17). In contrast, Rhinophylla pumilio and some stenodermatines (e.g. Uroderma bilobatum) have the dorsal fur bicolored. Finally, the dorsal fur is mostly tricolored in many stenodermatines (e.g. Mesophylla) and in Carollia brevicauda. For the purposes of comparison, I scored this character based on the fur banding pattern seen over the lower back so as to accommodate Ectophylla, which has entirely white fur over the upper back, and bicolor fur over the lower back (condition 2).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the banding patterns of dorsal fur of stenodermatines.

Many authors have used similar characters in phylogenetic analyses. Owen (1987: table 1 and appendix II, character 3) used it in his analysis of stenodermatine bats, and subsequently Owen (1991: 24, character 7) used it in his analysis of Dermanura species with the description of Koopmania. A similar character was used by Marques-Aguiar (1994, character 4) in her analysis of large species of Artibeus, Simmons (1996, character 1) in her analysis of Micronycteris species, and Wetterer et al. (2000) in their analysis of Phyllostomidae phylogenetic relationships.

The states as presently described agree with those above cited authors and the present scoring agrees with that of Wetterer et al. (2000), for species in common in this, and their work. I also agree with Wetterer et al. (2000), who considered the condition found in Ectophylla potentially homologous to that observed in other bicolor-haired stenodermatines.

Character 31: Banding pattern of ventral fur.

Ventral fur predominantly tricolored with dark base and tip, and pale medium band, with sparse fur with other banding patterns (0), or predominantly bicolored, with pale base and dark tip, with sparse unicolored and/ or tricolored fur (1), or predominantly unicolored with or without sparse bicolored fur (2).

The ventral fur is predominantly tricolored in Carollia brevicauda and some stenodermatines (e.g. Chiroderma villosum). In contrast, the ventral fur is predominantly bicolored in Rhinophylla pumilio and in many stenodermatines (e.g. Platyrrhinus helleri, Vampyrodes, Uroderma bilobatum). Finally, several stenodermatines have a predominantly unicolored ventral fur (e.g. Ectophylla, Stenoderma).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Marques-Aguiar (1994) first used this character in her phylogenetic analyses of Artibeus (Artibeus). A similar character was subsequently used by Simmons and Conway (2001), and Velazco (2005). I found intraspecific variation in some taxa described by previous authors as having a certain type of banding pattern in the ventral fur, and preferred to preserve potential homologies combining some states described previously by those authors (e.g. “fur unicolored” and “fur unicolored or bicolored” combined into one state “fur predominatly bicolored”).

Character 32: Hair on the noseleaf.

Noseleaf hairless or with fine hair (0), or with dense hair (1).

Carollia brevicauda and most stenodermatines have noseleaves that either lack hair or have only a sparse hair covering (e.g. Chiroderma villosum). In contrast, Sturnira lilium and Vampyressa melissa have hairy noseleaves.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 33: Bulb in hair shaft.

Bulb on hair shaft absent (0), or present (1).

There is no bulb or swelling in the bases of individual hairs in Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Mesophylla). In contrast, a bulb or swelling in the basal part of the hair shaft occurs in some other stenodermatines (e.g. Vampyrodes, Ariteus).

Variation in the morphology of the hair shaft of bat species was originally described by Benedict (1957) and has first appeared as a phylogenetic character in a component analyses conducted by Straney (1980). This character was subsequently used by Wetterer et al. (2000: character 2). My scoring is similar to Wetterer's et al. (2000). I made no original observations for this character.

Character 34: Scale margins on hair shafts.

Majority of scale margins on each hair entire (0), or toothed (1), or irregular (2).

Several phyllostomids have cuticle scale margins with smooth straight margins (e.g. Carollia brevicauda, Ectophylla). In contrast, most stenodermatines have toothed margins (Ariteus, Artibeus [Dermanura] cinereus). Yet a third condition is observed in Phyllostomus hastatus and Ardops, which both have irregular scale margins (Benedict, 1957; Wetterer et al., 2000).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Wetterer et al. (2000: page 46, character 2) first used this character in a phylogenetic analysis, based in the original descriptions of Benedict (1957). I made no original observations for this character.

Vibrissae and associated papillae

Character 35: Supercilliary vibrissae.

Supercilliary vibrissae present (0), or absent (1).

Phyllostomus hastatus, Carollia brevicauda and most stenodermatines (e.g. Sturnira lilium, Ardops) lack supercilliary vibrissae. In contrast, Centurio has a single supercilliary vibrissa (Wetterer et al., 2000: character 11).

This character first appeared as a character in the phylogenetic analyses of Wetterer et al. (2000), and subsequently in the analyses of Simmons and Conway (2001). My scoring is similar to that of Wetterer et al. (2000).

Character 36: Number of genal vibrissae.

Two genal vibrissae present (0), or either one or two (1).

Genal vibrissae are thick modified hair located ventral and posterior to the eye (Pocock, 1914; Brown, 1971; Velazco, 2005). Carollia brevicauda, Rhinophylla pumilio and most stenodermatines have two genal vibrissae. In contrast, one or two genal vibrissae may be present in Vampyressa brocki and V. nymphaea.

The number of genal vibrissae has appeared as a phylogenetic character in the analyses of Wetterer et al. (2000: character 12), and Simmons and Conway (2001: character 99). My scoring is in agreement to that of Wetterer et al. (2000) except in the case of V. nymphaea, which they scored as having two genal vibrissae.

Character 37: Interramal vibrissae.

No interramal vibrissae (0), or one (1), or two interramal vibrissae present (2).

Phyllostomus hastatus and several stenodermatines lack completely interramal vibrissae (e.g. Vampyressa bidens). In contrast, one interramal vibrissa is seen in in Platyrrhinus helleri. Finally, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Sturnira lilium, Vampyrodes) consistently have two interramal vibrissae.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in number of interramal vibrissae among stenodermatines.

This character has appeared in the phylogenetic analyses of Wetterer et al. (2000) and Velazco (2005). My scoring is in agreement to that of Wetterer et al. (2000) except in the case of Platyrrhinus helleri. In this case, I am in accordance with the scoring of Velazco (2005), who found one interramal vibrissa in P. helleri.

Character 38: Number of vibrissae in column adjacent to nose.

Three vibrissae in column adjacent to nose (0), more than three (1).

Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines have more than three vibrissae in the column adjacent to nose. In contrast, Ametrida, Centurio, and Sphaeronycteris have three vibrissae in the column adjacent to their noseleaves (fig. 4).

This character first appeared in the phylogenetic analyses of Wetterer et al. (2000: character 14) and of Velazco (2005). Velazco (2005) erected more characters to account for the exact number of vibrissae in the species of Platyrrhinus. I found variation in number of vibrissae in many species, and preferred to accommodate all the species with four or more vibrissae in a single state.

Character 39: Vibrissae on the upper lip.

No vibrissae on the upper lip (0), or a single vibrissa present on each side of upper lip (1), or one or two vibrissae present (2), or two vibrissae always present (3).

There is no vibrissa in the upper lip of Phyllostomus hastatus, Rhinophylla pumilio, and many stenodermatines (e.g. Centurio). In contrast, one vibrissa is located in the upper lip on each side of the face in several stenodermatines (e.g. Artibeus concolor, Phyllops falcatus). A third condition may be found in some other stenodermatines, in which one or two vibrissae may be located in the upper lip (e.g. Platyrrhinus helleri). Finally, two vibrissae always occur on the upper lip of Carollia brevicauda.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This character has previously been used in the phylogenetic analyses of Velazco (2005: character 6).

Character 40: Vibrissal papillae surrounding the noseleaf.

Vibrissal papilla surrounding the noseleaf connected, form padlike structure (0), or connected, form free skin flap (1), or separate, forming elongated cylindrical projections (2).

Vibrissal papillae are connected and form a padlike structure in Phyllostomus hastatus, Carollia brevicauda, and in most stenodermatines (e.g.

Artibeus [Dermanura] cinereus, Mesophylla, and see fig. 4). In contrast, fleshy skin flaps are formed by the vibrissae connected in some stenodermatines (e.g. Ametrida, and see fig. 4). A third condition is observed in Centurio and Sphaeronycteris, which have elongated, cylindrical, finger-like structures that are not connected with each other (see fig. 4).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This character first appeared in the analysis of Wetterer et al. (2000: 55, character 16). I am not in accordance with their scoring for Ardops ("free skin flap"), a species that in my opinion has a padlike structure surrounding its noseleaf.

Character 41: Genal papillae morphology.

Genal vibrissae arising from simple papillae (0), or arising from rounded, wart-like papillae (1).

The genal vibrissae arise from simple papillae in Phyllostomus hastatus, Carollia brevicauda and in several stenodermatines (e.g. Sturnira lilium, Artibeus jamaicensis). In contrast, the genal vibrissae arise from rounded, wart-like papillae in many stenodermatines (e.g. Sphaeronycteris, fig. 4).

Velazco (2005: character 4) first used this character in a phylogenetic analysis, and described the developed genal papillae as a basal protuberance where the vibrissae are implanted.

Body size, ear, eye, noseleaf, tragus, and oral papillae

Character 42: Body size.

Size large (weight over 37 g) (0), or medium (weight 21 to 36 g) (1), or small (weight 13 to 20 g) (2), or very small (weight 12 g or less) (3).

Phyllostomus hastatus and some species of stenodermatines (*e.g. Artibeus [Artibeus]* are fairly heavy. In contrast, several stenodermatines are medium-sized, weighting more than 21 g and up to 36 g (*e.g.* *Carollia brevicauda*, *Centurio*, *Pygoderma*). Several stenodermatines have a third condition and are small to medium sized, weighting 20-21 g (*e.g.* *Sturnira lilium*, *Enchisthenes*, *Vampyressa nymphaea*). Finally, some stenodermatines are very small and light, weighting 10-12 g or less (*e.g.* *Ectophylla*, *Vampyressa thyone*, *Mesophylla*).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 43: Pinna relative lenght.

Ear long (0), or short (1).

The pinna of *Carollia brevicauda* and some stenodermatines *(e.g. Vampyressa bidens*) is relatively long, *i.e*. it is higher than wider. In contrast, *Phyllostomus hastatus*, *Rhinophylla pumilio*, *Sturnira lilium* and several other stenodermatines (*e.g.* *Vampyressa* *pusilla*) have a relatively short pinna, with relatively proportional heigh and width.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 44: Pinna shape.

Ear triangular, tapering to an acute tip (0), or rounded (1).

The pinna of Phyllostomus hastatus, Carollia brevicauda, and Sturnira lilium is relatively triangular, i.e. with an acute tip. In contrast, Rhinophylla pumilio and stenodermatines (e.g. Platyrrhinus helleri, Vampyressa pusilla) have rounded pinnae.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 45: Anteromedial edge of ear pinna.

Anteromedial edge of ear pinna smooth, no lobes observed (0), or large lobe located in the proximal anteromedial edge of ear pinna (1).

Phyllostomus hastatus, Carollia brevicauda and most stenodermatines (e.g. Ametrida, Vampyressa bidens) have a smooth anteromedial edge of ear pinna, with no emarginations or lobes. In contrast, Centurio has a large lobe in the proximal anteriomedial edge of ear pinna bordered dorsally by a deep emargination.

Owen (1987, 1991) first used this character in a phylogenetic analysis.

Character 46: Dorsal emargination of lateral ear pinna.

Dorsalmost emargination of lateral ear pinna located in its distal half (0), or located in the proximal half of ear pinna (1).

The lateral edge of ear pinna has two lateral emarginations in stenodermatines. The dorsalmost lateral emargination of the pinna is generally shallow and coincides with the point of folding of the ear, being conspicuous when the ear is a little twisted or folded. The ventralmost emargination is deeper and basal (= proximal) and placed just anterior to a proximal lobe of skin with variable development in stenodermatines (see character 48).

The dorsalmost emargination of the lateral ear pinna is distal, located at or above the halfway point along the pinna in Phyllostomus hastatus, Carollia brevicauda and most stenodermatines (e.g. Uroderma bilobatum, Vampyressa thyone). In contrast, the dorsal emargination of the ear pinna is located in its proximal half in several stenodermatines (e.g. Ametrida, Sphaeronycteris, and see fig. 4).

Owen (1987, 1991) described a character related to the extent of the dorsalmost emargination of ear pinna. I found it difficult to precisely evaluate the length of that emargination because it may vary depending on the twisting or folding position of the ears of the bats. I therefore chose to describe variations related to the dorsal emargination of ear pinna in terms of its relative position to a vertical axis of the lateral pinna. For some bats, I also noticed that the dorsal emargination is only visible when the pinna is in certain positions, i.e. depending on the way it is folded (e.g. Platyrrhinus helleri appears often in pictures with rounded and smooth dorsal ear pinna lateral edges). This character is best observed in live animals and certain pictures of live animals.

Character 47: Color of inner pinna.

Ear pinna homogeneously dull of grayish color (0), or pale colored (yellowish or pinkish) area in the internal proximal shell present (1), or thin colored stripes *bordering lateral edges of ear pinna and large colored area in the internal proximal shell present (2), or most of ear pinna bright yellow colored (3)*.

Phyllostomus hastatus, *Carollia brevicauda*, *Sturnira lilium*, and most stenodermatines have a grayish, dull-colored ear pinnae, unadorned with highlighting contrasting colors such as white and yellow (*e.g.* *Chiroderma villosum*). In contrast, part of the internal pinna surface is pale-colored (pinkish or yellowish) in several stenodermatines (*e.g.* *Ametrida*, *Sphaeronycteris*, see fig. 4). A third condition is found in some other stenodermatines, in which there is a pale-colored stripe along the margin of the pinna, and also a large part of the internal pinna surface pale-colored (*e.g.* *Platyrrhinus helleri*, *Vampyressa* *bidens*; see fig. 4). Finally, a fourth condition is observed in *Mesophylla* and *Ectophylla*, which have the entire inner surface of the ear pinna colored bright yellow (fig. 4).

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps in the extent of coloration of internal ear.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 48: Extent of pale stripe on ear pinna.

Pale stripe along margin of pinna not continuous, tapers and disappears dorsolaterally (0), or pale stripe continuous along entire border of pinna (1).

Within stenodermatines that have colored margins in the ear pinna, the stripe may be continuous (*e.g.* *Uroderma bilobatum*), or interrupted in the dorsolateral part of ear pinna (*e.g.* *Vampyressa* *nymphaea*). Many species have a polymorphic condition, in which stripes may be either continuous or interrupted at tip (e.g. V. thyone), and such species were scored with both states in the data matrix.

Goldman (1920: 69) commented about the ear-edging pattern of "Vampyressa minuta" (= V. thyone), from Panama: "this color, more intense on the lower part of the ears, was somewhat duller toward the tips". Davis (1975) has also noticed this interrupted pattern of colored-edged ears of a collection of Vampyressa bidens from Iquitos, Peru.

All bats lacking a marging stripe in their pinna were scored "-".

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 49: Color of pale stripe on ear pinna.

Stripe on the border of pinna whitish cream or pale yellow (0), or stripes pure yellow (1).

Within stenodermatines that have colored margins on the ear pinna, the stripe may be whitish cream or pale yellow (e.g. Uroderma bilobatum) or, in contrast, a pure, bright yellow (e.g. V. bidens). This character may be hard to detect in museum specimens as the color of the pinna margin fades quickly after death.

All bats that lack a marging stripe in their pinna and those species that have a whole ear colored with yellow (e.g. Mesophylla) were scored "-".

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 50: Basal lobe in lateral pinna.

Basal lobe poorly developed and with dull colors (0), or well developed and colored with bright colors (1), or thick, well developed structure present, enlarged at the tip, colored similarly to skin of face (2).

A basal lobe is observed in the base of the lateral pinna in several stenodermatines, situated below the ventralmost emargination of lateral border of pinna. This lobe is poorly developed and has no bright colors in most stenodermatines (e.g. Sturnira lilium, Artibeus jamaicensis). In contrast, the basal lobe in the base of lateral pinna is well developed and colored with bright highlighting colors in several stenodermatines (e.g. Platyrrhinus helleri, Mesophylla, and see fig. 4). A third, autapomorphic condition is observed in Centurio, a species that has a well-developed thickened structure replacing the basal lobe. This structure is enlarged at the tip, and of the same color as the bare skin covering the face of this bat.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 51: Color of basal lobe.

Colored basal lobe either pale yellow or whitish (0), or bright yellow (1).

The colored lobe of base of lateral pinna is bright yellow in some stenodermatine bats that have a well-developed basal lobe (e.g. Platyrrhinus helleri, see fig. 4). In contrast, the lobe is whitish or pale yellow in several others (e.g. Uroderma bilobatum)

All species with dull colored lobes on pinna, and those that lack a basal lobe were scored "-".

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 52: Folds on inner surface of pinna.

Internal surface of ear pinna with well-marked parallel folds (0), or folds poorly marked (1).

The internal surface of the ear pinna in bats is frequently well-marked with parallel, scratch-like lines, which mark the points where the skin bends when the animal folds it's ears (e.g. Platyrrhinus helleri). In contrast, these parallel folding lines are poorly marked in some stenodermatines (e.g. Ectophylla, Mesophylla, Vampyressa thyone).

Velazco (2005) first described and used this character in a phylogenetic analysis.

Character 53: Tragus thickness.

Tragus roughly the same thickness throughout (0), or with a more thickened tip and medial attachment to head (1).

The tragus is of roughly equally thickness over all its extension in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in some stenodermatines (e.g. Sturnira lilium, Chiroderma villosum). In contrast, most stenodermatines have the tragus thickened at tip and at the latero-basal projection that attaches to the head (e.g. Vampyressa bidens).

This character has been used previously in the phylogenetic analyses of Simmons and Conway (2001). I however changed the definition of states to accommodate variation of this character within stenodermatines.

Character 54: Tragus color.

Tragus coloration pale, dull, does not contrast against the background color of internal ear pinna (0), or distal part of tragus is paler than and contrasts with the background of ear pinna (1), or most of the tragus colored and sharply contrasts with the background color of internal ear pinna (2).

I have noticed distinct patterns of combinations between the coloration of tragus and background skin of internal ear pinna, which make the tragus more or less visible or completely cryptic. Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines have a tragus with similar coloration as the internal pinna (e.g. Mesophylla, see fig. 4). Conversely, the distal tragus tip contrasts against the background color of internal ear pinna in some other stenodermatines (e.g. Vampyressa brocki, and see fig. 4). A third condition is observed in other stenodermatines, in which most of the tragus has a contrasting color against the background internal ear pinna (e.g. Platyrrhinus helleri, Uroderma bilobatum).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the extent of conspicuous coloration of the tragus among stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 55: Tragus lateral edge.

Tragus is with lateral edge smooth or nearly so (0), or irregularly toothed, with unequal projections in its lateral border (1), or finely serrated (2), or regularly toothed (3).

The tragus of Carollia brevicauda, Rhinophylla pumilio and some stenodermatines is virtually smooth in the lateral border above notch (see character 56 for a description of this notch) (e.g. Sturnira lilium). In contrast, the lateral border of tragus above basal notch is irregularly toothed in Phyllostomus hastatus and several other species of stenodermatines (Uroderma bilobatum, Artibeus). Other stenodermatines (e.g. Platyrrhinus helleri and Vampyressa brocki have a third condition, in which the lateral border of the tragus is finely serrated. Finally, the lateral border of tragus has subequal finger-like projections in some other stenodermatines (e.g. Sphaeronycteris).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 56: Notch in proximal lateral edge of tragus.

Tragus with either a shallow or no notch in the proximal lateral edge (0), or with a deep notch (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Sturnira lilium, Ectophylla alba) have a shallow notch or lack a notch in the lateral edge of the tragus. In contrast, the tragus of most stenodermatines has a deep notch located in its basal lateral edge (e.g. all Vampyressa species s.l.).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 57: Lateral attachment of tragus.

Lateral attachment of the tragus undeveloped (0), or often developed, sometimes swollen (1), always developed, often swollen and hirsute (2).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Sturnira lilium, Ectophylla alba) the lateral attachment of the tragus is a simple, poorly developed structure. In contrast, a relatively more developed structure, sometimes swollen, but not covered with black hair occurs in some other stenodermatines (e. g. Uroderma bilobatum, Vampyressa nymphaea). Finally, there is an always developed structure, often swollen and hirsute that lies in the anteromedial basal projection of the tragus in Vampyressa bidens.

Peterson (1968) suggested that the hairy structure found in Vampyressa bidens may be associated with a gland, and that it is sexually dimorphic for this species. I presently have no evidence to reinforce or to reject this hypothesis.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 58: Eyes size and exposition.

Almond-shaped eyes, usually little exposed out of orbit sockets (0), or big round eyes, often well exposed out of orbit sockets (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and many stenodermatines (e.g. Vampyressa thyone) have almond-shaped eyes, which are little exposed out of the orbit sockets. In contrast, some other stenodermatines (e.g. Chiroderma villosum, Pygoderma) have eyes that usually stay broadly open and exposed out of orbit sockets, conferring to the bats a "big-globular eye" appearance. Although this suggests differences in visual acuity possibly associated with foraging strategies, studies to test this hypothesis have not yet been attempted.

This character is only observable in live animals.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 59: Iris coloration.

Iris brownish, black pupil does not contrast sharply with darker-colored background of iris (0), or iris pale, black pupil contrasts with paler-colored background of iris (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines have a brownish iris against which the black pupil does not strongly contrast, giving an overall brownish appearance to the eye (e.g. Uroderma bilobatum). In contrast, several stenodermatines (e.g. Chiroderma villosum, Pygoderma) have pale-colored irises, and their black pupils sharply contrast with this background.

This character may only be observable in live animals.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 60: Presence of noseleaf.

Presence of a complete noseleaf with horseshoe and spear at all ages (0), or no trace of a noseleaf at any age after birth (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Platyrrhinus helleri, Vampyressa) have noseleaves with spear and lancet at all ages. In contrast, Centurio has no noseleaf at any age after birth.

Whether or not Centurio has a noseleaf has been controversial in the literature. Some authors have argued that Centurio has a noseleaf (e.g. Lim 1993) while others have stated that it does not (e.g. Miller, 1907, Wetterer et al., 2000). I concur with the authors that consider Centurio as not having a true noseleaf, suggesting that it may have been lost as part of a complex set of evolutionary changes that make the face of this species unique among bats. However, in my definition of states I emphasize the lack of a noseleaf “at any age after birth” making it explicit the fact that from newborns to adults there is no trace of a noseleaf. This contrasts with the situation of the only other phyllostomids with undeveloped noseleaves, the three monotypic species of vampire bats (Chiroptera: Phyllostomidae, Desmodontinae: genus Diphylla, Diaemus, Desmodus), which may sometimes have traces of spears, and have a developed horseshoe. Finally, I argue that even if Centurio would have had traces of noseleaf structures in early stages of its embryological development (as might be demonstrated by ontogenetic studies), this should be treated as a separate issue and in separate characters.

Lacking a noseleaf is therefore an autapomorphic condition for Centurio in the context of this study, and in all subsequent characters related to the noseleaf structure, I scored Centurio “-”.

Character 61: Shape of the noseleaf.

Noseleaf triangular, greatest breadth of the lancet located in the proximal spear (0), or noseleaf broad and ovate with an expanded distal spear, the greatest breadth of the lancet located above proximal third of noseleaf height (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Vampyressa bidens) have a triangular noseleaf, with a large base. In this case, the greatest width of the noseleaf is located clearly proximally, and the noseleaf tapers continuously towards the tip. In contrast, several other stenodermatines (e.g. Chiroderma) have ovate-shaped noseleaves in which the lateral lancet is expanded distally (see fig. 4).

Centurio that lacks a noseleaf was scored “-“.

This is the first use of this character in a phylogenetic analysis.

Character 62: Spear folds.

Lateral edges of spear with shallow folds separating them from the central rib (0), or lateral edges of spear form deep folds (1).

The lateral edges of the spear of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Mesophylla) are demarcated from the central rib by shallow folds (see fig. 4) and the edges of the lancet do not usually fold behind the rib. In contrast, the lateral edges of the spear of many stenodermatines are large and have deep folds separating them from the central rib of spear, sometimes giving the impression of a free rib column (e.g. Uroderma bilobatum, Vampyressa brocki, and see fig. 4).

Peterson (1968), in his description of Vampyressa brocki noted that the “terminal margins of the lancet [of the noseleaf] tend to wrap around the mid-rib and come together on its posterior margin near the apex". This condition conforms to state 1 as described here.

Centurio that lacks a noseleaf was scored "-".

This is the first use of this character in a phylogenetic analysis.

Character 63: Size of the noseleaf spear in relation to the horseshoe.

Spear of noseleaf short, less than the twice the height of horseshoe (0), or spear long, more than twice the height of horseshoe (1).

The spear of the noseleaf of most stenodermatines is long (Wetterer et al. 2000) but it has variable proportions when compared to the horseshoe, which may be higher or shorter. The noseleaf is short compared to the height of the horseshoe in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and in several other stenodermatines (e.g. Enchisthenes). In contrast, the horseshoe is long in comparison to the length of the spear in several other stenodermatines (e.g. Mesophylla).

Centurio that lacks a noseleaf was scored "-".

This character has previously been used by Owen (1987: character 2, 1991: characters 2-5), Marques-Aguiar (1994: character 9), Wetterer et al. (2000: character 19). I have adapted this character to accommodate variation within stenodermatines.

Character 64: Distal extent of central rib of spear.

Central rib of noseleaf restricted to proximal spear (0), or extends to the tip of spear (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and Sphaeronycteris have the central rib restricted to the proximal part of the spear (see fig. 4). In contrast, in most stenodermatines a central rib of the noseleaf reaches the tip of the spear (e.g. Vampyressa bidens).

Centurio that lacks a noseleaf was scored "-".

This character has appeared in the phylogenetic analyses of Wetterer et al. (2000: character 24).

Character 65: Noseleaf patterns of coloration.

Noseleaf unicolored or with gradations of colors not sharply separate (0), or distinctively bicolored (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Sturnira lilium, Chiroderma villosum, Ectophylla) have noseleaves with indistinctive divisions of colors with either a single overall color (e.g. all brownish or all yellow, see fig. 4) or sometimes gradations of colors often in a "dégradé" pattern, without clear borders between colors (e.g. pinkish to orangey, see character 65, and see fig. 4) In contrast, several stenodermatines (e.g. Uroderma bilobatum, Vampyressa nymphaea, and see fig. 4) have distinctively bicolored noseleaves, with the colors clearly defined and sharply separated (e.g. whitish or creamy and brown, yellow and brown).

Centurio that lacks a noseleaf was scored "-".

A character similar to this has appeared in the phylogenetic analyses of Wetterer et al. (2000: character 18). I however treated the colors patterns in unicolored and bicolored noseleaved bats, and the distribution of patches of color in bicolored noseleaved bats in separate characters to explain the variation I observed (see characters 66 to 68).

Character 66: Color of unicolored noseleaf.

Noseleaf uniformly brownish or grayish (0), or “dégradé”; ranges from fade yellow to orangey or pinkish, or a mix of these tonalities (1), or uniformly bright yellow (2).

The color of the noseleaf within unicolored noseleaved bats is variable. The noseleaves of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most unicolored noseleaved stenodermatines (e.g. Sturnira lilium, Chiroderma villosum) are uniformly brownish or grayish (see fig. 4). In contrast, the noseleaves of some short-faced stenodermatines (e.g. Ametrida, Pygoderma, Phyllops) have a “dégradé”, blended pattern, in which the coloration ranges from fade yellow to orangey or pinkish, or a mix of these tonalities. Finally, the noseleaves of Ectophylla and Mesophylla are uniformly colored with bright yellow (see fig. 4).

All species with distinctively bicolored noseleaves and Centurio that lacks a noseleaf were scored “-“.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the patterns of coloration of unicolored noseleaves.

This is the first use of this character in a phylogenetic analysis.

Character 67: Patterns of coloration of bicolored noseleaves.

Dorsal half of lateral horseshoe, sometimes trailing edge of ventral margin horseshoe, and approximately one-fourth of lateral flap of lancet pale, remainder of horseshoe and noseleaf brown (0), or most of horseshoe and 1/4 to 1/2 of the lancet flap pale, remainder of noseleaf brown (1), or most of horseshoe, including virtually all lateral edge and approximately one-half the height of the whole ventral margin; and two thirds or more, often the whole lateral flap of lancet pale colored; remainder of noseleaf brown (2).

The pale spots of color (whitish-cream, pale yellow or pure yellow, see character 68) of bats with distinctively bicolored noseleaves have different patterns of distribution. The dorsal half of the lateral horseshoe, sometimes the trailing edge of the ventral margin of the horseshoe, and approximately one-fourth of the lateral flap of lancet may be pale-colored and the remainder of the horseshoe and noseleaf is brown in some stenodermatines (e.g. Vampyressa thyone). In contrast, most of the horseshoe and one-fourth to one-half of the lancet lateral flap is pale-colored in other stenodermatines (e.g. Platyrrhinus helleri, Uroderma bilobatum). Finally, Vampyressa bidens, V. brocki and V. nymphaea have most or their horseshoe, including virtually all of the lateral edge and approximately one-half (in height) of the ventral margin and two thirds or more of the lateral flap of lancet (often the whole lateral flap) pale colored, with the column of the central rib brown (fig. 4).

All stenodermatines with unicolored noseleaves and Centurio were scored "-".

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a phylogenetic analysis.

Character 68: Colors of bicolored noseleaves.

Color patches of bicolored noseleaved bats are whitish or cream-colored (0), or are pale to bright yellow (1).

The color patches of the noseleaves of bicolored-noseleaved stenodermatines are either whitish or cream-colored (e.g. Artibeus cinereus) or yellow (e.g. Vampyressa bidens).

All stenodermatines with unicolored noseleaves and Centurio were scored with "-".

This is the first use of this character in a phylogenetic analysis.

Character 69: Leaflet in posterior spear.

No leaflet present behind spear (0), or small scalloped leaflet present in posterior spear (1).

No leaflet is observed behind the lancet of the noseleaf in most stenodermatines (e.g. Vampyressa bidens, V. nymphaea) and in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, Rhinophylla pumilio and Sturnira lilium. In contrast, a leaflet with variable morphology is present just behind the noseleaf in Vampyressa thyone and Mesophylla (see fig. 7). This does not appear to be sexually dimorphic.

The leaflet in Mesophylla varies from a large unifid leaf (e.g. USNM 579602, from Bolivia, and the holotype of M. macconnelli flavescens from Trinidad AMNH 186433) to a bifid leaflet (e.g. USNM 549428, from Brazil), whereas in Vampyressa thyone it varies from a single tipped leaflet (e.g. DZSJRP 14133, from Brazil) to a short trifid leaflet (e.g. USNM 575599, from

Bolivia). Therefore the morphological structure of the leaflet appears too variable to be of taxonomic value. It may be a different case with the analysis of a larger number of fluid specimens and live individuals since this is a character that cannot be studied in dried skins.

Centurio that lacks a noseleaf was scored “-“.

This character has been previously used by Wetterer et al. (2000: character 29), but a facial skin outgrowth found in Sphaeronycteris (see character 89) was considered homologous to the leaflet described in the present character. I disagree that those structures (the leaflet, this character, and the outgrowth, character 89 of this listing may be homologous and described them separately.

Character 70: Proximal rib of the noseleaf.

Central rib terminates abruptly proximally, does not grade into horseshoe (0), or proximal rib grades gently into horseshoe (1).

The proximal rib in Carollia brevicauda and Rhinophylla pumilio terminates abruptly at the horseshoe. In contrast, the proximal rib of Phyllostomus hastatus and of all stenodermatines progressively vanishes in a gentle gradation where it connects to the horseshoe.

Centurio that lacks a noseleaf was scored “-“.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 71: Shape of lateral horseshoe.

Lateral horseshoe with a cup-like lateral projection at nostril level (0), or with a rough edge (1), or with a generally smooth lateral border (2).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and many other stenodermatines (e.g. Artibeus jamaicensis, Vampyressa bidens) have a single cup-like lateral projection at nostril level. In contrast, Chiroderma and Mesophylla have a third condition, a rough-edged lateral horseshoe (see fig. 4). Finally, several other species of stenodermatines have a generally smooth and rounded lateral horseshoe (e.g. Ametrida, Artibeus cinereus, Vampyressa thyone) (see fig. 4).

Centurio that lacks a noseleaf was scored “-“.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 72: Inferior border of horseshoe.

Inferior border of horseshoe forms a thin, free flap of skin at junction with upper lip (0), or forms a thickened ridge (1), or forms a continuous surface with upper lip (2).

The inferior border of the horseshoe forms a thin, free-flap of skin in Phyllostomus hastatus and in several stenodermatines. In contrast it forms a thickened ridge in some other stenodermatines (e.g. Ariteus). Finally, the inferior border of the horseshoe is a continuous surface bound to the upper-lip skin in Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and Enchisthenes.

Centurio that lacks a noseleaf was scored “-“.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This character has appeared previously in analyses of Straney (1980: G16-17), Marques-Aguiar (1994: 10), Simmons (1996: 7), and Wetterer et al. (2000: 25).

Character 73: Shape of inferior border of horseshoe.

Inferior border of thickened horseshoe smoothly curved or straight (0), or v-shaped projection present (1).

The inferior border of the horseshoe of most stenodermatines with a thickened inferior border of the horseshoe is a smoothly straight to slightly curved surface (e.g. Ametrida, Phyllops). In contrast, Ardops and Ariteus have a v-shaped inferior border.

Centurio that lacks a noseleaf was scored “-“.

This character has first appeared in the analysis of Wetterer et al. (2000).

Character 74: Protuberance in free-flapped horseshoe.

Rounded protuberance in the middle of ventral edge of the free-flapped horseshoe bats present (0), or absent (1).

Within stenodermatines, many have a rounded protuberance in the middle of the ventral edge of the horseshoe (e.g. Platyrrhinus helleri). In contrast, other species of stenodermatines (e.g. Mesophylla) have a smooth ventral edge of horseshoe, without a protuberance.

Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and Enchisthenes, which have no free-flaped ventral margins of their horseshoes and Centurio that lacks a noseleaf were scored “-”.

This is the first use of this character in a phylogenetic analysis.

Character 75: Papillae in the chin.

Chin with multiple, well-developed dermal papillae (0), or smooth or with a few poorly developed papillae (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Chiroderma villosum, Mesophylla) have the chin covered with multiple papillae. In contrast, Centurio and Sphaeronycteris have a smooth, unpapilated chin.

This character has been first used by Wetterer et al. (2000: character 30) in a phylogenetic analysis.

Character 76: Large papillae below lip line.

Two elongated large papillae running roughly parallel sided to midline of chin (0), or central papilla present just ventral to midline of lower lip (1).

Phylllostomus hastatus has two elongated papillae running roughly parallel to midline of chin. In contrast, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines have a large central papilla just ventral to midline of lower lip.

Centurio and Sphaeronycteris, which both lack papillae below their lip line were scored "-"

This character has been previously used by Wetterer et al. (2000: character 33) in a phylogenetic analysis. I have changed the states to conform to the variation I have found within Stenodermatinae.

Character 77: Small papilla below central large papilla.

Small papilla present just below central large papilla (0), or absent (1).

The chin of many stenodermatines is characterized by a large central papilla. There appears a small papilla just below central large papilla in some stenodermatines (e.g. Vampyressa bidens). In contrast, a small papilla just below central papilla is absent in several other stenodermatines (e.g. Ardops, Ariteus).

Taxa lacking a central papillae in the chin (Centurio and Sphaeronycteris) and Phyllostomus hastatus that have elongated papillae in the chin (see character 76) were scored “-”.

This is the first use of this character in a phylogenetic analysis.

Character 78: Arrangement of the chin papillae.

Papillae surrounding central papilla arranged in “v” (0), or in “u” (1).

Carollia brevicauda and Rhinophylla pumilio have two convergent lines of papillae surrounding the central papillae and forming a “v”. In contrast, Sturnira lilium and all stenodermatines have a “u” shaped line of papillae surrounding the central papilla.

Taxa lacking a central papillae in the chin (Centurio and Sphaeronycteris) and Phyllostomus hastatus that have elongated papillae in the chin (see character 76) were scored “-”.

This is the first use of this character in a phylogenetic analysis.

Character 79: Internal oral papilla.

Internal oral papillae absent (0), or limited to the lip line (1), or widespread (2).

In stenodermatines the inner surface of lips and cheeks is covered with many small projections, the internal labial papillae (Silva-Taboada and Pine, 1969). Wetterer et al. (2000: character 34) noticed fine differences in the morphology of these papillae, which vary from flat to triangular or conical structures. Internal oral papillae are absent in Phyllostomus hastatus, Carollia brevicauda and Rhinophylla pumilio. In contrast, internal oral papillae are present and limited to the lower lip line in the species Artibeus cinereus, Sturnira lilium, Uroderma bilobatum, Ectophylla, Mesophylla, and in all Vampyressa (s.l.) species. Finally, many stenodermatines (all species from subtribe Stenodermatina, e.g. Centurio, Pygoderma) have widespread internal oral papillae covering their inner cheeks.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Wetterer et al. (2000) first used this character in a phylogenetic analysis.

Character 80: Forelimb skin coloration.

Thumb, metacarpals and forearm dull and not contrasting with the color of overall wing covering skin (0), or sometimes with yellow parts (1), or always with parts yellow colored (2).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines have the skin covering their forearms, thumbs and metacarpals that is brown and does not contrast with the color of the wing membranes. In contrast, many individuals of Mesophylla have thumbs, second and third metacarpals yellow colored (e.g. USNM 530981, from Amazonas, Brazil), and all Ectophylla had thumbs, metacarpals and forearm skin yellow.

Many individuals labeled as Mesophylla macconnelli have yellow colored foredigits, but others have uncolored digits (e.g. UNIVALLE 11394, from Cauca, Colombia). This variation, apparently independent of other yellow-colored body parts of Mesophylla, will be described and analyzed further in a forthcoming review of this taxon.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Lim (1991) first used this character in a phylogenetic analysis.

Patagium

Character 81: Relative size of dactylopatagium minus.

Dactylopatagium minus narrow (0), or broad (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and many stenodermatines have narrow dactylopatagium minus (e.g. Enchisthenes, Vampyrodes). In contrast, many other stenodermatines (all species from subtribe Stenodermatina, e.g. Ametrida, Phyllops) have very broad dactylopatagium minuses.

The dactylopatagium minus is the part of the chiropteran patagium located between the second and third digits. Vaughan (1970) studied variation in the size and pigmentation of dactylopatagium minus and the articulation of the metacarpal bones in some Neotropical bats. The dactylopatagium minus ranges from a narrow and pigmented membrane that ends proximal to the third metacarpophalangeal joint (e.g. species of the family Thyropteridae) to a broad and transparent/little pigmented membrane that extends to, or go slightly beyond to the distal end of the first phalanx of the third digit (e.g. in Emballonuridae, Natalidae, and most Phyllostomidae) (Vaughan, 1970).

Having a broad dactylopatagium might affect flight capabilities, providing a larger wing surface and reflecting in lift increasing, more sustainability for the flight, and enhancing camber ability. The dactylopatagium minus may be important for species with low and maneuverable flight. Vaughan (1959), for instance, observed that in some species with broad wings, the dactylopatagium minus angles sharply downwards during flight thus increasing the camber of the chiropatagium.

The evolution of a broad, and/or permanently open (see characters 81 and 82) and/or transparent (see character 83) dactylopatagium minus membrane may be correlated with roosting habits of the bats and avoidance of predation. When transparent, the dactylopatagium minus membrane may work as a “window” throughout which bats can observe the environment even with folded wings (Vaughan, 1970).

This is the first use of this character in a phylogenetic analysis.

Character 82: Dactylopatagium minus extension.

Digits two and three permanently partially open (0), or digits two and three total and permanently spread (0).

Vaughan (1970) noticed that the arrangement of second and third metacarpals in some species of stenodermatines increases the surface area of the dactylopatagium minus ensuring that the membrane stays permanently open (e.g. Sturnira lilium and Centurio senex). This arrangement involves a special organization of the bones of the wrist coupled with convergent curved second and third metacarpals (Vaughan, 1970). The dactylopatagium minus appears to stay permanently only partially open in several stenodermatines (e.g. Vampyressa bidens). In contrast, the dactylopatagium minus appears to stay totally spread and permanently open in Sturnira lilium, Ardops, Ariteus, Phyllops falcatus, Stenoderma, Sphaeronycteris, Ametrida, Centurio and Pygoderma. A finer study of the wrist bones organization, and of roosting behavior of stenodermatines may be required for a better understanding of this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 83: Pigmentation of dactylopatagium minus.

Dactylopatagium minus moderately to heavily pigmented (0), or lightly pigmented (1), or virtually transparent (2).

The dactylopatagium minus is heavily pigmented in Phyllostomus hastatus, Carollia brevicauda and in several stenodermatines (e.g. Uroderma bilobatum). In contrast, the dactylo-minus is semi-transparent and lightly pigmented in several other stenodermatines (e.g. Artibeus [Dermanura] cinereus, Vampyressa bidens). A third condition is found in many other stenodermatines (e.g. Phyllops falcatus, Ectophylla), which have a translucid dactylominus.

The consequences of having a semi-transparent or totally translucid dactylominus might reflect in adaptations related to roosting habits of the bats and avoidance of predators and are poorly understood.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the pigmentation of the dactylopatagium minus membrane of stenodermatines.

Although transparency in some species was early noticed by some authors (e.g. Allen, 1898, for Ectophylla), the occurrence of variable pigmentation in the dactylopatagium minus membrane has never been used in a phylogenetic analysis before.

Character 84: Patterns of coloration of chiropatagium.

Chiropatagium (except dactylopatagium minus) is uniformly colored (0), or has lattice pattern alternating pigmented and transparent stripes in between fourth and fifth fingers (1).

The chiropatagium (except the dactylopatagium minus, see characters 5. 81-83) is uniformly colored in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in most stenodermatines. In contrast, Centurio has a striped patagial membrane between the fourth and fifth fingers, alternating dark brownish stripes (the color of most of its wing membrane) with transparent, unpigmented stripes. This condition, although much less conspicuous, has also been observed in a single skin of Sphaeronycteris from “Rio Madeira, Brazil” (AMNH 92248). Since this is the only specimen that I observed with the lattice pattern, I scored Sphaeronycteris with (0), pending further investigation of additional specimens from Brazil. This lattice pattern was also noticed in one fluid specimen of Vampyressa sp. (USNM 520851, from Bocas del Toro, Panama that pertains to an undescribed species).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 85: Insertion of plagiopatagium onto hind limb.

Posterior edge of plagiopatagium inserts onto lower leg or ankle region (0), or onto lateral surface of metatarsals (1).

In Carollia brevicauda and Sturnira lilium, the posterior attachment of the plagiopatagium is located on the distal portion of the lower limbs, either on the lower leg or ankle. In contrast, Phyllostomus hastatus, Rhinophylla pumilio and most stenodermatines the posteriormost edge of the plagiopatagium attaches to the hindfoot along the lateral surface of the metatarsals.

This character has been previously used in the phylogenetic analyses of Straney (1980: characters G9-13), Owen (1987: character 6), Owen (1991: characters 14, 15, and 16), Marques-Aguiar (1994: character 7), Wetterer et al. (2000: character 88), and Velazco (2005: character 60). My definition of character states and scoring agree with those of Wetterer et al. (2000) and Velazco (2005).

Character 86: Uropatagium size and shape.

Uropatagium very broad, almost the size of tibia and little or no notched (0), or broad, with shallow medial notch, length of uropatagium at the notch is more than ½ length of tibia (1), or uropatagium broad and with deeper medial notch, length of uropatagium at the notch is more than 1/3 and less than 1/2 tibia length (2), or uropatagium narrow, length of the uropatagium at the notch is less than 1/3 tibia (3), or rudimentary (4).

The uropatagium of Phyllostomus hastatus is very broad with a virtually straight (not notched) posterior margin. In contrast, the uropatagium of Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Chiroderma villosum) is broad with a shallow notch. A third condition might be observed in several other stenodermatines, which have the uropatagium, although still broad, with a deeper medial notch (e.g. Vampyressa bidens). A fourth condition is observed in Vampyressa melissa that has a narrow uropatagium. Finally, Sturnira lilium has a rudimentary uropatagium that consists of only a thin flap of skin along the legs.

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps observed in the relative size of the uropatagium of stenodermatines.

To erect this character, I united one state described by Wetterer (2003: character 12) to define the condition of Sturnira lilium (character state 3) with the suggestions of several authors for the relative size and form of uropatagium (e.g. Peterson, 1968, Marques-Aguiar, 1994).

Character 87: Shape of notch of uropatagium.

Distal edge of uropatagium is “v” shaped (0), or circular shaped (1).

The form of the notch in the distal edge of uropatagium tends to be circular in Carollia brevicauda, Sturnira lilium, and many stenodermatines (e.g. Vampyressa melissa). In contrast, the notch of the uropatagium tends to be v-shaped, or triangular, in some others (e.g. Uroderma bilobatum, Vampyressa bidens).

Phyllostomus hastatus was scored with “-” since I considered that this species has virtually no notch in the uropatagium (see previous character).

Velazco (2005) first used this character in a phylogenetic analysis.

Glands, swollen, skin modifications

Character 88: Prominent eyelids and periorbital glands.

Eyelid region smooth, without periorbital gland or swelling (0), or with prominent, swollen eyelid region indicating large periorbital glands (1).

Periorbital glands consist of a doughnut-shaped mass of glandular tissue surrounding the eyes. This condition has been described for Ametrida (Peterson, 1965) and for Pygoderma (Myers, 1981). A prominent eyelid is also observed in Centurio and Sphaeronycteris although it is not as well developed as in Pygoderma and Ametrida (see fig. 4). In contrast, there are no other phyllostomids with such modification in the eyelid.

Myers (1981) suggested that the periorbital swollen of Pygoderma is a sexually dimorphic character (males having better developed glands) but my observations suggest that it varies individually in development within both sexes.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 89: Outgrowth above nose.

Sexually dimorphic outgrowth in form of visor located in the interorbital region above nose (0), or no outgrowth behind the spear (1).

A dermal outgrowth in form of a visor is present in the interorbital region in Sphaeronycteris.

This structure is sexually dimorphic and much more developed in males than in females. In contrast, Phyllostomus hastatus, Carollia brevicauda and all other stenodermatines have no such dermal outgrowth in form of visor.

Contrarily to Wetterer et al. (2000: character 29), I did not consider this structure homologous to the leaflet present behind the noseleaf lancet of Mesophylla and Vampyressa as it lies in a different position and is structurally distinct (see figs. 4 and 7, and for discussion on this respect, see character 69).

This character has been previously used by Wetterer et al. (2000: character 29), but the outgrowth of Sphaeronycteris was considered homologous, i. e. one of the conditions of a character describing the leaflet found in Mesophylla and Vampyressa thyone (see character 69).

Character 90: Dermal outgrowth in lip.

Dermal outgrowth of skin in the labial region absent (0), or fold of skin present in the chin/labial region present, forming a "double lower lip" (1).

There are no folds of skin in the neck or labial region of most stenodermatines. In contrast, Pygoderma has a fold of skin in the lower lip region and exhibits a "double-lipped appearance".

This is the first use of this character in a phylogenetic analysis.

Character 91: Submandibular mass of tissue.

Submandibular mass of tissue absent (0), or present (1).

A submandibular mass of tissue under the chin of Pygoderma was first noticed by Johann Natterer, who drew it in detail in a plate of 1889, from a female he captured in Ipanema, São Paulo, Brazil (Viena Archives, reproduced by Riedl-Dorn, 1999).

A submandibular mass of tissue (probably a gland, although it has not been studied histologically yet) is absent in *Phyllostomus hastatus*, *Carollia brevicauda* and in most stenodermatine bats (*e.g.* *Artibeus cinereus*, *Sturnira lilium*). In contrast, a submandibular mass of tissue is present under the chin of *Pygoderma* and *Centurio*.

This is the first use of this character in a phylogenetic analysis.

Character 92: Dermal outgrowth in neck.

Dermal outgrowth or fold of skin in the neck region absent (0), or large fold of skin in the neck present (1).

There are no folds of skin in the neck region of most stenodermatines. In contrast, *Centurio* and *Sphaeronycteris* have skin folds in their necks that can be pulled up to cover their faces (Paradiso, 1967, Nowak, 1991).

Those dermal outgrowths are more developed in the males of these species. According to Reid (1997) the folds of skin in *Centurio* are small, naked and pinkish in females, and large, velvety, white, and with transparent patches in males. The significance of those differences between sexes is unknown.

Lim (1993: character 3) and Wetterer *et al*. (2000: character 38) have used this character in phylogenetic analyses.

Character 93: Gular gland.

Gular gland absent (0), present (1).

Phyllostomus hastatus has a gular (throat) gland that produces a thick white substance of unknown function, similar to the gular gland seen in many other phyllostomine bat species (V. Tavares person. obs.). In contrast, Carollia brevicauda, Rhinophylla pumilio, and all stenodermatines lack a gular gland.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 94: Forelimb swellings.

Sweelings in the dorsal forelimbs absent (0), or sometimes developed in males (1).

There are gland-like structures in the forelimbs of some males of Pygoderma. Those structures are elongated swellings covered by bare skin, varying from an almost imperceptible linear swelling to a v-shaped or z-shaped conspicuous and well-developed swellings. The epithelial tissue covering this swelling under the microscope is very similar in texture and appearance to that of the doughnut-glands surrounding the eyes of some stenodermatines, which enclose glandular tissue (Myers, 1981, and see character 88). The swellings are situated on the lateral/distal edge of the forearm, extending distally onto the proximal end of the 5th metacarpal and to the distal/medial edge of the forearm (Tavares et al., ms submitted). I have not found forelimb swellings in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, or any other stenodermatine species.

This is the first use of this character in a phylogenetic analysis.

Character 95: Pendulus chest gland.

Glands absent in the chest region (0), or pendulus, bifid gland present on chest (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatine bats usually do not have any glandular structures on their chests other than mammae. In contrast, Ametrida has a pair of bifid pendular glands on the chest, apparently better developed in males. The function of these structures is unknown.

This is the first use of this character in a phylogenetic analysis.

Sexual dimorphism

Character 96: Sexual dimorphism in size.

No sexual dimorphism in size (0), or dimorphism only in size, with females being larger than males (1).

Phyllostomus hastatus, Carollia brevicauda, Sturnira lilium, and most stenodermatines (e.g. Platyrrhinus helleri) are not sexually dimorphic either in body dimensions or in other external characters. In contrast, Ametrida, Ardops, Ariteus, Phyllops, Pygoderma, Stenoderma and Vampyressa bidens are dimorphic in size, with females being significantly larger than males, independent whether they have other non-morphometric sexually dimorphic differences.

There occurs dimorphism other than body size differences in several stenodermatines (e.g. the dermal outgrowth in form of a visor is present in the interorbital region in the species Sphaeronycteris, character 89) and those were described separately in several previously listed characters (89-95) as they do not appear homologous (e.g. the submandibular gland described in character 91 that appear in Centurio and Pygoderma, compared to the above mentioned "visor" of Sphaeronycteris). On the other hand, the "concerted" development of a set of characters that result in sexually dimorphic stenodermatine taxa could perhaps be treated as a multistate character, which will be discussed elsewhere in the context of character evolution within stenodermatines.

This is the first use of this character in a phylogenetic analysis.

Skull ontogenesis

Character 97: Timing of development of the nasal bone.

Nasal ossification appears early in development, while other facial bones are in earlier stages of development and before any bone is present in the vertebral column (0), or ossification of nasal appears later in development, and nasal remains little developed while other facial bones are well-developed (1).

The nasal bone is variable in shape and relative position within adult stenodermatine bats. Paths and timing of development of the nasal bone may also vary independently even when the nasal of adult bats appears similar. Straney (1983) observed that the ossification process of of the nasal begins earlier than the development of other facial bones in Sturnira lilium and Uroderma bilobatum. In contrast, the ossification process of the nasal bone begins later, in comparison with the development of other facial bones, in Chiroderma villosum.

Straney (1983) examined series of fetuses of three species of phyllostomids (Chiroptera: Phyllostomidae) in a comparative study to understand the ontogeny of nasal bones of Chiroderma species. All Chiroderma species described at that time had nasal bones that remain poorly developed in the adult forms, a character that led some authors in the past to the misleading interpretation that Chiroderma lacked a nasal bone (e.g. Goodwin and Greenhall, 1962). Studies focusing on the ontogeny of facial bones of species are scarce and will certainly help to clarify many questions raised through the observation of the profuse amount of anatomic variations in their rostral adult skull.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 98: Shape and direction of growth of initial ossifying nucleus of nasal.

Initial ossifying nucleus of nasal circular, located rostral to the medial anterior edge of frontal, growth takes place primarily along transversal axis (0), or initial nucleus is a slender ossified rod connected to facial maxilla and medial edge of frontal, growth takes primarily place along lateral axis (1).

The nasal of Sturnira lilium begins development as a round-shaped osseous nucleus that grows more or less simultaneously in the medial/lateral and anterior/posterior directions, becoming wider caudad and consequently longer posteriorly (Straney, 1983). In contrast, the nasal of Chiroderma villosum and Uroderma bilobatum develops first into an elongated rod and later grows laterally to a rectangular shape.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 99: Position of slender initial ossifying nucleus.

Early slender nasal nucleus situated medially (0), or laterally (1).

There is variation in relative position of this structure among bats that have a slender initial ossifying nucleus. Uroderma bilobatum has a medial positioned initial ossifying nucleus of the nasal. In contrast, Chiroderma villosum has a laterally positioned initial ossifying nucleus of the nasal (Straney, 1983).

Straney (1983) suggested that the large nasal cleft observable in adult Chiroderma is a result of both later development (see character 93) and of the lateral displacement of the ossifying nucleus. The lateral position of initial ossification nucleus of Chiroderma may be a synapomorphy for this genus if the close correlation between this position and the occurrence of a large cleft in the adult as suggested by Straney (1983) is proven. This would make other characters describing the nasal bone in adult Chiroderma correlated to the present character (see characters describing size and relative position of nasal in the next section). However, according to my personal observations of stenodermatines that also have a less developed nasal bone in the adult (e.g. an extreme example is Stenoderma, which has a large vacuity replacing part of nasals) lead me to the decision of setting apart characters related to the adult nasal and to the nasal ontogenesis until there are further studies describing the ontogenesis of facial bones and potential correlations are elucidated.

I scored Sturnira lilium, which have a circular initial nasal nucleus, with (-), “inapplicable”.

This is the first use of this character in a phylogenetic analysis.

Skull morphology

Antero-dorsal and posterior skull

Character 100: Shape of maxillary ramus in dorsal profile.

Maxillary rami are roughly straight and triangular (0), or are arched (1).

In Phyllostomus hastatus and Carollia brevicauda, the maxillary rami tend to diverge in a straight line posterior to the second premolar so that they appear triangular-shaped in dorsal aspect. In contrast, all stenodermatines have arched maxillary rami.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 101: Angle at anterior arched maxilla.

Anterior section of arched maxillary bones narrowly spread, angle inscribing outermost edge of the canine and the next outermost tooth on each side is acute (less than 90^o) (0), or widely spread, angle obtuse (greater than 90^o) (1).

Freeman (1988) noted differences in the angle formed by the right and left maxillary bones in the context of her discussions about differences in palatal structure among bats. She measured the angle that inscribes the outermost edges of the canine and the next outermost tooth (generally the fourth upper premolar) on both sides of the jaw in order to describe differences among species.

The anterior maxillary rami are relatively narrowly spread in most stenodermatines (e.g. Pygoderma, Ardops). In contrast, these bones are widely spread in Ametrida, Centurio, and Sphaeronycteris (fig. 8). I coded Phyllostomus hastatus and Carollia brevicauda with "-" (inapplicable), based in the hypothesis that the orientation of maxillary bones in these two species is not homologous to the condition found in all stenodermatine bats (see character 100).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 102: Orientation of premaxilla.

Premaxilla is obliquely positioned relative to a vertical plane formed by the anterior face of canines and to a horizontal plane formed by the hard palate (0), or is roughly vertically oriented, parallel to a plane formed by anterior face of canines and perpendicular to a horizontal plane formed by the hard palate (1).

The profile of the rostrum in bats depends on the shape and placement of several facial bones including the premaxilla, the maxillae, and the nasals. The facial process of the premaxilla defines a small anteriormost part of the rostrum in phyllostomid bats. The ventral end of the premaxilla is twisted forward, and the premaxillary bone is obliquely positioned in relation to a vertical plane formed by the anterior face of canines, and to a horizontal plane formed by the hard palate, in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in many stenodermatines (e.g. Sturnira lilium, Vampyressa bidens). In contrast, in many stenodermatines the premaxilla is roughly vertical oriented, parallel to a plane formed by anterior face of canines, and perpendicular to the horizontal plane formed by the hard palate (e.g. Uroderma bilobatum, Pygoderma, Vampyressa pusilla).

The variation in the orientation of bones that compose the rostrum in stenodermatine bats was originally used in a phylogenetic analysis by Lim (1993: character 7) in a general character describing the form of the rostral profile of stenodermatines (“gradually sloping” or “dorso-ventral compressed”). Wetterer et al. (2000, character 47) subsequently built a binary character to account for the variation in rostrum profile within phyllostomid bats. Both Lim (1993) and Wetterer et al. (2000) included forehead orientation and placement of narial openings in their definition of the character describing rostrum profile, thus accommodating the variation in shape of the rostrum of stenodermatines in a single character. However I found that forehead orientation, shape and relative size of the nasal bone, and relative position of nasal aperture vary in a complex fashion within stenodermatines that may not easily be described in a single character. I therefore treated orientation of premaxilla (this character), shape and orientation of facial maxilla, relative size of the nasal bone, forehead orientation, and placement of edges of the narial aperture separately, rather than attempting to describe rostral shape in a single character.

To cite one example: the rostral profile in Stenoderma appears to slope continuously from the braincase when seen in lateral view. However, the dorsal surface of the rostrum of Stenoderma is actually abruptly disrupted by a depression where the nasals lie respectively below and between the developed temporal and supraorbital ridges, as if they were pushed dorso-ventrally between them. Posterior to the depressed nasals in Stenoderma the forehead lies perpendicular in relation to a palatal plane, a condition seemingly homologous to the perpendicular forehead of Ametrida and Sphaeronycteris (see character 115). Therefore the orientation of the premaxilla in Stenoderma is clearly independent from the orientation of other facial bones.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the orientation of premaxilla observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 103: Oblique premaxilla.

Premaxilla strongly oblique, ventral premaxilla situated in plane dorsal and not parallel to the plane formed by the anterior face of the canines (0), or slightly oblique, roughly follows inclination of the plane formed by the anterior face of the canines (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and many stenodermatines have the premaxilla much twisted with the ventral part forward, and situated in a plane that is not parallel to that formed by the anterior face of the canines (e.g. Ametrida, Mesophylla macconnelli, Vampyressa nymphaea). In contrast, several other stenodermatines have a slightly obliquely positioned premaxilla located in a plane roughly parallel to that formed by the anterior face of the canines (e.g. Ectophylla alba).

All stenodermatines with a non-oblique positioned premaxilla were coded "-".

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 104: Surface of premaxilla.

Premaxilla is smooth, not marked by grooves outlining incisors roots (juga) (0), premaxilla marked by grooves outlining roots of the incisors (1).

The bone of premaxilla is smooth and slightly or not marked at all by grooves outlining tooth roots (juga) in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Vampyrodes, Centurio, and see fig. 8). In contrast, the bone of premaxilla appears thinner, and has a corrugated appearance as it is marked by grooves outlining the roots of the incisor teeth (jugae) in many other stenodermatines (e.g. Vampyressa brocki).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 105: Shape of facial process of maxilla.

Facial process of maxilla not compressed (0), or only slightly compressed from P3 backwards (1), or compressed laterally at level of premolars (2), or compressed laterally at level of the entire series of upper teeth, from canines to molars, forming a concave surface (3), or facial process of maxilla is compressed dorsoventrally and oriented horizontally, roughly parallel to palatal processes (4).

The facial process of the maxilla covers the largest part of anterolateral rostrum in bats. This process lies roughly perpendicular to the palatal process of the maxillary bone in most phyllostomids (Wetterer et al., 2000), but has a variable form and orientation among species of stenodermatine bats (see fig. 8). The facial process of the maxilla has no lateral or dorsoventral compressions in many stenodermatines (e.g. Sturnira lilium, Ardops, and see fig. 8), instead being slightly convex. In contrast, the facial process of the maxilla is slightly compressed laterally at the level of *P3* and posteriorly in *Ectophylla*. A third condition is observed in some stenodermatines, in which the lateral facial process of the maxilla is compressed at level of premolars (*e.g. Chiroderma villosum, Ectophylla, Vampyressa bidens, V. brocki*).

All species of *Phyllops* (*Phyllops falcatus* and the two fossil forms, *P. silvai*, and *P. vetus*) have a fourth condition in which the facial process of the maxilla has a concave surface situated between the anterior edge of orbits and the maxillary toothrow, giving an excavated appearance to the bone (Tavares and Mancina, 2008). As a result, in *Phyllops* it is possible to see the part of the facial process that lies close to and dorsal the maxillary toothrow when the skull is viewed in dorsal aspect (see fig. 10). This condition appears to be unique to the genus *Phyllops*, and is seemingly intermediate between the “flat and perpendicular” facial process commonly found in phyllostomids (including most stenodermatines) and the extreme dorsoventral compression and horizontal orientation of the facial process of the maxilla seen in *Ametrida* and *Sphaeronycteris toxophyllum*. In these two species, a fifth condition is observed, in which the entire facial process of the maxilla is oriented horizontally, lying roughly parallel to the palatal process. As a result, the facial process of the maxilla appears dorsoventrally compressed when the skull is viewed in lateral aspect, and virtually the entire facial maxilla is visible in a dorsal view of the skull.

I scored *Phyllostomus hastatus* and *Carollia brevicauda* with “-” since I am hypothesizing that the orientation of maxillary bones in these two species is not homologous to the condition found in all stenodermatine bats (see character 100).

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps. Within this hypothesis, conditions of the maxilla described as “compressed” and “concave” are intermediate between “uncompressed” and “horizontal”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 106: Surface of facial process of maxilla.

Facial process of maxilla marked by grooves outlining roots of cheek teeth (0) or smooth or only slightly marked by grooves outlining roots of cheek teeth (juga) (1).

The facial process of the maxilla is marked by grooves shaped by the tooth roots (juga) in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many other stenodermatines (e.g. Vampyressa brocki, and see fig. 8). In contrast, the facial process of the maxilla is virtually smooth or only slightly marked by the roots of teeth in many stenodermatines (e.g. Sturnira lilium, Vampyressa pusilla, and see fig. 8).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 107: Direction of opening of external nares.

Narial opening faces anteriorly (0), or anterodorsally (1), or dorsally (2).

In most bats (e.g. Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Artibeus) the narial opening (= external nare) opens anterodorsally in a plane that is oblique to both the occlusal plane of the teeth and to the plane defined by the anterior surfaces of the upper inner incisors. Within stenodermatines, this condition occurs in most species. In contrast, the narial opening is located in a plane that faces primarily anterior (and perpendicular to that passing through occlusal plane of upper dentition) in some stenodermatines (e.g. Pygoderma and an undescribed species of Vampyressa, from Bocas del Toro, Panama, and see fig. 8). A third condition is observed in some other stenodermatines (e.g. Vampyressa brocki, Stenoderma, in which the narial opening faces dorsally along most of its extension, being mostly located in a parallel plane to that formed by the hard palate (see fig. 8).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the direction of opening of external nares observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 108: Location of posterodorsal edge of external nares.

Posterodorsal edge of narial opening lies level with anterior P3 (0), or posterior P3 (1), or anterior P4 (2), or posterior P4 (3), or posterior M1 (4), or posterior M2 (5).

The position of the edges of external nares along the long axis of the skull can be determined by comparing the positions of anteroventral and posterodorsal edges of the narial openings relative to the toothrow. The dorsal edge of external nares is formed by the anterior nasals and varies in a complex fashion among the taxa in this study independently of the direction of narial openings, as described in character 109. This edge is located at the level of anterior P3 in Vampyressa sp. (Bocas del Toro) and Ectophylla. In contrast, the edge is displaced to the level of posterior P3 in Carollia brevicauda and in several stenodermatines (e.g. Enchisthenes, Vampyressa pusilla). A third condition is observed in some other stenodermatines, which have which have the dorsal narial edge displaced to lie at the level of anterior P4 (e.g. Artibeus [Dermanura] cinereus, Mesophylla, Vampyressa bidens). A fourth condition is observed in Phyllostomus hastatus and many stenodermatines (e.g. Sturnira lilium, Vampyressa brocki), which have the dorsal narial edge of the nares located at the level of posterior P4. Stenoderma and Sphaeronycteris have a fifth condition, in which the dorsal edge of nare located at the level of posterior M1. Finally, Ametrida has the posteriormost position of the dorsal edge of nares within stenodermatines, this dorsal edge located at the level of posterior M2.

This character has been ordered 0⇔1⇔2⇔3⇔4⇔5 to reflect a series of logically intermediate steps in the location of posterodorsal edge of external nares observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 109: Placement of anteroventral edge of external nares.

Anteroventral of the narial opening located directly dorsal to upper incisors, barely separated from roots of incisors (0), or conspicuously separated from roots of incisors by the bone bar formed by facial process of premaxilla and located in the same plane of anterior face of incisors (1), or displaced caudad, to the level of a plane passing through posterior face of upper outer incisors (2), or to the level of a plane formed by canines (3), or to the level of a plane running through the distal half of P3 (4), or to the level of a plane running through the distal half of P4 (5).

The anteroventral edge of the nares is formed by the premaxilla and facial process of the maxilla, which also forms the anterolateral wall of the nasal cavity.

The location of the ventral edge of the narial opening varies within Stenodermatinae independent of both the orientation of nasal apertures (see character 107) and of the morphology of posterorostral elements of the rostrum (see character 108).

In Centurio, there is virtually no separation between the ventral edge of external nare and the roots of upper incisors because they are located directly dorsal to the upper incisors. In contrast, the narial opening is conspicuously separated from the roots of the incisors by an expanse of bone and situated in the same plane as the anterior surface of the upper incisors in some stenodermatines (e.g. Uroderma bilobatum, Ardops, Vampyressa sp. from Bocas del Toro). A third condition is observed in Carollia brevicauda and some Vampyressa, in which the ventral edge of the nares is slightly displaced posteriorly to the level of a plane passing through posterior face of upper outer incisors (e.g. Vampyressa melissa, V. pusilla and V. thyone). Phyllostomus hastatus and most stenodermatines (e.g. Sturnira lilium, Ectophylla alba) have a fourth condition, in which the ventral edge of the narial opening is located roughly at the level of the upper canines. Stenoderma has yet a fifth, unique condition, in which the ventral edge of the nares is located approximately at the level of the distal half of P3. Finally, Ametrida and Sphaeronycteris have a sixth condition, in which the anteroventral edge of the narial opening is situated dorsal to the distal half of P4.

This character has been ordered 0⇔1⇔2⇔3⇔4⇔5 to reflect a series of logically intermediate steps in the placement of anteroventral edge of external nares observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 110: Relative size and shape of ventral edge of the nares.

Ventral margin of each nare slopes to a v-shape and has virtually no straight base (0), or with a relative narrow straight base, lateral edges terminating at level of I1 (1), or with a relatively large straight base, lateral edges terminating at level of I2 (2), or polymorphic, either “v-shaped” or with a narrow straight base (3).

In the midst of attempting to understand the variation of ventral narial margin within stenodermatines I found two apparent independently evolved features. In the present character, I define this margin based on the presence of a narrow or broad straight margin or on its absence (v-shaped margin), and in the next character I convey the presence/absence of a medial notch (see character 111). The ventral margin of each narial opening slopes to a v-shaped surface that have virtually no straight base in some stenodermatines (e.g. Sturnira lilium). In contrast, the ventral margin of the nares has a straight and narrow base reaching up the I1 level in Carollia brevicauda, Rhinophylla pumilio and in some other stenodermatines (e.g. Vampyressa pusilla). A third condition is found in Phyllostomus hastatus and many stenodermatines (e.g. Ametrida, Vampyressa brocki), in which the straight base of ventral margin of nare is broader and reaches I2 level. Vampyressa thyone may have either a narrow straight base or a completely v-shaped ventral margin of nares, and was coded here as a separate, fourth state.

Peterson (1968) described the occurrence of a broad straight ventral margin of the narial opening for Vampyressa brocki as an useful character to distinguish between Vampyressa brocki and V. p. pusilla and V. p. thyone (currently recognized as two separate species, Lim et al., 2003). Indeed, the relative extension of the straight margin is consistently larger in Vampyressa brocki than in all specimens of V. thyone and V. pusilla that I examined, and a v-shaped ventral narial edge with virtually no straight base is never found in the currently available specimens of V. brocki. On the other hand, whether the shape of the ventral narial opening of V. thyone is actually polymorphic within this taxon or it is a diagnostic character to define species within a complex needs to be further investigated. With the evidence at hand, V. thyone appears polymorphic, with either a narrow straight band in the ventral margin of nare or a totally v-shaped edge, but never with a broad ventral margin.

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps in the relative size and shape of ventral edge of the nares observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 111: Notch in the ventral margin of the external narial opening. Ventral margin of external narial opening smooth and unnotched (0), or with notch (1).

The ventral edge of the external narial opening is not notched in Phyllostomus, Carollia brevicauda, Rhinophylla pumilio, and in some individuals of Vampyressa pusilla and V. thyone. In contrast, a v-shaped notch occurs in the medial part of the ventral edge of the narial opening in most stenodermatines (e.g. Mesophylla macconnelli). Vampyressa pusilla and V. thyone appear polymorphic for this character and were scored 0/1.

Species with a “v-shaped” ventral margin of nare were scored “-“ for this character (see character 110).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 112: Relative size of the nasal bone in the adult.

Nasal long, occupying all extension of the rostrum, and slender, tapers from the posterior to anterior direction (0), or nasal short, occupying 2/3 of the rostrum, anterior tip not forming a continuous edge with the anterodorsal maxilla and thus creating a recess (1), or nasal very short, occupying approximately half of the rostrum (2), or nasal extremely truncated, occupying one-third or less of the rostrum (3).

The nasal in most bats is a narrow, elongate bone that is usually broad at the posterior end and slightly tapered anteriorly where it meets the anterodorsal ramus of the facial process of the maxilla. Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and several stenodermatines have a rectangular slender nasal bone that tapers toward anterior rostrum meeting and forming a continuous border with the anterodorsal maxilla (e.g. Vampyrodes, Ardops). In contrast, Vampyressa melissa, V. pusilla, and V. thyone have somewhat shorter nasal bones that occupy approximately 2/3 of the rostrum. In these forms the anterior tip of the nasal ends posterior to the edge of the anterodorsal maxilla ramus, thus creating a recess between those bones (see fig. 8). A third condition is observed in Vampyressa bidens and V. brocki, in which the nasal is even shorter, occupying roughly half of the rostrum but again meets and forms a continuous anterior border with the anterodorsal ramus of maxilla. The nasal of Vampyressa nymphaea is further shortened, “v-incised” and occupies less than half rostrum in this species, a condition herein interpreted as a fourth state. Finally, some other stenodermatines (e.g. Chiroderma villosum, Stenoderma) have a fourth condition, in which the nasals are much shortened, to the extreme among stenodermatines, occupying one-third or less of the rostrum longitudinal axis.

Although the nasal bone may be very shortened in the adults of certain species of stenodermatine bats (e.g. Ametrida) due to ontogenetic constraints as in the case of Chiroderma villosum (see characters above, about skull ontogenesis) there is no current available data on the ontogenesis of other species of stenodermatines with or without shortened nasals for testing homologies of these conditions. If the ontogenetic paths of bats with shortened or truncated nasals prove to be similar then a single character (either based on ontogenesis or adult skulls) may explain and express this condition.

Goldman (1920: 69) cited the recess formed by the shortening of the nasal as diagnostic for “Vampyressa minuta” (= V. thyone), commenting in his account of Chiroderma, comparing this latter genus with Vampyressa: “the apparent absence of nasals [in Chiroderma], their excision foreshadowed in Vampyressa having progressed to the extreme degree”.

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps in the relative size of the nasal bone in the adults, observed within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 113: Nasal shape and relative placement in the rostrum.

Nasal flat or only slightly convex, forming a continuous surface with facial processes of maxilla and premaxilla (0), or obliquely positioned with lateral part situated in the same plane as the dorsal maxilla, and its medial part shifted down (1), or bowed in the antero-posterior axis, rostrum is disrupted by a concavity observable as a curved surface in lateral aspect (2), or twisted with medial part up and forming an arch above surfaces of facial processes of maxilla and premaxilla (3), or located into a deep depression below and between the supraorbital ridges (4), or primate-like, placed horizontal above facial maxilla (5).

The nasal articulates posteriorly with the frontal, anteriorly with the premaxilla, and laterally with the facial process of the maxilla. Although the nasal may be either flat or slightly convex dorsally in many noctilionoids (Simmons and Conway, 2001) and forms a continuous surface with the other bone elements of the rostrum, its position and orientation is variable within stenodermatines. The nasal is flat to slightly convex forming a continuous surface with facial processes of maxilla and premaxilla in Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Uroderma bilobatum, Pygoderma bilabiatum, *Vampyressa melissa*). In contrast, some stenodermatines have the nasals slightly twisted along the lateromedial axis (with the medial part down) (*e.g.* *Mesophylla*). A third condition occurs in *V. bidens*, *V. brocki* and *V. nymphaea*, which have a bowed nasal bone in the anteroposterior direction forming a concave surface that disrupts the lateral profile of the rostral skull of these bats. Several other stenodermatines have a fourth condition in which nasals are arched and elevated above facial maxilla (*e.g.* *Enchisthenes hartii*, *Ectophylla alba*, *Phyllops falcatus*, *Ardops nichollsi*). *Stenoderma* has a fifth condition, with the nasal located into a deep depression in the rostrum between the two thick elevated rostral ridges observed in this species. Finally, the nasal bone is retracted between the orbits in *Ametrida* and *Sphaeronycteris*, located in a plane above the plane of their dorso-ventrally compressed facial premaxilla and maxilla, with distal tips shaped as a small rounded projection that can be seen both in lateral and dorsal views. This condition resembles that seen in many primates with shortened rostra.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 114: Posterior extent of nasal.

Nasal distal tip terminates at level of anterior rim of orbit (0), or posterior to anterior rim of orbit (1).

The distal part of the nasal in many bats ends at the level of the anterior orbital rim. This condition is seen in *Phyllostomus hastatus*, *Rhinophylla pumilio*, Carollia brevicauda, and several stenodermatines (e.g. Chiroderma villosum, Ametrida). In contrast, the distal tip of the nasal lies posterior to the level of the anterior rim of the orbit in many other stenodermatines (e.g. Enchisthenes, Vampyrodes, Phyllops falcatus, Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 115: Inflations in the rostral skull.

Rostral skull without inflations (0), or anterodorsal maxilla slightly inflated (1), or postorbital region of skull inflated (2), or anterodorsal maxilla and postorbital region of skull with inflations (3), or most part of dorsal maxilla inflated, including anterior and laterodorsal maxilla and postorbital region of the skull (4), or posterior part of dorsal maxilla inflated, from a medial point toward distal aspect and postorbital region of the skull (5), or anterior portion of orbital wall with a rounded inflation, possibly encompassing part of frontal, lachrymal, and orbitopalatine bones (6), or large area of rostral skull inflated, from anterodorsal maxilla to posterior orbital wall, possibly encompassing maxilla, frontal, lachrymal, orbitopalatine, and orbitosphenoid bones (7).

Most stenodermatines appear at first sight to have a smooth and not inflated rostral skull, with the exception of the aberrant skull of Pygoderma that has a throughly swollen rostrum (see state 8 of this character). However, under careful investigation I have observed that the occurrence of swellings in the rostral skull is actually a recurring character within stenodermatines that varies in extension, encompassing different sets and parts of rostral bones. The hypothesis implicit in the present character is that those inflations in the rostral skull are potentially homologous features that are best explained by a multistate character. I however treated swellings in the ventral palatine bone separately (see character 131) as it seemed difficult to trace a straight relationship between those swellings and the ones I describe in the present character.

The rostral skulls of *Phyllostomus hastatus*, *Rhinophylla pumilio, Carollia brevicauda*, and of several stenodermatines (*e.g.* *Ametrida*) have no inflated bones. In contrast, *Sturnira lilium* has the postorbital region inflated (as well as other species of *Sturnira*, such as *S. tildae*). A third condition is observed in some stenodermatines (*e.g.* *Platyrrhinus helleri*, *V. nymphaea*, and *Vampyressa brocki*) that have a slightly inflated anterodorsal maxilla. A fourth condition found in other stenodermatines (*e.g.* *Vampyressa bidens*) is the occurrence of inflations both in the anterodorsal and postorbital portions of the skull. Several other stenodermatines (*e.g.* *Artibeus [Dermanura]*, *Enchisthenes hartii*, *Ectophylla alba*) have yet another condition in which the fronto-maxilar junction has an inflation located just anterior to the postorbital region. *Vampyressa pusilla*, *V. thyone*, and *V. melissa* have a sixth condition, in which most part of the dorsal maxilla along the nasals is slightly inflated. *Sphaeronycteris* has a rounded inflation located in the anterior portion of orbital wall, possibly encompassing part of frontal and lachrymal. The inflations are hidden in a frontal view by the modified anterior orbital edges. The impression is that because of the extremely shortened rostrum of *Sphaeronycteris* and of the anterior displacement of its orbits, little space has remained for the nasal cavity, and the paired rounded inflations seem to provide it. This condition is unique among bats and to the best of my knowledge it has not been previously described. Finally, a ninth condition observed in Pygoderma is a large area of rostral skull inflated, from anterodorsal maxilla to posterior orbital wall, apparently encompassing maxillary, frontal, lachrymal, orbitopalatine, and orbitosphenoid bones.

Although I at first considered this character as a good candidate for ordering, I found that there are still many questions about homologies within it that must be be left unresolved until clues from ontogenetic studies are available. The orbital wall in bats, for example, is a complex mosaic of bony elements (e.g. dermal bones such as the frontal, and endochondral bones such as the alisphenoid), the boundaries of which often obscured in adult and even juvenile bat skulls by the fusion of adjacent elements (Novacek, 1993). In the absence of sutures it is hard to make definitive statements about positional homology of the skull bones among species with such diversity in skull morphology.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 116: Fronto-maxillary suture and supraorbital ridge.

Supraorbital ridge, fronto-maxillary suture, and coronal lines of rostrum unmarked or only faintly marked (0), or at least partially marked (1), or distinct throughout (2), or modified and laminar-shaped (3).

The rostral shield in bats is highly variable, depending on the morphology and relative contribution of rostral bones, the occurrence of inflations (see character 115) and of ridges. Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Vampyressa pusilla) have neither well-defined suture lines nor well-marked supraorbital ridges in the posterior rostrum of their adult skulls, even when in some cases the postorbital process is developed (see character 117). In contrast, Platyrrhinus helleri, Phyllops falcatus, and Vampyressa nymphaea have these lines partially marked by ridges and sutures: in these the coronal line of skull partially develops into a ridge, starting from a midpoint between the vertex (point of meeting with interparietal line) and the orbital rim, and the supraorbital ridge may be distinct. A third condition may be found in Phyllostomus hastatus and several other stenodermatines (e.g. Artibeus jamaicensis, Ariteus), which have marked coronal lines and supraorbital ridges that open in an inverted “v” down to rostral skull. Finally, Ametrida, Sphaeronycteris, and Stenoderma have coronal and supraorbital ridges modified into laminar shaped ridges. The combination of this character with others (e.g. characters related to the nasal shape and placement) makes the morphology of the rostro-medial skull of Stenoderma unique among bats.

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps in the development of facial lines and ridges in the adult skull of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 117: Postorbital process.

Postorbital process well-developed (0), or poorly developed (1).

The postorbital process is relatively well developed and clearly defined in Phyllostomus hastatus, Carollia brevicauda and in some stenodermatines (e.g. Chiroderma villosum). In comparison, this process is poorly developed and faintly defined in most stenodermatines (e.g. Uroderma bilobatum). This character appears to be variable within Vampyressa nymphaea and was coded as a polymorphism “0/1” in the data matrix; such variation will be treated separately elsewhere in a revisionary study of this species.

Variation in the development of the postorbital process of bats was previously used by Marques-Aguiar (1994: character 15) in her study of Artibeus and by Velazco (2005: character 19) in his study of Platyrrhinus.

Character 118: Forehead relative orientation.

Forehead (= anterior part of the skull posterior to the nasal) continuous in the anterodorsal plane, lateral profile of rostrum slopes gently postero-anteriorly from forehead to nasal bones (0), or forehead protrudes, lateral profile of rostrum broken (1), or forehead flexed vertically, placed in a plane roughly perpendicular to palatal plane (2).

The frontal bone is often difficult to delimit precisely in the adult chiropteran skull because of the fusion of bone elements and disappearance of suture lines. I therefore define the forehead, without delimiting precisely the frontal bone location, as the anterior region of the skull located immediately dorso-posterior to the distal end of the nasal bone.

The forehead region of the skull of Phyllostomus hastatus, Carollia brevicauda, Sturnira lilium, and most stenodermatines is continuous with the nasal region in postero-antero dorsal outline, and it slopes gently towards its meeting with the distal portion of nasal (e.g. Sturnira lilium, Phyllops vetus, Vampyressa melissa). In contrast, Vampyressa nymphaea have a protruding forehead that breaks the rostral profile when viewed from lateral view. A third condition occurs when the forehead is roughly perpendicular in relation to the palatal plane, which appears in Ametrida, Sphaeronycteris, and Stenoderma.

Lim (1993) and Wetterer et al. (2000) described the change in orientation of the forehead and of the premaxilla and maxilla to account for the variation in the sloping of the rostrum outline among phyllostomids. However, I found that the forehead orientation is an independent character in relation to maxilla and premaxilla orientation within stenodermatines. For example, Stenoderma shares the vertically-oriented forehead with Ametrida and Sphaeronycteris (this character) but does not share the horizontally-oriented premaxilla and maxilla of these species (characters 102 and 105). The roughly perpendicular orientation of the forehead of Ametrida and Sphaeronycteris was not explicitly mentioned in the character described by Lim (1993) for the variation in rostrum sloping of stenodermatine bats. Yet the forehead morphology of Vampyressa nymphaea has not been previously described as a separate, unique condition among stenodermatines. The extent of forehead protrusion in V. nymphaea appears variable and will be treated separately in another study.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the in forehead orientation in the adult skulls of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 119: Breadth of postorbital constriction.

Postorbital constriction relatively narrow, minimum width less than or equal to 50 % of braincase breadth (0), or moderate, minimum width greater than or equal to

55 % the breadth of the braincase (1), or or broad, more than 70 % the breadth of the braincase (2).

Phyllostomus hastatus and some stenodermatines (*e.g.* *Ametrida*, *Vampyressa nymphaea*) have a narrow postorbital constriction, approximately 50% or less of their braincase breadth. In contrast, *Carollia brevicauda*, *Rhinophylla pumilio* and most stenodermatines (*e.g.* *Artibeus jamaicensis*, *Chiroderma villosum*) have a moderately broad postorbital constriction, equal to or greater than approximately 55 % of the braincase breadth. A third condition, found in *Pygoderma*, is a broad postorbital constriction of more than 70 % the breadth of the braincase.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 120: Comparative breadth of post and interorbital constriction. *Postorbital constriction is conspicuously narrower than interorbital constriction (0), or breadth of postorbital constriction is virtually equal the breadth of the interorbital constriction (1).*

The postorbital constriction is always narrower than the interorbital constriction in *Phyllostomus hastatus*, *Carollia brevicauda*, *Rhinophylla pumilio*, and in most stenodermatines (*e.g.* *Vampyressa* *melissa*). In contrast, the postorbital constriction has roughly the same breadth as the interorbital constriction in some stenodermatines (*e.g.* *Ametrida*, *Mesophylla*, *Vampyressa pusilla*).

According to my observations, although the postorbital constriction is sometimes slightly larger than the interorbital constriction in some individuals of Vampyressa (s.l.) (e.g. Vampyressa bidens, n = 96; V. brocki, n = 13) and slightly narrower than the interorbital constriction in some individuals of Vampyressa (s.l.) (e.g. V. nymphaea, n = 95) it averaged roughly equal in breadth, and all averaged proportionately same values when divided by braincase breadth in most individuals of these species (Vampyressa bidens, V. brocki, V. nymphaea, and V. thyone). In spite of this apparent general pattern, I conservatively scored those four species "0/1", polymorphic, for this character recognizing the need of statistical revisions of morphometrics of these species. Those measurements cited above and others were taken as part of revisions of those taxa and will be accordingly published within this context elsewhere.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 121: Development of sagittal crest.

Sagittal crest absent (0), or poorly developed (1), or always well developed, with a raised surface (2).

Although the development of a sagittal crest is often variable in bats, in stenodermatines it appears to be consistently absent in some taxa (e.g. Mesophylla, Vampyressa pusilla), configuring one state detected for the present character. In contrast, the sagittal crest is poorly developed, i.e. it is often marked but not raised thick in many stenodermatines (e.g. Sturnira lilium, Phyllops falcatus, Vampyressa bidens), and in Carollia brevicauda. Finally, the sagittal crest is developed and forms a raised surface in Phyllostomus hastatus and in some stenodermatines (e.g. Ardops nichollsi, Vampyressa melissa).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the development of a sagittal crest within stenodermatines.

The development of a sagittal crest has not been used in a chiropteran phylogenetic study previously.

Character 122: Relative depth of the rostrum.

Rostrum relatively long, skull length approximately twice rostrum length (0), or relatively shortened, skull length approximately 2 1/2 rostrum length (1), or very shortened, skull length much less than 2 1/2 rostrum length (2).

The rostrum is relatively long and measures approximately 1/2 of total skull length in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and in many stenodermatines (e.g. Uroderma bilobatum, Mesophylla, Vampyressa melissa, Vampyressa pusilla). In contrast, the skull length is comparatively shorter and measures approximately two and a half the length of rostrum in several other stenodermatines (e.g. Enchisthenes, Vampyressa nymphaea). A third condition is found in some other stenodermatines, in which the skull length is much less than two and a half the length of rostrum (e.g. Ametrida).

Although there is a lot of variation in relative size and shape of the bony elements of the rostrum of stenodermatines (nasal, facial maxilla), the relative contribution of rostral length to the total skull length is important itself to distinguish among some genera of stenodermatines (e.g. Uroderma, Artibeus and Enchisthenes), and to sort evolutionary lines of Vampyressa s.l. (e.g. represented by the subgenus Vampyressa, Vampyriscus, and Metavampyressa Peterson, 1965).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps in the relative depth of the rostrum of stenodermatines.

The relative deepness of rostrum has traditionally been used to distinguish between a clade formed by short-faced bats (subtribe Stenodermatina) from long-faced bats (all other stenodermatines) and I only refined these observations recognizing shortened rostra among customarily categorized as “long-faced” species (e.g. Artibeus cinereus) and elongated rostra amid species by tradition categorized as “short-faced” bats (e.g. Pygoderma) based on relative proportions. Yet another source of independent variation in relative skull dimension is the size and shape of the braincase, which is described in the next character (see character 123).

Character 123: Relative width and height of the braincase.

Braincase height greater than width (0), or roughly subequal or width slightly greater than height, anterior ceiling of braincase conspicuously rounded (1).

The shape of the braincase in bats is determined largely by the proportions of its width, length, and height. In Phyllostomus hastatus and Centurio height of the braincase is greater than width. In contrast, height and width of the braincase are nearly subqual or the width is slightly greater than the height in many stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum, Mesophylla macconnelli). Relative braincase length was accounted for the character 122, and consequently was not considered here.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 124: Shape of posterior border of dorsal skull.

Posterior border of skull triangular in dorsal view (0), or round (1), or flattened (2).

The posterior border of dorsal skull of bats is formed by supraoccipital and dorsoposterior portion of parietal. However there are no current ontogenetic studies and studies of young skulls of stenodermatine bats showing the limits of these bones in posterior skull, which is variable in shape and orientation. I therefore describe my observations of the morphology of the posterior skull (characters 124, 125, and 126) without reference to individual bones.

The posterior border of dorsal skull approaches a triangular shape in Phyllostomus hastatus, Carollia brevicauda and some stenodermatines (e.g. Chiroderma villosum) In contrast, this border has a rounded shape in several stenodermatines (e.g. Vampyressa bidens, V. nymphaea). A third condition is observed in other stenodermatines, which have a flattened posterior edge of the dorsal posterior border of the skull (e.g. Pygoderma, Vampyressa pusilla).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 125: Posterior midline protuberance in dorsal skull.

No posterior protuberance in caudal skull when seen in dorsal view (0), or rounded posterior protuberance present (1), or triangular protuberance present (2).

A midline caudal protuberance in the dorsal skull is absent in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla). In contrast, the parietal region conspicuously protrudes in a rounded shape, and the marginal constriction siding it creates clear boundaries with the lateral portion of the parietals in several stenodermatines (e.g. Vampyressa brocki, V. pusilla). Finally, a triangular protuberance is present in Artibeus concolor and Chiroderma villosum, constituting a third condition.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 126: Orientation of the occipital bone.

Occipital bone not rotated in the anteroventral direction, foramen magnum directed primarily caudally (0), or occipital bone axis flexed anteroventrally, foramen magnum directed primarily ventrally (1).

The occipital region in the chiropteran skull is often positioned as a slightly oblique wall in relation to the palatal and dorsal planes of the skull, with the foramen magnum mostly directed caudally. This is the case of Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Sturnira lilium, Artibeus [Dermanura] cinereus, Ectophylla alba). In contrast, in some other stenodermatines (e.g. Ametrida, Phyllops falcatus, P. vetus) the occipital bone is rotated anteroventrally toward the basal plane of the skull, and the foramen magnum is oriented to the ventral, basicranial plane in its most part.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 127: Relative position of the occipital vertex.

Intersection of the lambdoid and interparietal crest located above level of the zygomatic arch (0), or roughly at the level of the zygomatic arch (1).

All stenodermatines that have the occipital axis oriented ventrally also have the intersection of lambdoid and interparietal crests located in a point at the level of zygoma or a little below it, suggesting that these are linked conditions. On the other hand, phyllostomids that have the occipital axis oriented mostly caudally exhibit variation in the position of the vertex between lambdoid and interparietal crests. Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Artibeus jamaicensis, Pygoderma bilabiatum, Vampyressa pusilla) have the intersection located in a point much above the level of zygoma. In contrast, some other stenodermatines (e.g. Chiroderma villosum, Vampyressa brocki) have the interparietal/lambdoid vertex located in a point close to the zygoma level.

All stenodermatines that have the occipital axis oriented ventrally were scored “-“.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 128: Mastoid process.

Mastoid process projects laterally (0), or does not project laterally (1).

The mastoid process of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Vampyrodes) projects laterally and can be easily observed in dorsal view of the skull. In contrast, no lateral projection of the mastoid process occurs in many stenodermatines (e.g. Mesophylla). In these forms, the mastoid process cannot be seen in a dorsal view of the skull.

This is the first use of this character in a chiropteran phylogenetic analysis.

Ventral skull

Character 129: Palatal branch of premaxilla.

Palatal branch of premaxilla poorly developed, incisive foramina separated from the incisors by a narrow bar of bone whose anteroposterior length is equal to or less than 1/8 of the length of the incisive foramina (0), or palatal branch of premaxilla relatively well developed, the anterior rim of incisive foramen is concave in outline, incisive foramina conspicuously separated from the incisors roots by a breadth of bone twice or more the length of incisor foramen (1).

In many bats, the palatal branches of the premaxilla form the anterolateral walls of the incisive foramina, which are located anteriorly on the palate near the roots of upper incisors. In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla), the palatal branches of the premaxilla are poorly developed so that the incisive foramina are separated from the incisor roots by a very narrow bar of bone whose anteroposterior length is equal to or less than 1/8 of the length of the incisive foramina. In contrast, several other stenodermatines (e.g. Ametrida, Platyrrhinus helleri) have the incisive foramen conspicuously separated from the incisor roots by a breadth of bone equivalent to at least half the length of the incisive foramen. Additionally, the anterior rim of the incisive foramen in these species is concave in outline.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 130: Bucal ceiling shape (= osseous ventropalate shape).

Hard palate concave, slightly to moderately arched, degree of arching is much less than height of molar tooth crown (0), or palate concave, strongly arched, degree of arching roughly equal to or exceeds height of molar tooth crowns, slope of arch continuous (1), or palate strongly arched, degree of arching exceeds height of molar tooth crowns, slope of arch greatest laterally so that palate cross-section is roughly squared (lateral walls vertical, medial palate horizontal) (2), or palate convex, medial portion bordered by lateral depressions that parallel toothrow (3).

The osseous palate is a complex association of the palatal process of premaxilla, maxilla, and the horizontal process of the palatine bone. Microchiropteran bats exhibit a wide range of shapes and degree of palatal. Palatal arching in bats ranges from nearly nonexistent (so that the palate is flat) to steeply arched, variation that is possibly correlated with different feeding habits. The palate is flat to slightly vault and the degree of arching is much less than the height of molar teeth crowns in Phyllostomus hastatus, Carollia brevicauda, and some stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum, Vampyressa nymphaea, V. bidens). In contrast, the palate is strongly arched (arching equals or exceeds the height of the molar crowns) with the slope of arching continuous across the palate in several other stenodermatines (e.g. Centurio, Ectophylla alba, Mesophylla macconelli, V. melissa, V. pusilla). Stenoderma and Phyllops falcatus have also a strongly arched palate but one that does not slope continuously: the lateral walls (right above cheek teeth) are roughly vertical, and the medial palate is horizontal, roughly flat. The condition of low crowned molars set in high alveoli was described for catarrhine monkeys by Hershkovitz (1977), and is uncommon among bats. The palatal arching is even more modified in the Antillean endemic species Ardops, Ariteus, and in the mainland species Pygoderma. In these species, the palate is nearly convex, due to the occurrence of depressions alongside the bases of the maxillary molar series of teeth.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 131: Inflation in the palatal process of the maxilla.

Palatal process of maxilla without inflation (0), or ventropalatine bone with inflation (1).

In most bats, the palatal process of maxilla does not have inflations. This is the case in Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum, Ametrida, Centurio).

In contrast, Phyllops falcatus and the fossil form P. vetus have a rounded inflation in the palatal process of maxilla, which is often perforated (see fig. 10). The inflations seem to be more strongly developed in Phyllops falcatus from Haiti (four females AMNH 236696, 236691, 236692, and one specimen from unknown locality, labeled as “presumably Haiti”, AMNH 143662) than in those from Cuba (three specimens with unknown sex, AMNH 176191, 176192, 41008), and are very poorly developed in two of them (AMNH 176192 and 41008).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 132: Proportional distance between cheek teeth, and shape of posterior maxilla in occlusal view.

Greatest width between the cheek teeth occurs between the last molars and smallest between the third upper premolar and the second lower premolar, width between canines is much smaller than width between last molars, posterior maxillary toothrows divergent (0), or width between the cheek teeth is approximately sub-equal along posterior upper molar series, posterior toothrows roughly parallel (1), or toothrows converge at last upper molar but smallest width between cheek teeth is larger than distance between canines (2), or toothrows converge posteriorly, the smallest width between the cheek teeth occurs between the last molars (second or third), and width between last molars is roughly equal to the width between canines (3).

The maxillary arch of stenodermatines varies in shape in ventral outline independently of the form of the anterior toothrow (incisors and canines) premaxilla and anterior maxilla.

Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and some stenodermatines have a steadily divergent posterior maxilla and toothrows, and the greatest distance between the upper tooth series is located at the level of the last molar. In contrast, the distance between the right and left cheek teeth remains more or less constant along the posterior upper teeth series in many stenodermatines, so that the posterior maxillary toothrow are roughly parallel sided (e.g. Sturnira lilium, Uroderma bilobatum). In these forms, all molar teeth are nearly equidistant from their contralateral counterparts. A third condition is observed in several other stenodermatines, in which the last molar is displaced in the medial direction, shifted inward toward the bucal cavity (e.g. Mesophylla, Vampyressa bidens, V. melissa, V. pusilla, V. thyone). The maximum breadth between the toothrows in these forms occurs anterior to the posterior molars. Finally, Ariteus, Pygoderma, and Phyllops falcatus exhibit a fourth condition in which the least distance between the toothrows occurs posteriorly, between the last upper molars, and the largest breadth occurs at level of the fourth upper premolar (e.g. Ariteus) or first upper molar (e.g. Pygoderma). In these forms, the posterior upper tooth series is circular and the posterior teeth are arranged in a practically complete arch.

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps detected according to the observation of the morphology of the occlusal arch of maxilla within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 133: Posterior extension of hard palate.

Hard palate long, extends posterior into interorbital region (0), or short, does not extend posteriorly beyond insertion of zygomatic process of frontal (1).

The posterior hard palate border extends into the interorbital region in Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Artibeus [Dermanura] cinereus, Ectophylla). In contrast, the hard palate does not extend into the interorbital region in some stenodermatines, namely the short-faced (Stenodermatina) bats (e.g. Ametrida, Ariteus, Phyllops).

Variations in the posterior extent of the hard palate have been described previously by several authors (e.g. Owen, 1987, 1991, Lim, 1993, Wetterer et al., 2000). Owen (1987, 1991) described the variation in length of posterior hard palate through continuous parameters and Lim (1993) incorporated shape and size in a single character, using a discrete framework in a phylogenetic analysis. Simmons (1998) and Simmons and Geisler (1998) described the hard palate of bats in terms of its extension into the interorbital region (Simmons, 1998: 14, character 15, Simmons and Geisler, 1998: 173, character 15), and the present character is similar to theirs. Wetterer et al. (2000:69-70, characters 44 and 45) described a single character considering both horizontal palatal extension and emargination. They concluded that Ametrida could not be scored for a character considering palatal extension (and emargination, in the case of their description) but my interpretation of the condition of this species is that it lacks a posterior extension into the interorbital region (contra Wetterer et al., 2000), just like other stenodermatines, such as Pygoderma: I scored Ametrida with (1). Variation on the degree of emargination in the posterior border of hard palate is treated in the character 134.

Character 134: Depth of emargination in posterior border of hard palate. Emargination in posterior border shallow, never parallels upper tooth series, ends posterior to distal face of M3 (0), or relatively deeper, ends at level of anterior M2 (1), or very deep, ends at level of posterior M1 (2), or extremely deep, extends to anterior M1 (3).

There is almost no emargination or a very shallow notch in the posterior hard palate of Ametrida and Pygoderma, which ends posterior to M3. In contrast, Centurio and Sphaeronycteris have an emargination that reaches maximally anterior M2. A third condition is found in Phyllops falcatus, in which the palatal emargination reaches posterior M1. Finally, Ardops, Ariteus, Stenoderma have a deep emargination reaching up to anterior M1.

My scoring generally agrees with the treatment given by Lim (1993) for a character similar to the present. My scoring of Ametrida for this character is in disagreement with Wetterer et al. (2000), who scored Ametrida as “-” for a character similar to this (Wetterer et al., 2000, character 44: 69). My definitions of states and scorings for this character are otherwise similar to that found in Wetterer et al. (2000: 69), although with no reference to the palatal extension (see discussion under character 133).

All bats with a hard palate that extends into interorbit were scored with “-“.

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps concerning to the depth of the emargination of the posterior border of hard palate in stenodermatines.

Tavares and Mancina (2008) used this character to distinguish fossil and extinct forms of species of genus Phyllops (P. vetus and P. silvai), and from the short-faced (sutribe Stenodermatina) fossil Cubanycteris.

Character 135: Shape of shortened (emarginated) posterior border of palate.

Posterior border of shortened (emarginated) hard palate wide U – shaped (0), or forming a closed "u" or "v" constricted roughly at level of M2 with a rounded anteriormost tip (1), or always "v" shaped (2).

The shape of the notch in the posterior border of hard palate was identified as an informative character for bats with emarginated palates (lacking extensions of the palate into the interorbital regions) by Wetterer et al. (2000). Some stenodermatines have a wide u-shaped posterior border of the hard palate (Ardops and Ariteus). In contrast, Phyllops falcatus have a constricted emargination, roughly "v" or "u" shaped and often constricted at level of M2. Finally, Ametrida, Centurio and Sphaeronycteris have a v-shaped emargination in the posterior palate.

All bats with a hard palate that extends into interorbit were scored with "-".

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Lim (1993: 163, character 4) coupled depth, shape, and width of the posterior palatal emargination in a single character. I concur with Wetterer el al. (2000) that shape of the emargination appears to be an independent condition in relation to depth. The palate of species of Phyllops, for example, is deeply emarginated but varies in shape. My definitions for this character and the scoring is different from that of Wetterer et al. (2000) in some points, since I treated palatal extension separately from emargination, scored Ametrida as having a v-shaped palatal emargination, and described the condition of P. falcatus as unique for this species.

Character 136: Orientation of palatine lamina of bats with emarginated palate.

Palatine vertical laminae posterior to wide "u-shaped" emargination run roughly parallel (0), or clearly diverge (1).

Variation occurs in the orientation of posterior (vertical) palatal lamina (presumably composed of the palatine bones) within stenodermatines with "u-shaped" emarginated palate. The vertical laminae run roughly parallel to each other in Ardops and Ariteus. In contrast, the vertical laminae diverge broadly in Pygoderma and Stenoderma.

All the species without and emarginated palate, those with acute-shaped emarginations, and Phyllops falcatus (which has a unique condition of the posterior border of the horizontal palate, see character 135) were scored with "-" for this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 137: Shape of posterior border of extended ventropalate.

Caudal border of hard palate extension into interorbit roughly "v" shaped (0), or "u" shaped and without a median projection (1), or straight and "w"- shaped, with a median projection (2).

I agree with Wetterer et al. (2000) that the border of palate may not be homologous in species with and without emarginated palates, and accordingly described the shape of posterior hard palate in two distinct sets of characters. On the other hand, Wetterer et al. (2000) suggested that the shape of posterior border of hard palate is too variable within species with hard palate extending to interpterigoyd fossa but according to my observations, the caudal hard palate appears to be an informative source to detect homologies among stenodermatines with consistent conditions related to its shape and relative extension.

The posterior border of palate is "v-shaped" (i.e. with an acute vertex) in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, Ectophylla and Vampyressa melissa. In contrast, this border is "u - shaped" (i.e. with a rounded shaped border) and never has a median projection in several stenodermatines (e.g. Uroderma bilobatum, Vampyressa pusilla). A third condition is found in other stenodermatines, in which the posterior border of hard palate is larger and straighter, and often approaches to a "w-shaped" form because it also has a median projection (e.g. Vampyressa brocki).

All bats without an extension of the posterior hard palate into interorbit were scored "-".

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 138: Placement of anteriormost point of extended ventropalate.

Anteriormost, middle point of posterior border of palate in bats with extended palate relatively shallow, terminates in a point up to the level of posterior half of interorbital wall (0), or relatively deep, terminates at a point at the level of the anterior half of interorbital wall (1).

The middle point of the posterior palate is shallow and terminates at the level of the posterior half of the interorbital wall in Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and in several stenodermatines (e.g. Chiroderma villosum). In contrast, this point is displaced ending up to the posterior half of the interorbital wall in Enchisthenes, Mesophylla and Vampyressa pusilla.

All bats without an extension of the posterior hard palate into interorbit were scored “-“.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 139: Choana proportions.

Choana width greater than height (0), or width and height subequal (1), or choana height greater than width (2).

The choana (= internal narial aperture) is wider than higher in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda and in many stenodermatines (e.g. Artibeus concolor, Ardops). In contrast, the choana is roughly as wide as high in several other stenodermatines (e.g. Chiroderma villosum, Ectophylla, Vampyressa bidens). A third condition found in some other stenodermatines is a higher than wider choana (e.g. Ametrida).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 140: Mesopterygoid fossa.

Mesopterygoid fossa length great than width (0), or length and width subequal (1), or length less than width (2), or virtually nonexistent (3).

The mesopterygoid fossa is relatively longer than than it is wide in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and in many stenodermatines (e.g. Platyrrhinus helleri, Mesophylla). In contrast, length and width of the mesopterygoid fossa are subequal in several other stenodermatines (e.g. Vampyressa brocki, V. pusilla). A third condition observed in Vampyressa bidens is the presence of a mesopterygoid fossa that has a length somewhat shorter than its width. Finally a unique, forth condition, is observed in Ametrida, which have evolved to the reduction of the mesopterygoid fossa to an extreme that it is actually nonexistent.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Characters taking into account the extension or “shape” of mesopterygoid fossa have been used by several authors (Marques-Aguiar, 1994: character 21, Lim, 1993: character 4, Wetterer et al., 2000: character 45) but I focused only in the proportional extent of the fossa rather than in the shape or other conditions related to the hard palate, which were considered in several (above) characters of the present account.

Character 141: Basisphenoid pits relative proportions and depth.

Basisphenoid pits wide and deep (0), or narrow and deep (1), or narrow and shallow (2).

Phyllostomus hastatus, Carollia brevicauda, and some other stenodermatines (e.g. Pygoderma, Ectophylla) have basisphenoid pits that are wide and deep. In contrast, some other stenodermatines have narrow and deep basisphenoid pits (e.g. Enchisthenes, Mesophylla, Vampyressa nymphaea). Finally, the basisphenoid pit is narrow and shallow in some stenodermatines (e.g. Artibeus concolor, V. bidens).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

I am not aware of the use of this character in previous chiropteran phylogenetic analysis.

Character 142: Basisphenoid pits position.

Basisphenoid pits lie at level of cochlea (0), or pushed to lie anterior to cochlea (1).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and most stenodermatines (e.g. Chiroderma villosum, Phyllops falcatus) lie at the level of cochlea and posterior to it. In contrast, the basisphenoid pits of Ametrida and Sphaeronycteris are pushed to a region just anterior to the cochlea.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 143: Postglenoid process and orientation of glenoid fossa. *Postglenoid process poorly developed, articular surface of glenoid fossa is mostly directed ventrally (0), postglenoid moderately developed, as little as 1/8 to 1/4 of the medial articular surface of glenoid fossa is anteriorly oriented (1), or postglenoid process well developed, large part of the postgleonid process overhangs the glenoid fossa covering up more than 1/4 of the articular surface (2), or approximately half of the articular surface of glenoid fossa is directed ventrad, with the other half directed rostrad roughly perpendicular to the frontal process of squamosal bone (3)*.

The post glenoid process is situated just posterior to the glenoid (= mandibular) fossa, which articulates with the condyloid process of mandible. The post-glenoid process is poorly developed and the articular glenoid surface is mostly directed ventrally in *Carollia brevicauda*, *Rhinophylla pumilio* and in many stenodermatines (*e.g.* *Sturnira lilium*, *Artibeus cinereus*, *Vampyressa* sp. from Bocas del Toro, Panama). In contrast, a small medial part of the postglenoid process, as little as 1/4 to 1/8 of the medial articular surface of glenoid fossa develops and bends over the articular surface of the glenoid fossa in *Phyllostomus hastatus* and many other stenodermatines (*e.g.* *Sturnira lilium*, *Vampyressa nymphaea*). A third condition is observed in some other stenodermatines, which have a large part of the post glenoid process bent over the articular fossa of the mandible to form a curved surface that comprises a large part of the articular surface of glenoid fossa, which is accordingly oriented to face rostrally; those forms are Ectophylla and the Caribbean Stenodermatina Ardops, Ariteus, Phyllops falcatus and Stenoderma. Finally, some stenodermatines have well developed postglenoid processes that are oriented roughly perpendicular to the glenoid fossa. As a result, half of the articular surface of the glenoid fossa faces ventrally and and the other half rostrally; those species are the continental Stenodermatina bats Ametrida, Centurio, Pygoderma, and Sphaeronycteris).

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps detected according to the observation of the variation of the posglenoid process and orientation of glenoid fossa of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 144: Size of ectotympanic bulla relative to the cochlea.

Ectotympanic bulla extends across one-third of cochlea (0), or extends across more than one-third, and up to one-half of the cochlea external surface (1).

Carollia brevicauda, Rhinophylla pumilio and many stenodermatines (e.g. Platyrrhinus helleri, Vampyressa brocki) have a relatively short ectotympanic bulla, which extends maximally up to 1/3 of over the cochlear surface. In contrast, Phyllostomus hastatus and some others stenodermatines (e.g. Sturnira lilium, Phyllops falcatus) have the ectotympanic bulla extending to cover more than one-third, up to one half of the cochlea.

This character has been previously used in the phylogenetic analysis of Simmons and Geisler (1998).

Character 145: Cochlear wall.

Cochlea phanerochlear (0), or cryptocochlear (1).

Novacek (1991) studied the variation in thickness of the cochlear wall of microchiropteran bats. *Phyllostomus hastatus* and many stenodermatines (*e.g. Vampyressa nymphaea*, *V. melissa*) have a “phanerocochlear” condition, in which the cochlear walls are thin and sometimes even translucent. In contrast, *Carollia brevicauda*, *Rhinophylla pumilio* and several stenodermatines (*e.g. Chiroderma villosum*, *Sturnira lilium*) have a thick cochlea, the “cryptocochlear” condition as defined by Novacek (1991).

This character has been previously used in the phylogenetic analysis of Simmons and Geisler (1998).

Lateral skull

Character 146: Number and location of infraorbital foramina.

Single infraorbital foramen present in anterior maxilla (0), or two infraorbital foramina, with the dorsal foramen usually anterior to the ventral (1).

There is usually a single infraorbital foramen located in the maxilla anterior to the anteriormost orbital rim in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Sturnira lilium, Ectophylla). In contrast, most stenodermatines normally have two foramina, the dorsal foramen often a little displaced anteriorly in relation to the ventral foramen (e.g. Chiroderma villosum, Vampyressa pusilla).

Some other conditions related to the infraorbital foramen are variable among some species of stenodermatines, such as relative size of the foramina, when there are two foramina, as in the case of Vampyressa (s.l.). Although in some cases those conditions appear to have taxonomic value (e.g. Vampyressa thyone), I conservatively retained only the information related to the number of infraorbital foramen due to apparent within taxon variation.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 147. Position of infraorbital foramina.

Infraorbital foramen(ina) located dorsal to first upper molar (0), or infraorbital foramen(ina) located dorsal to fourth upper premolar (1), or infraorbital foramen(ina) located in a point comprised in the space between dorsal third upper premolar and fourth upper premolar (2), or infraorbital foramen(ina) located in a point comprised in the space between dorsal fourth upper premolar and first molar (3).

The infraorbital foramen is located dorsal to the first upper molar in Phyllostomus hastatus Rhinophylla pumilio and Carollia brevicauda. In contrast, the infraorbital foramen (ina) is (are) dorsal to fourth upper premolar in several stenodermatines (e.g. Sturnira lilium, Stenoderma, Ectophylla). A third condition may be observed in some stenodermatines (e.g. Artibeus concolor, Ariteus, Vampyressa brocki), which are infraorbital foramina located in a point comprised in the space between dorsal third upper premolar and fourth upper premolar. Finally, infraorbital foramina are located in a point comprised in the space between dorsal fourth upper premolar and first upper molar in Ametrida, Sphaeronycteris and Mesophylla.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 148. Position of posterior end of infraorbital canal.

Posterior end of infraorbital canal located dorsal to M2 (0), or posterior end of infraorbital canal located dorsal to M2 (1).

The posterior end of infraorbital canal extends to level of dorsal M2 in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and Pygoderma. In contrast the posterior end of infraorbital canal extends to level of dorsal M1 in Sturnira lilium and many stenodermatines (e.g. Vampyressa melissa, Vampyrodes).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 149: Position of anterior rim of the orbit.

Anterior rim of the orbit above anterior M1 (0), or anterior rim of orbit located above posterior M1 to anterior M2 (1), or reaching the level of posterior M2 to anterior M3 (2), or variable within species, located in a point between posterior P4 to anterior M1 (3), or above posterior P4 (4), or above P3 (5).

The anterior edge of the orbit forms a distinct rim in many bats, and may be located in different positions relative to the toothrow (Simmons and Conway, 2001). I observed the position of the anterior rim of the orbit by tracing an imaginary line from the anteriormost edge of the orbital rim to the correspondent tooth locus immediately ventral to it.

The anteriormost edge of the orbital rim is located dorsal to anterior M1 in Phyllostomus hastatus and in several stenodermatines (e.g. Ardops, Mesophylla, Vampyressa nymphaea). In contrast, the anterior rim of the orbit is positioned dorsal to either the posterior M1 or anterior M2 in Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and Pygoderma. A third condition seen in Ametrida and Sphaeronycteris was a much more posteriorly located rim of the orbit, located above the posterior M2 or even more posteriorly, reaching the level of the dorsal M3. A forth condition that I observed was an anteriormost edge of the orbital rim variably located in points between posterior P4 and anterior M1 in some stenodermatines (e.g. Uroderma bilobatum, Vampyressa melissa). A fifth condition that occurred in Chiroderma villosum and Vampyressa bidens was an anteriormost edge of the orbital rim located dorsal to posterior P4. Finally, the anterior rim of anteriormost edge of the orbital rim is located above P3 in Centurio.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Simmons and Conway (2001) first used this character in a chiropteran phylogenetic analysis.

Character 150: Orientation of zygomatic process of squamosal.

Zygomatic process oriented obliquely towards dorsal aspect, forms angle with the jugal and zygomatic process of maxilla (0), or zygomatic process of squamosal not strongly oblique, does not produce an angle with the jugal and zygomatic process of maxilla, which are oriented mainly horizontally (1).

The zygomatic process of the squamosal bone is strongly ascendant in many bats, as it is in Phyllostomus hastatus and many stenodermatines (e.g. Vampyressa brocki). In contrast, the zygomatic process of the squamosal bone is not strongly ascendant, and the zygomatic arch is predominantly oriented horizontally in several stenodermatines (e.g. Sturnira lilium, Vampyressa sp. from Bocas del Toro, Panama).

Carollia brevicauda was scored “-” as this species lacks a zygomatic arch.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 151: Thickness of zygomatic complex along its length.

Zygomatic arch of of variable thickness, some parts zygomatic wider in lateral view than other parts (0), or of uniform thickness when seen in lateral view (1).

The relative thickness of the zygomatic complex of bones is variable along its axis in Phyllostomus hastatus and several stenodermatines (e.g. Platyrrhinus helleri). In contrast, the height along axis of the zygomatic complex of bones is roughly constant along the length of the arch in many other stenodermatines (e.g. Chiroderma villosum, Sphaeronycteris).

Carollia brevicauda was scored "-" as this species lacks a zygomatic arch.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 152: Relative width of zygomatic when arch complex is of variable thickness along its lenght

Largest height of zygoma located proximal to the zygomatic process of squamosal (0), or proximal to the zygomatic process of maxilla (1).

In Phyllostomus hastatus and most stenodermatines with variable thickness along the length of zygomatic arch (Artibeus [Dermanura] cinereus, Platyrrhinus helleri, Ariteus, Vampyressa brocki) the largest height of zygoma is located proximal to the zygomatic process of squamosal. In contrast, the largest height of zygoma lies at the zygomatic process of maxilla in Vampyressa pusilla.

All species with the zygomatic arch complex of uniform breadth and Carollia brevicauda that lacks a zygomatic arch were scored "-".

This is the first use of this character in a phylogenetic analysis.

Character 153: Relative width of zygomatic when arch complex is of uniform breadth.

Zygoma thin, with height much less than 1/5 the length of the maxillary toothrow (0), or enlarged, with largest height roughly 1/5 or more the length of maxillary toothrow (1), or laminar, with largest height equals to or more than 1/4 the length of maxillary toothrow (2).

The zygomatic complex of bones when with roughly uniform breadth along its length is thin overall in many stenodermatines (e.g. Sturnira lilium, Pygoderma). In contrast, the zygoma with relatively uniform breadth is enlarged, with its largest height roughly 1/5 or more of the maxillary toothrow in several other stenodermatines (e.g. Ardops, Ariteus, Phyllops). Finally, a third condition is observed in Ametrida, Sphaeronycteris, and Stenoderma, which have the zygoma overall much enlarged to the extreme among stenodermatines, with the largest height more than 1/4 of the length of the maxillary toothrow.

Species that shown variation in thickness of zygomatic complex along its length and Carollia brevicauda, which lacks a zygomatic arch, were scored “-“ for this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 154: Development of paraoccipital process.

Paraoccipital process well developed (0), or poorly developed (1).

The paraoccipital process is well developed in Phyllostomus hastatus and in some other stenodermatines (e.g. Phyllops falcatus, Vampyressa melissa). In these forms, the paroccipital process varies from roughly half the size of the condyle to being almost as large as the occipital condyle. In contrast, the paraoccipital process is poorly developed in Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Vampyressa pusilla).

This character has previously appeared in the phylogenetic analyses of Marques-Aguiar (1994: character 20), Straney (1980: character J – 6), Owen (1987: character 12), and Velazco (2005: character 20).

Character 155: Presence of an apophysis on the paraoccipital process.

Apophysis on the paraoccipital process absent (0), or present (1).

There is no apophysis, no knob, on the paraoccipital process of Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Sturnira lilium, Enchisthenes hartii, Ectophylla, Vampyressa bidens). In contrast, an apophysis may be present on the paraoccipital process of some stenodermatines (e.g. Ardops).

This character has appeared in the phylogenetic analyses of Velazco (2005: character 21).

Character 156: Fossa in the frontal process of squamosal.

Fossa on the squamosal where the zygoma meets the braincase very reduced or absent (0), or present (1).

Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Sturnira lilium, Pygoderma) lack a fossa posterior to or at the junction of posterior squamosal zygoma with braincase. In contrast, a fossa is present on the squamosal bone just when it meets with the braincase (e.g. Vampyrodes, Vampyressa melissa).

I have not scored all the species of this study for this character, which was one of the last I selected as potentially informative over the course of the studies of cranial variation within stenodermatines, due to the lack of a sufficient number of observations within populations (i.e. individuals of a same species). These species thereafter not scored were Rhinophylla pumilio, Artibeus concolor, Enchisthenes, Ardops, Sphaeronycteris, Stenoderma, Ectophylla, Mesophylla, Vampyressa nymphaea and V. thyone), and they were coded with “?“ in the data matrix.

Velazco (2005: character 22) has first used this character in a phylogenetic analysis.

Character 157: Sutura squamosa.

Sutura squamosa poorly marked (0), or well marked, with ridge (1).

The sutura squamosa, which lies between the squamosal and occipital bone is poorly marked in Carollia brevicauda, Rhinophylla pumilio and in many stenodermatines (e.g. Ametrida, Mesophylla, Vampyressa nymphaea). In contrast, this suture is well-marked in Phyllostomus hastatus and several stenodermatines *(*e.g. Chiroderma villosum, Phyllops falcatus*)*.

This is the first use of this character in a chiropteran phylogenetic analysis.

Internal surface of skull

Character 158: Clinoid process.

Clinoid process absent (0), or present (1).

The clinoid process is a vertical prolongation of the sphenoid bone located in the sella turcica (Stromsen, 1947, Velazco, 2005). This process is absent in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Centurio, Vampyressa thyone). In contrast, some other stenodermatines have a developed clinoid process (e.g. Enchisthenes, Platyrrhinus helleri, Vampyressa brocki).

I have not scored all the species of this study for this character, which was one of the last I selected as potentially informative over the course of the studies of cranial variation within stenodermatines, due to the lack of a sufficient number of observations within populations (i.e. individuals of a same species). The species thus not scored were Artibeus [Dermanura] cinereus, Artibeus concolor, and Ardops), which were coded "?" in the data matrix.

Velazco (2005: character 23) has first used this character in a phylogenetic analysis.

Mandible

Character 159: Symphyseal region.

Well-developed "osseous" chin absent (0), or squared-shaped, well-developed osseous chin present (1).

In many bats there is no formation of a well-defined osseous chin, and the anteriormost tip of the mandible either projects slightly forward in relation to a basal mandibular plane, or it is gently curved. This condition is observed in Phyllostomus hastatus, Carollia brevicauda and in many stenodermatines (e.g. Sturnira lilium Ectophylla, Vampyressa bidens). In contrast, a well-developed, "primate-like" chin occurs in some stenodermatines (e.g. Ardops, Stenoderma, Sphaeronycteris). The symphyseal region in these species is high and perpendicular to the basal mandibular plane, forming a 90° angle with it.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 160: Anterior mental surface.

Anterior mental surface straight (0), or with rounded ventral projections (1).

The anterior mental surface has a smooth ventral border with no ventral projection in Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines (e.g. Chiroderma villosum, Vampyressa melissa). In contrast, the anterior mental surface has two ventral projections in some stenodermatines (e.g. Ametrida, Phyllops falcatus).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 161: Mandibular ramus orientation.

Tip of mandibular ramus twisted upwardly, ascendant, does not follow the horizontal plane formed by ventral surface of mandibular body (0), roughly straight, follow the plane formed by ventral surface of mandibular body (1).

The posterior tip of the mandibular ramus is twisted upward, ascendant, and does not follow an horizontal, roughly straight plane formed by the ventral surface of the mandibular body in Phyllostomus hastatus and several stenodermatines (e.g. Ardops, Vampyressa nymphaea). In contrast the posterior mandibular ramus is not ascendant but straight, roughly following the plane formed by the ventral surface of the mandibular body in many other stenodermatines (e.g. Sturnira lilium, Chiroderma villosum), Carollia brevicauda, and Rhinophylla pumilio.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 162: Coronoid process orientation in relation to longitudinal plane.

Coronoid process directed dorsally, anterior border of coronoid process forming roughly an straight angle (~ 90°) with the occlusal plane of the molar teeth (0), or anteriorly, anterior border of coronoid process forming roughly an acute angle (<90°) with the occlusal plane of the molar teeth (1).

The coronoid process of mandible is directed dorsally in Phyllostomus hastatus and in most stenodermatines (e.g. Sturnira lilium, Vampyressa pusilla), its anterior border forming an angle near to straight (~ 90°) with the occlusal plane of the molar teeth. In contrast, the coronoid process is displaced anteriorly towards rostral plane in Ardops, Ariteus and Stenoderma, its anterior border forming an angle smaller than straight (< 90°) with the occlusal plane of the molar teeth.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 163: Coronoid process orientation in relation to transverse plane.

Coronoid processes do not diverge, project straight dorsally (0), or diverge only slightly dorsally (1), or diverge strongly dorsally (2).

The coronoid processes of Ametrida are virtually not divergent, projecting straight dorsally. In contrast, the coronoid processes of Phyllostomus hastatus, Carollia brevicauda and most stenodermatines have coronoid processes that diverge only slightly dorsally (e.g. Chiroderma villosum, Vampyressa bidens). A third condition observed in some stenodermatines (e.g. Artibeus jamaicensis, Enchisthenes) is the occurrence of strongly divergent coronoid processes.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in the direction of the coronoid processes of the mandible according to transversal plane.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 164: Posterior mental foramen.

Posterior mental foramen located ventral to second lower premolar (0), or ventral to space between second and fourth lower premolar (1).

The posterior mental foramen is located in the lateral body of the mandible at a point just below second lower premolar in Carollia brevicauda, Rhinophylla pumilio, and in most stenodermatines (e.g. Vampyressa nymphaea). In contrast, the posterior mental foramen is ventral to some point between the second and the fourth lower premolars in Ectophylla.

I have not scored all the species of this study for this character, which was one of the last I selected as potentially informative over the course of the studies of cranial variation within stenodermatines, due to the lack of a sufficient number of observations within populations (i.e. individuals of a same species). These species not scored were Artibeus [Dermanura] cinereus, Artibeus concolor, Artibeus jamaicensis, Enchisthenes, Vampyrodes, Chiroderma villosum, and Ametrida), and they were coded “?“ in the data matrix.

This is the first use of this character in a chiropteran phylogenetic analysis.

Tooth morphology

Upper incisors

Character 165: Breadth of upper inner incisor crown.

Upper inner incisor crown breadth subequal along most of length from base to tip (0), or breadth of upper inner incisor crown clearly unequal along length (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Mesophylla) have roughly subequal breadths along most of the longitudinal axis of upper inner incisor. In contrast, several stenodermatines have an upper inner incisor that is of unequal breadth along its length from base to tip (e.g. Chiroderma villosum, Ametrida, Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 166: Shape of the upper inner incisor.

Upper inner incisor roughly rectangular when seen in anterior view, height somewhat greater than breadth, often with a ventral straight margin (0), or quadrate, breadth and height subequal, often with a rounded ventral margin (1), or elongated cylinder with a rounded ventral margin (2), or triangular, conic shaped with a pointed ventral margin (3).

The upper inner incisor of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and Sturnira lilium is roughly rectangular in shape and often has a straight occlusal margin. In contrast, some stenodermatines have the upper inner incisor tending to quadrate proportions (breadth and height subequal), with a rounded occlusal margin (*e.g.* *Artibeus*, *Enchisthenes, Uroderma bilobatum, Vampyressa melissa*). A third condition is observed in some stenodermatines, in which the upper inner incisor approaches to the form of an elongated cylinder (*e.g.* *V. nymphaea*, fig. 9). Finally, the upper inner incisor of several stenodermatines (*e.g.* *Ariteus*, *Ectophylla*) has a triangular, conic shape with a pointed tip (see fig. 4). In this last case, even when the conic upper inner incisor has accessory cusps (see character 170), those are also conic, triangular shaped.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Characters describing the occlusal margin shape and the size of upper inner incisors were used by several previous authors (Pacheco and Patterson, 1991: character 11, Lim, 1993: character 10, Marques-Aguiar, 1994: character 24, Wetterer *et al*., 2000: character 50, Simmons and Conway, 2001: character 29).

The main difference between the present character and those that appeared previously is that I recognized four clearly separated trends in the evolution of the proportions and shape of upper inner incisors within stenodermatines: rectangular, squared, cylindrical, and conic, whereas previous authors (Pacheco and Patterson, 1991; Lim, 1993; Marques-Aguiar, 1994; Wetterer *et al*., 2000; Simmons and Conway, 2001) generally distinguished between triangular and squared incisors. Those different treatments are due to an attempt, in this study, to describe fine-grained variation within stenodermatines, while the descriptions made previously (e.g. Wetterer et al., 2000, Marques-Aguiar, 1994) were either in broader or in specific taxonomic revisionary contexts (e.g. broader, in the case of the study of Wetterer et al., 2000 about the phylogeny of Phyllostomidae, and specific, in the case of the revision of Artibeus by Marques-Aguiar, 1994).

Character 167: Orientation of the upper inner incisor.

Upper inner incisor tips directed ventrally, not convergent (0), or directed medially so tips appear to converge (1), or tips sometimes slightly divergent (2).

The tips of upper inner incisors are relatively straight and directed ventrally so that they do not converge medially in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla alba, Chiroderma villosum, Ametrida, some individuals of Vampyressa thyone). In contrast, the tips of upper inner incisors are directed medially so that the tips converge in several other stenodermatines (e.g. Mesophylla, Vampyressa bidens). Finally, some stenodermatines have sometimes slightly divergent upper inner incisors (e.g. Stenoderma).

Vampyressa thyone was coded “0/1” in the data matrix because both states were observed within populations of this species.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 168: Proportions of triangular upper inner incisor.

Crown of triangular upper inner incisor noticeably higher than it is wide (0), or roughly as high as it is wide (1), or wider than than it is high (2).

When triangular, the upper inner incisor is noticeable higher than it is wide in some stenodermatines (e.g. Ectophylla, Pygoderma, and see fig. 5). In contrast, Ardops and Ariteus have a triangular upper inner incisor with a crown that is roughly as high as it is wide. Finally, Centurio has as a unique condition in which the crown of upper inner incisor is wider than it is high.

Miller (1907) noticed the differences between upper inner incisors relative proportions for the Caribbean bats Ariteus and Ardops vs. Phyllops falcatus.

Species without triangular shaped upper inner incisors were scored "-" for this character.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in relative proportions of the triangular upper incisor of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 169: Secondary cusps on triangular upper inner incisor.

Crown of triangular upper inner incisor with no accessory cusps (0), or with one or more accessory cusps (1).

Several stenodermatines with a triangular shaped upper inner incisor have no accessory cusps (e.g. Ametrida, Ectophylla). In contrast, other stenodermatines with a triangular shaped upper inner incisor have accessory cusps (e.g. Ardops, Pygoderma). Accessory cusps on the upper inner incisor of stenodermatines were observed by Miller (1907) and Wetterer et al. (2000).

Species without triangular shaped upper inner incisor were scored “-“ for this character.

I have modified this character from that described by Wetterer et al. (2000) to encompass all secondary cusps on upper inner incisor, including the small lateral cusp of Pygoderma. In doing so, I scored more species with the second state (“with cusps”, state 1) than did Wetterer et al. (2000), who first used this character in a phylogenetic analysis.

Character 170: Main cusp position on the triangular upper inner incisor.

Main cusp of upper inner incisor offset mesially (0), or centered (1).

The main cusp on the upper inner incisor of most stenodermatines with triangular upper inner incisor is not centered but rather placed mesially relative to a midline through the tooth (e.g. Ardops, Centurio, and Ectophylla). In contrast, Ametrida and Sphaeronycteris have a main cusp on the upper inner incisor that is centered in the middle of the tooth.

Miller (1907) described the main cusp of the upper inner incisor of Centurio as “centered”. Although one specimen of Centurio had a cusp that indeed appears centered (AMNH 177419), most specimens that I examined had a mesially offset main cusp.

Species without triangular shaped upper inner incisors were scored “-“ for this character.

This character has previously been used by Wetterer et al. (2000, character 51: 76), and my scoring for this character is similar to theirs.

Character 171: Cusp proportions on triangular upper inner incisor.

Main cusp of upper inner incisor slightly longer than lateral cusp (0), or main cusp 2 x the length of the lateral cusp (1).

Several stenodermatines with triangular upper inner incisors have more than one cusp on that tooth. The main cusp is slightly longer than the secondary cusp (e.g. Ardops, Ariteus, Centurio, and Phyllops falcatus). In contrast, Pygoderma and Stenoderma have a main cusp that is twice as long as the lateral cusps in their upper inner incisors.

Species without triangular shaped upper inner incisors were scored “-“ for this character.

The variation in the relative length of the cusps in the upper inner incisor of some species of stenodermatines was noted by Miller (1907), and described and scored in a phylogenetic analysis by Wetterer et al. (2000). My scoring is similar to Wetterer et al. (2000).

Character 172: Bilobation on quadrate and cylindrical upper inner incisors.

Upper inner incisor when either quadrate or cylindrical generally without notch in its distal margin and never bilobed (0), or sometimes bilobed (1), or often bilobed (2), or always bilobed (3).

The upper inner incisor of stenodermatines with cylindrical and quadrate/rounded shaped upper inner incisor (Sturnira lilium, Uroderma bilobatum, Platyrrhinus helleri, Vampyrodes caracciolli, Chiroderma villosum, Mesophylla, Vampyressa bidens, V. brocki, V. nymphaea, V. pusilla, V. thyone, and V. melissa) have distinct basic patterns of the occlusal margin depending on presence, relative position and extension of a notch, and permanence of the bilobation due to wearing.

Many stenodermatines (e.g. Sturnira lilium, Chiroderma villosum) generally have no notch in the distal margin of their upper inner incisor. In contrast, Mesophylla sometimes has a bilobed upper inner incisor (e.g. AMNH 207068) but this tooth is often not bilobed. The extent of this variation within Mesophylla and its taxonomic implications will be analyzed separately in another study. Some other stenodermatines have a third condition, which is in most cases having a bilobed upper inner incisor, but not always (e.g. Vampyressa bidens). Finally, another condition may be observed in Uroderma bilobatum, Vampyressa thyone, V. melissa, V. pusilla, and other undescribed species of Vampyressa sp. (from Bocas del Toro, Panama) which all have always a notched, bilobed upper inner incisor although variable in extent of notching and variably affected by wearing.

All species without bilobed or cylindrical upper inner incisors were scored “-” in the data matrix.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Some discrepancies between my scoring of presence/absence of a notch are Pacheco and Patterson (1991), whom described the upper inner incisor of Sturnira lilium as bilobed, and Wetterer et al. (2000) whom described the upper inner incisor of Mesophylla (included in Ectophylla by these authors) as “round or straight”, whereas I found that it might be sometimes bilobed. Wetterer et al.

(2000) used a similar character in their analysis of phyllostomid bats phylogeny, but they only described the shape of the occlusal margin of incisors.

Character 173: Depth of the notch in the bilobed upper inner incisor.

Notch of upper inner incisor deep and open (0), or shallow (1).

The notch of the upper inner incisor in stenodermatines that have them bilobed is deep and open distally, in general encompassing approximately 1/4 or more the height of tooth in some species (e.g. Uroderma bilobatum, Vampyressa melissa). In contrast, the notch is shallow in some other stenodermatines (e.g. Vampyressa bidens, V. pusilla, and see fig. 5).

All species without bilobed or cylindrical upper inner incisors were scored "-" in the data matrix.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 174: Wear pattern of bilobed upper inner incisor.

Bilobed upper inner incisor is generally little affected by wear, remains bilobed throughout most or all of life of individual (0), or bilobed upper inner incisor often shows wear and partial or complete loss of bilobed condition (1).

In the present character, I describe my observations on susceptibility to wear leading to the loss of the bilobed condition in the stenodermatines with an always, often or sometimes bilobed upper inner incisor. The bilobed upper inner incisor appears to have no propensity to wear in some stenodermatines (e.g. Uroderma bilobatum). In these forms the tooth remains bilobed throughout most or all of the life of the individual (as judged by wear on other teeth and overall condition of skulls and skins, and by also illustrated by my personal observations of the teeth conditions related to elderly in several adult individuals alive – such as weared molars and rough black skin nipples surrounded by bare skin in females). In contrast, the I1 is often affected by wear to the point of inducing to the complete loss of the bilobed condition in several other stenodermatines (e.g. some individuals of V. thyone).

The propensity for wear has taxonomic implications particularly in the case of Vampyressa (s.l.) because characters related to variation in the distal (occlusal) margin of upper inner incisor have been largely used to define species limits within the genus. Many species of Vampyressa exhibit total occlusion of the incisors when the jaws are closed, which may contribute to the erasure of the bilobed condition especially when the notch is shallow. Although the degrees of wear on the incisor may be intimately linked to the occlusion patterns, propensity to wear and loss of the bilobed condition is apparently an independent variable within Vampyressa: most specimens of V. melissa and other undescribed species of Vampyressa (from Bocas del Toro, Panama and from Southern Colombia) that I examined showed little wear on the upper incisors in spite of having their incisors closely in contact, whereas the upper inner incisor in V. thyone seems to be often much affected by wear though they are not in tight occlusion with the lower incisors when jaws are closed: yet it may be due to the limitation in number of specimens available for these species. In anyway, the specimen with its upper incisor most affected by wear among the individuals of V. melissa that I examined was the AMNH 233769 from Paucartambo, Peru but even in this individual, the bilobed condition was clearly visible. Also, one other specimen of a new, undescribed species of Vampyressa (from Bocas del Toro) had the most weared molars and premolars of all Vampyressa (s.l.) that I examined but preserved the bilobed condition as regarded in this character.

Another example of the taxonomic importance of wear is the genus Mesophylla. Some characters related to the upper inner incisor, although they at a first sight appear to be important to trace species limits within this genus, must be interpreted with caution. In cases in which the upper inner incisor of individuals of Mesophylla is clearly much affected by wear, some characters must be disregarded in comparisons.

All species without bilobed upper inner incisors were scored with “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 175: Relative size of lobes on the bilobed upper inner incisor.

Inner and outer lobe of bilobed upper inner incisor virtually subequal (0), or inner lobe always wider and longer than outer lobe (1), or inner lobe sometimes longer (2).

The bilobed upper inner incisor has subequal lobes in some stenodermatines, the inner being sometimes a little wider and slightly longer (e.g. Uroderma bilobatum). In contrast, the inner lobe is clearly much wider and longer than the outer lobe in some other stenodermatines with a bilobed upper inner incisor (e.g. Vampyressa bidens). Some individuals of Vampyressa thyone have the first condition, some other the second, and still others have a third condition, which is an internal lobe much longer but not wider than the external lobe.

Vampyressa thyone was coded with “0/1/2” and this variation will be examined separately in a revisionary study of this taxa.

All species without bilobed upper inner incisors were scored “-” in the data matrix.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 176: Lingual cingulum on upper inner incisor.

Lingual cingulum absent on upper inner incisor (0), or present (1).

A lingual cingulum is absent on the upper inner incisor of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and of most stenodermatines (e.g. Mesophylla). In contrast, a lingual cingulum is present on the upper inner incisor of Chiroderma villosum.

This character has been previously used in the phylogenetic analysis of Simmons and Conway (2001: character 31).

Character 177: Upper outer incisor relative size.

Upper outer incisor less than or equal to one third the length of upper inner incisor (0), or greater than or equal to one half or more of the length of upper inner incisor (1).

The upper outer incisor is much smaller than the upper inner incisor in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and in most stenodermatines (e.g. Vampyressa nymphaea). In contrast, the upper outer incisor is roughly one-half or more of the length of upper inner incisor in some other stenodermatines (e.g. Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 178: Shape of upper outer incisor.

Upper outer incisor simple, peg-like and without posteromedial cusp (0), or peg-like and often with a minute posteromedial tip (1), or peg like and deep longitudinally grooved (2), or bilobed, with subequal lobes and resembling a small upper inner incisor (3), or irregularly bilobed, with large inner lobe directed medially (4), or single-tipped, pointed, and resembling a small upper inner incisor (5).

There is a large amount of morphological variation in the design of upper outer incisor within stenodermatines. Phyllostomus hastatus, Carollia brevicauda, and some stenodermatines (e.g. Sturnira lilium, Platyrrhinus helleri, Mesophylla) have a simple acuspidate peg-like upper outer incisor. In contrast, Vampyressa bidens has a peg-like upper outer incisor that often has a minute posteromedial cusp (fig. 11). Several stenodermatines have a third condition in which upper outer incisor is longitudinally deep grooved (e.g. Ardops, Sphaeronycteris). Some other stenodermatines have a bilobed upper outer incisor, which resembles the bilobed upper inner incisor in these taxa although it is much smaller (e.g. Uroderma bilobatum, Vampyressa melissa). A fifth condition consists of an asymmetrically bilobed upper outer incisor in which the inner lobe is larger than the outer and directed medially (e.g. Artibeus concolor, Phyllops falcatus, Vampyressa brocki). Finally, Ectophylla has a single-tipped and pointed upper outer incisor that looks like a small version of the conic upper inner incisor of this species.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 179: Alignment of the upper incisors.

Upper incisors arranged in an arch, upper inner incisor in front of outer in ventral view (0), or arranged in a straight line (1).

Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines have the upper incisors arranged in arch, and the upper inner incisor lie in front of the upper outer incisor when seen in lateral aspect (e.g. Artibeus concolor, Mesophylla). In contrast, several stenodermatines have the upper incisors arranged in a straight line between the canines and may not be seen in lateral view (e.g. Ardops nichollsi, Pygoderma bilabiatum).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 180: Upper inner incisors position relative to vertical plane.

Upper incisors proodont, project forward in a plane not parallel to that of the anterior face of canines (0), or roughly parallel to such plane (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and Sturnira lilium have proodont upper incisors that lie forward in a plane that is not parallel to that of the anterior face of the canines. In contrast, the upper incisors lie in a plane roughly parallel to that formed by the anterior face of canines in stenodermatines (e.g. Vampyressa bidens).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 181: Number of lower incisors.

Often one lower incisor present, rarely two lower incisors (0), or always two lower incisors present (1).

Carollia brevicauda, Sturnira lilium, Rhinophylla pumilio and most stenodermatines (e.g. Vampyressa melissa) have two lower incisors. In contrast, Vampyressa bidens has often one lower incisor, and rarely if ever has two (see comments below). There is no study with clues on which tooth has been lost, whether is it the lower outer incisor or the lower inner incisor so I had been unable to identifying which one is the lower incisor that is present in V. bidens.

Davis (1975) reported variation in the typical incisor formula of Vampyressa bidens (i 2/1-2/1) in two Peruvian specimens: one male was 2/2-2/2 and another was 2/3-2/3. Brosset and Charles-Dominique (1990) also reported a specimen of V. bidens with three lower incisors explaining this condition as it was an aberration due probably to the loss of the fourth. On the other hand, all museum specimens of Vampyressa bidens that I was able to examine had a single lower incisor. The occurrence of more than one incisor in Vampyressa bidens could be either one exception to the typical pattern observed in V. bidens or a misidentification (e.g. those specimens could be attributable to V. brocki instead). Since I was unable to examine such specimens I conservatively scored V. bidens as occasionally having two lower incisors.

Character 182: Relative size of inner lower incisor.

Lower inner incisors smaller than outer (0), or lower incisors subequal (1), or lower outer incisors slightly larger than lower inner incisors (2).

The inner lower incisor is smaller than the outer in Carollia brevicauda and some individuals of Vampyressa brocki. In contrast, the lower incisors (outer and inner) are subequal in size in most stenodermatines (e.g. Ectophylla). A third condition occurs in many individuals of Vampyressa nymphaea and in most individuals of V. brocki, which have the outer lower incisor slightly larger than inner lower incisor.

Due to the limited number of specimens available of V. brocki, I have conservatively scored this taxon with states 0 and 1 in the data matrix. I scored Vampyressa nymphaea with 1 and 2 in the data matrix, as it appears that relative size of lower incisors is actually variable within this taxon. I scored Vampyressa bidens, which generally has only a single lower incisor, with "-".

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 183: Arrangement of the lower incisors.

Lower incisors are arranged in an arch (0), or form a nearly straight line between lower canines (1).

The lower incisors are arranged in a curved arch like the upper incisors in Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Vampyressa thyone). In contrast, the lower incisors form a nearly straight line between lower canines in Phyllostomus hastatus and many other stenodermatines (e.g. Chiroderma villosum) independently of the arched arrangement of its upper incisors.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 184: Groove pattern on lower incisors.

Lower incisors with shallow groove on anterior face of tooth, grooved surface when present often restrict to cutting edge of tooth (0), or anterior face of tooth deeply grooved (1), or never grooved, a blunt cone (2).

The lower incisors have a shallow, longitudinal groove on the anterior tooth face in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Sturnira lilium, Vampyressa pusilla) although this groove may be virtually absent in some species (e.g. Mesophylla). In contrast, the lower incisors have a deep groove in several stenodermatines (e.g. Ardops, Vampyressa bidens). Ectophylla always has a third condition, in which the lower incisors have the form of cones with a curved anterior face that always lacks a groove.

I did not account for the bilobation of the occlusal surface of the lower incisors in the present character because this appeared quite variable among the species analyzed. The occlusal surface of the lower incisors vary from being entire (straight) to slightly emarginated (e.g. individuals of Carollia brevicauda), slightly bilobed (e.g. most Uroderma bilobatum) to trilobed (e.g. U. bilobatum AMNH 209475, and many specimens of Sturnira lilium). Among the many specimens of S. lilium analyzed, the occlusal margin of the inner lower incisors (i1) was trilobed in most specimens (e.g. AMNH 213357, 213366, 230588, 230589, 230591), and was irregular in a few others (e.g. AMNH 219923, AMNH 213358). The variation in the morphology of the crown shape of both inner lower incisor and outer lower incisor may probably be due in many cases to the erosion of the enamel due to wear.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 185: Orientation of the crown of the lower incisors.

Lower incisors oriented roughly vertically, perpendicular to horizontal plane formed by molars crown (0), or directedly somewhat lingually (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and many stenodermatines (e.g. Sturnira lilium, Vampyrodes) have the lower incisors directed vertically, perpendicular to the horizontal plane formed by the crown of the molars. In contrast, several other stenodermatines have the lower incisors directed somewhat lingually (e.g. Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 186: Relative position of the outer lower incisor in relation to canine.

Outer lower incisor medial to or only slighly overlapping canine when seen in anterior view (0), or most of outer lower incisor located anterior to canine (1).

Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and many stenodermatines (e.g. Ectophylla) have a lower outer incisor that lies largely or completely anterior to the canine. In contrast, in Phyllostomus hastatus and several other stenodermatines (e.g. Vampyressa melissa) only a small part of the lateral portion of the outer lower incisors overlaps the canine in lateral view, the rest of the tooth lying more medial to the canine.

Vampyressa bidens that generally has only one lower incisor was scored "-" for this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Upper canine

Character 187: Relative position of upper canine in the toothrow.

Most of the anterior surface of upper canine faces laterally, following the upper tooth series (0), or faces anteriorly (1).

Phyllostomus hastatus, Carollia brevicauda and the majority of stenodermatine species (e.g. Sturnira lilium, Platyrrhinus helleri, Chiroderma villosum) have most of the anterior (vestibular) surface of the canine positioned laterally, following the position of the anterior (vestibular) surface of the postcanine upper tooth series. In contrast, many other stenodermatines (e.g. Enchisthenes, Pygoderma, Sphaeronycteris) have the vestibular face of upper canine positioned mostly rostrad, following the position of the anterior (vestibular surface) of the upper incisors.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 188: Upper canine posterior cingulum.

Posterior cingulum of canine poorly developed (0), or well developed (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Vampyressa melissa) have a poorly developed posterior cingulum on the upper canine. In contrast, some other stenodermatines have a well-developed posterior cingulum on the canine (e.g. Mesophylla).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 189: Relative height of the upper canine in the upper toothrow.

Upper canine more than twice as high as third upper premolar (0), or roughly twice or less (1), or of approximate size, upper canine only a little larger than third upper premolar (2).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio*,* and several stenodermatines (e.g. Sturnira lilium, Vampyressa nymphaea) have an upper canine more than twice higher than the third upper premolar (e.g. Vampyressa pusilla, and see). In contrast, many other stenodermatines have an upper canine roughly twice, or only a little less the height of the upper third premolar (e.g. Enchisthenes). Finally, other stenodermatines have the upper canine and third upper premolar roughly of approximate size as the upper canine is only a little higher than the upper canine (e.g. Ametrida).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the proportional size of the upper canine in relation to the third upper premolar in stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 190: Orientation of the upper canine.

Canines directed laterally so that the tips are divergent (0), or canine directed ventrally, tips not divergent (1).

Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Ectophylla) have an upper canine that is somewhat laterally oriented so that the tips of the right and left canines are divergent. In contrast, Phyllostomus hastatus and most stenodermatines have a roughly ventrally directed canine so that the tips of the right and left teeth are not divergent laterally (e.g. Vampyressa bidens).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 191: Secondary cusp on upper canine.

Secondary cusp on upper canine absent (0), or present (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Vampyressa nymphaea) lack secondary cusps on the upper canines. In contrast, some other stenodermatines have secondary cusps in their upper canines (e.g. Vampyressa melissa). The relative position of the secondary cusp is discussed in the next character (character 192).

The species Vampyressa pusilla and V. thyone are polymorphic for this character and were scored “0/1” in the data matrix.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 192: Relative position of the secondary cusp on upper canine.

Secondary cusp on upper canine located posterolaterally, visible only in lateral view (0), or located posterolingually (= displaced lingual), may be visible in anterior view (1).

Most stenodermatines with a secondary cusp on the upper canine have this positioned posterolaterally so that it can be observed in lateral view (e.g.

Vampyressa melissa, V. pusilla). In contrast, Ectophylla has a posterolingually positioned secondary cusp on the upper canine that may be seen in anterior view.

All species lacking a secondary cusp in the upper canine were scored “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Lower canine

Character 193: Cingulum of the lower canine.

Cingulum of lower canine poorly developed (0), or moderately developed (1), or well-developed (2).

A poorly developed or even an undeveloped posterior cingulum occurs on the lower canine of Carollia brevicauda, Rhinophylla pumilio, and many other stenodermatines (e.g. Vampyressa pusilla). In contrast, the canine has a moderately developed cingulum in Enchisthenes and Vampyressa nymphaea. Finally, a well-developed cingulum is seen on the lower canine in many other stenodermatines (e.g. Ardops, Uroderma bilobatum).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the relative development of cingula in the lower canines in stenodermatines.

A character similar to this has been used by Pacheco and Patterson (1991) in their analysis of the phylogeny of the genus Sturnira.

Character 194: Relative height of the lower canine.

Lower canine only slightly higher than the second lower premolar (0), or twice as high as the height of second lower premolar (1), or more than twice the height of second lower premolar (2).

The lower canine and the second lower premolar are of approximate size, and the lower canine is only slightly higher than the second lower premolar in Stenodermatina bats (short-faced). In contrast, Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many other stenodermatines (e.g. Vampyressa thyone) have a lower canine that is approximately twice as high as the second lower premolar. Finally, some stenodermatines have a lower canine that is more than twice the height of the second lower premolar (e.g. Vampyressa brocki).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in the relative height of lower canines in stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 195: Shape of the lower canine.

Lower canine roughly conical (0), or shaped like a flattened spear (1).

Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Sturnira lilium, Enchisthenes, Vampyressa thyone) have a conical lower canine. In contrast, some stenodermatines have a canine that is compressed anteroposteriorly, so it appears flattened, spear-like (e.g. Ametrida, Stenoderma).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 196: Orientation of the lower canine.

Lower canine curved anteroposteriorly and divergent laterally (0), or lower canine straight anteroposteriorly and divergent laterally (1), or virtually straight (2).

Unlike the upper canines, the lower canines of all taxa in this study vary in orientation both in lateromedial and anteroposteriorly directions. Phyllostomus hastatus and many stenodermatines (e.g. Artibeus jamaicensis) have a lower canine that is recurved anteroposteriorly and divergent lateromedially. In contrast, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Chiroderma villosum, Ectophylla) have a lower canine that is straight anteroposteriorly and divergent laterally. Finally, the lower canine is virtually straight (not divergent laterally and not recurved anteroposteriorly) in several other stenodermatines (e.g. Ariteus).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in anteroposterior and lateromedial orientation of lower canines in stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 197: Secondary cusp on lower canine.

Secondary cusp on lower canine absent (0), or present (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Vampyressa thyone) lack a secondary cusp on the lower canine. In contrast, Uroderma bilobatum has an anterolingual cusp on the lower canine, which is formed from a prolongation of the internal cingulum.

This is the first use of this character in a chiropteran phylogenetic analysis.

Third upper premolar

Character 198: Relative proportions of third upper premolar.

Third upper premolar higher than than it is long (0), or height and length subequal (1), or third upper premolar longer than it is high (2).

There appear to be two evolutionary trends in upper premolar morphology within stenodermatine bats. The third upper premolar is either a slender, styliform tooth as in the case of some Vampyressa (s. l.), Platyrrhinus and others, or a broad quadrangular tooth, as in the case of Artibeus and the short-faced bats (Stenodermatina). In the case of Chiroderma, Ectophylla, Mesophylla, and Vampyressa (s. l.), the reduction of third upper premolar associated to other characters contributes to the formation of a lateral gap when jaws are occluded (see characters related to the occlusion patterns). Other characters that make third upper premolar a highly variable tooth are the variation in shape of the base of the tooth in contact with maxillary alveoli, and how it is implanted in the upper jaw.

The development of a broad third upper premolar may indicate that this tooth preserved the primary function of slashing food, whereas the reduction of third upper premolar may indicate that this tooth has been displaced to another function (e.g. to leave space for a gap formation, as a proximate cause).

Although third upper premolar is generally the lowest tooth among the upper post-canine teeth series in stenodermatines, it varies in relative proportions and development. Phyllostomus hastatus and most stenodermatines (e.g.

Sturnira lilium, Enchisthenes, Centurio) have a third upper premolar that is higher than it is long. In contrast, the third upper premolar is roughly as high as it is long in Carollia brevicauda and in some other stenodermatines (e.g. some Vampyressa thyone). A third condition is observed in other stenodermatines (e.g. Chiroderma villosum, V. bidens), which have a third upper premolar that is longer than it is high.

This character is variable within Vampyressa brocki with some individuals having a third upper premolar that is as long as it is high and others having this tooth longer than it is high. Within Vampyressa melissa and V. thyone third upper premolar is either higher than it is long or as long as it is high. These polymorphisms were scored by using multiple states for every taxon with more than one state.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in the relative proportions of the third upper molars within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 199: Shape of third upper premolar in lateral profile.

Third upper premolar triangular, broad and with a straight base (0), or third upper premolar styliform with straight base (1), or third upper premolar conical with at least 1/3 of the anterior portion of base obliquely oriented and situated at level of posterior cingulum of canine (2), or third upper premolar quadrangular, base and tip triangular with roughly same proportions (3).

Viewed from in lateral outline, the third upper premolar is a broad triangular tooth with a straight base in Carollia brevicauda and Rhinophylla pumilio. In contrast, third upper premolar is a styliform tooth with a straight base in Phyllostomus hastatus, Vampyressa melissa, V. pusilla, and Vampyressa sp. (undescribed species from Bocas del Toro, Panama). However, in most stenodermatines a third condition appears, in which part of the anterior portion of the third upper premolar base is oriented obliquely and the remainder is relatively straight (i.e. parallel to molar crown), the anteriormost third upper premolar cingulum situated generally at level of posterior cingulum of canine and then ascending towards the alveolar surface (e.g. Platyrrhinus helleri, Vampyressa bidens). Finally, a fourth condition is observed in several other stenodermatines (e.g. Sturnira lilium, in which the third upper premolar is quadrangular as its base and its tip are triangular-shaped, with roughly equal proportions.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a phylogenetic analysis.

Character 200: Relative sizes of third and fourth upper premolars.

Third upper premolar is two-thirds or more the height of fourth upper premolar (0), or less than two-thirds the height of fourth upper premolar (1).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in most stenodermatines (e.g. Chiroderma villosum) the third upper premolar is more than 2/3 of the size of the fourth upper premolar. In contrast, in some stenodermatines (e.g. Vampyressa nymphaea), the third upper premolar may be shorter, generally a half or less the size of the fourth upper premolar.

This character was previously used by Velazco (2005: character 27) in his analysis of Platyrrhinus phylogeny. I have changed the definition of the states to accommodate variation within stenodermatines.

Character 201: Alignment of the third upper premolar in the toothrow.

Third upper premolar displaced lingual (0), or aligned with upper tooth series (2).

The third upper premolar is displaced lingual in relation to the other upper postcanine teeth in Phyllostomus hastatus, Platyrrhinus helleri, and Vampyrodes. In contrast, the third upper premolar is roughly aligned with the upper postcanine tooth series in most stenodermatines (e.g. Ectophylla).

Velazco (2005: character 26) first used this character in a phylogenetic analysis.

Character 202: Plane of insertion of the third upper premolar on alveolar surface.

Third upper premolar implanted in the same plane of insertion of the fourth upper premolar (0), or above it (1).

The third upper premolar is implanted in a horizontal alveolar surface roughly in the same plane as the fourth upper premolar in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in most stenodermatines (e.g. Sturnira lilium). In contrast, the third upper premolar is implanted in an excavated alveolar surface and its base lies in a plane dorsal to the base of the fourth upper premolar in several other stenodermatines (e.g. Ectophylla, Vampyressa nymphaea).

This is the first use of the character in a phylogenetic analysis.

Fourth upper premolar

Character 203: Vestibular cingulum on fourth upper premolar.

Vestibular (labial) cingulum on fourth upper premolar poorly developed (0), or well developed (1).

Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla, Mesophylla) have a poorly developed vestibular cingulum on their fourth upper premolar. In contrast, a vestibular cingulum is well developed on the fourth upper premolar of Phyllostomus hastatus and several other stenodermatines (e.g. Vampyrodes, Vampyressa brocki).

This is the first use of the character in a phylogenetic analysis.

Character 204: Stylar cusps on posterior fourth upper premolar.

Stylar cusps on posterior fourth upper premolar absent (0), or sometimes present (1), or one present (2), or two always present (3).

Stylar cusps in addition to the main cone of the fourth upper premolar are always absent in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Ectophylla and Mesophylla). In contrast, stylar cusps on the posterior part of the fourth upper premolar are sometimes present in some stenodermatines (e.g. Vampyressa brocki). A third condition is observed in Vampyressa (s.s.) species (e.g. Vampyressa melissa), in which one stylar cusp appears on the posterolateral fourth upper premolar. Finally, Uroderma bilobatum, Platyrrhinus helleri, and Vampyrodes always have two stylar cusps on the posterior part of fourth upper premolar.

My observations indicate the occurrence of a stylar cusp generally arising from the postero-lateral cingulum of fourth upper premolar in several individuals of Vampyressa (s. l.), contrarily to the conclusions of Wetterer et al. (2000), who scored Vampyressa as having no stylar cusps on posterior fourth upper premolar. I describe my observations about the differential development of this structure within Vampyressa (s. l.) in the next character (character 205).

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps detected according to the observation of the variation in the occurrence of stylar cusps on the posterior fourth upper premolar.

Lim (1993) first used this character in a phylogenetic analysis, followed by Wetterer et al. (2000), who further noticed polymorphism in this character within species of phyllostomid bats. I agree with Lim (1993) for the scoring of Uroderma bilobatum, and with this later author and Velazco (2005) for the scoring of Platyrrhinus helleri and Vampyrodes, and disagree with Wetterer et al. (2000).

Character 205: Relative size of stylar cusp on posterolateral cingulum of fourth upper premolar.

Fourth upper premolar with small stylar cusp on posterolateral cingulum, cusp size of less than 1/3 of that of main cone of fourth upper premolar (0), or with stouter stylar cusp, between 1/3 and 1/2 size of main cusp on (1).

Some stenodermatines (e.g. Vampyressa bidens, V. brocki) have a small, slender cusp-like projection arising from the posterolateral part of the cingulum of the fourth upper premolar. In contrast, some other stenodermatines (e.g. Vampyressa melissa, V. pusilla) have a stouter and larger postero-lateral cusp arising from the cingulum of the upper fourth premolar, reaching up to 1/3 to a little less than 1/2 the height of its main cusp.

All species lacking a postero-external, cusp-like stylar projection on upper fourth premolar were scored “-”.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 206: Depth of hypoconal fossa on the fourth upper premolar. Fossa on the hypoconal basin of fourth upper premolar shallow (0), or deep (1).

The fossa on the hypoconal basin of the fourth upper premolar is shallow in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Platyrrhinus helleri, Chiroderma villosum, Vampyressa bidens). In contrast, the fossa in the hypoconal basin of the upper fourth premolar is deep in some other stenodermatines (e.g. Uroderma bilobatum).

Velazco (2005) first used this character in a phylogenetic analysis. My scoring coincides with his with the exception of Vampyrodes. Velazco (2005) found intraspecific variation within Vampyrodes whereas I observed a shallow fossa in the hypoconal basin consistently in specimens of this taxon.

Character 207: Shape of the fourth upper premolar in lateral view.

Upper fourth premolar triangular and straight in lateral view (0), or triangular but slightly curved posteriorly at tip (1).

Rhinophylla pumilio, Carollia brevicauda, Sturnira lilium, and most stenodermatines have a triangular and straight fourth upper premolar when observed in lateral view. In contrast, the fourth upper premolar of some stenodermatines, while still triangular, is slightly curved posteriorly at the tip (e.g. Ectophylla, Mesophylla, Vampyressa nymphaea).

This is the first use of the character in a phylogenetic analysis.

Second lower premolar

Character 208: Second lower premolar proportions.

Second lower premolar with length either equal to or greater than height (0), or height greater than length (1).

The second lower premolar is long, with length either equal to or greater than height, in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in several stenodermatines (e.g. Chiroderma villosum, Vampyressa bidens, V. nymphaea). In contrast, the second lower premolar height is clearly greater than length in many other stenodermatines (e.g. Artibeus, Vampyressa melissa).

This is the first use of the character in a phylogenetic analysis.

Character 209: Second lower premolar relative size in toothrow.

Second lower premolar is roughly a half of height of the lower canine, and two-thirds of height of the lower fourth premolar (0), or is roughly two-thirds of height of the lower canine and two-thirds or more of height of the lower fourth premolar (1), or is one-fourth to one-third of height of the lower canine and a half or less of height of the upper fourth premolar (2).

The second lower premolar is roughly half of height of the lower canine and two-thirds or more of height of the lower fourth premolar in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Vampyrodes, Vampyressa melissa). In contrast, the second lower premolar is approximately two-thirds of the lower canine and two-thirds or more of the fourth lower premolar in several other stenodermatines (e.g. Ametrida, Centurio). Finally, some stenodermatines (e.g. Vampyressa bidens, V. brocki) have a second lower premolar that is one-fourth to one-third of height of the lower canine and a half or less of the height of the fourth lower premolar.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of the character in a phylogenetic analysis.

Character 210: Shape of the second lower premolar.

Second lower premolar triangular (0), or comma-shaped, forming a spike displaced forward (1), or blade-like (2), or flat-crowned, much reduced (3).

The second lower premolar is a sharp triangle in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Vampyrodes). In contrast, the second lower premolar is roughly comma-shaped with a sharp, spike-like cusp located anteriorly the tooth in some other stenodermatines (e.g. Ectophylla, Vampyressa melissa, V. thyone). A third condition observed in some Vampyressa s.l. (e.g. Vampyressa bidens, V. nymphaea) is a blade-like second lower premolar. Finally, the second lower premolar of Chiroderma villosum is reduced to a flat crown.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of the character in a phylogenetic analysis.

Character 211: Median ridge on lingual face of second lower premolar.

Median ridge absent on lingual face of second lower premolar (0), or present (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla, and Mesophylla) lack a median ridge on the lingual face of second lower premolar. In contrast, a dorsoventrally oriented medial ridge is present on the lingual face of the second lower premolar of many stenodermatines (e.g. Uroderma bilobatum, Vampyressa bidens, V. nymphaea) (fig. 12).

This is the first use of this character in a chiropteran phylogenetic analysis.

Fourth lower premolar

Character 212: Median ridge on lingual face of fourth lower premolar.

Median ridge present on lingual face of fourth lower premolar (0), or absent (1).

Phyllostomus hastatus and many stenodermatines (e.g. Vampyressa bidens, V. melissa) have a dorsoventrally oriented median ridge on the lingual face of their fourth upper premolar (fig. 12). In contrast, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla, and Mesophylla) lack a median ridge on the lingual face of their fourth lower premolar.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 213: Cusps on the posterior face of the fourth lower premolar.

No cusps on the posterior face of fourth lower premolar (0), or one posterolabial cusp sometimes present (1), or two cusps present (2).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines lack cusps onto the posterior face of fourth lower premolar. In contrast, some stenodermatines sometimes have a posterolabial cusp on fourth lower premolar (e.g. Ardops). A third condition occurs in Platyrrhinus helleri and Vampyrodes caracciolli that have two cusps on their posterior fourth lower premolar.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation of the variation in the occurrence of stylar cusps on the posterior face of the fourth lower premolar.

The occurrence of cusps on posterior face of the lower fourth premolar was first used by Velazco (2005) in a phylogenetic analysis. The scoring for species common to his and the present study is similar.

Character 214: Stylar cusps on anterior fourth lower premolar.

No stylar cusps on anterior fourth lower premolar (0), or one cusp present (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Ectophylla, Vampyressa pusilla) lack stylar cusps on the anterior face of fourth lower premolar. In contrast, some stenodermatine taxa have one stylar cusp on the anterior fourth lower premolar (e.g. Platyrrhinus helleri).

Velazco (2005) previously used this character in a phylogenetic analysis. My scoring for species common to his and to the present study is similar.

Upper molars

Character 215: Labial cingulum on first upper molar.

Labial cingulum absent or poorly developed on first upper molar (0), or well developed but without stylar cusps (1), or well developed but sometimes with posterior stylar cusp (2), or well developed and always with a well-developed posterior stylar cusp (3).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Ectophylla, Vampyressa melissa) have a poorly developed cingulum on the labial face of first upper molar. In contrast, some other stenodermatines have a well-developed labial cingulum on first upper molar that lacks any stylar projections or cusps (e.g. Platyrrhinus helleri). A third condition observed in the first upper molar of several other stenodermatines (e.g. Vampyrodes, Uroderma bilobatum, Vampyressa brocki) is a well-developed labial cingulum that sometimes develops in a posterolateral, cusp-like stylar projection. Finally, Vampyressa nymphaea has a developed labial cingulum with a well-developed cusp-like projection on the posterior part of the labial cingulum that may reach the size of one-third of the length of the metacone.

Artibeus jamaicensis that sometimes have a developed labial cingulum was scored 0/1 for this character.

This character has been ordered 0⇔1⇔2⇔3 to reflect a series of logically intermediate steps detected according to the observation on the development of labial cingula and stylar cusps on the first upper molar.

Velazco (2005: character 34) used a similar character to account for variation on the labial cingulum of the M1 metacone among species of Platyrrhinus. The states as presently defined in this study were differently built compared to those of Velazco (2005) and may not be directly comparable.

Character 216: W-shaped ectoloph on the first and second upper molars.

W-shaped ectoloph on first and second upper molars present (0), or absent (1).

A w-shaped ectoloph is present on the upper molars of Phyllostomus hastatus. In contrast, Carollia brevicauda, Rhinophylla pumilio, and all stenodermatines lack ectolophs on their upper molars. W-shaped ectolophs are also present on the lower molars of Phyllostomus hastatus among the species analyzed in this study, and will not be described in a separate character since presence/absence of lophs in the upper and lower dentition is correlated.

Griffiths (1985) suggested that many stenodermatines have w-shaped ectoloph, but I have found no trace of such pattern on any of the species of stenodermatines included in this analysis.

Wetterer et al. (2000: character 60) first used this character in a phylogenetic analysis.

Character 217: Protocone on the first upper molar.

Well developed protocone onto first upper molar (0), or little developed (1), or absent (2).

There is a well-developed protocone in the first upper molar of Phyllostomus hastatus and several stenodermatines (e.g. Vampyrodes, Ariteus). In contrast, there occurs a poorly developed protocone on the M1 of Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Platyrrhinus helleri, Vampyressa bidens). Finally, some other stenodermatines do not have a protocone on their first upper molars (e.g. Chiroderma villosum, Mesophylla).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the observation on the development of a protocone on the first upper molar.

Velazco (2005: character 38) used a similar character in his phylogenetic analysis of the genus Platyrrhinus. However the present character is not comparable to Velazco's (2005) because he described degrees of development of the protocone in a different scale for a set of species that all had protocones in their first upper molar ("well developed", "moderately developed", "small and blunt").

Character 218: Hypocone basin on first upper molar.

Hypocone basin distinct on first upper molar (0), or absent (1).

The hypocone basin is is present on the first upper molar of Phyllostomus hastatus, and several stenodermatines (e.g. Uroderma bilobatum, Phyllops falcatus). In contrast, the hypocone basin is absent on the first upper molar of Carollia brevicauda and many stenodermatines (e.g. Chiroderma villosum, Mesophylla, see fig. 8).

Wetterer et al. (2000: character 61) first used this character in their phylogenetic analysis of phyllostomid bats.

Character 219: Hypocone onto the first upper molar.

Hypocone indistinct (0), or often developed (1).

Phyllostomus hastatus and some stenodermatines (e.g. Pygoderma) have an indistinct hypocone despite having a well-developed hypoconal basin (see character 218). In contrast, several other stenodermatines have often a developed hypocone (e.g. Phyllops, Sphaeronycteris).

All species with a poorly developed or undeveloped hypoconal basin were scored “-“ for this character.

Wetterer et al. (2000: character 61) described a character including the development of a hypoconal basin and the occasional occurrence of a hypocone in a single character.

Character 220: Presence and size of metacone on the first upper molar.

Metacone subequal to or greater than paracone in height (0), or metacone approximately two-thirds of height of the paracone (1), or less than two third but more than a half the height of the paracone (2), or much shorter than paracone, less than a half (3), or metacone rudimentary or absent (4).

The metacone on the first upper molar is subequal to the paracone in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio and some stenodermatines (e.g. Sturnira lilium). In contrast, the metacone on upper first molar is approximately two-thirds of the height of the paracone of upper first molar in several stenodermatines (e.g. Ametrida, Vampyressa brocki). A third condition is a smaller metacone on upper first molar, up to half the height of paracone of upper first molar (e.g. Chiroderma villosum, Vampyressa melissa). Some stenodermatines (e.g. Pygoderma) have a metacone on the upper first molar that is less than a half the height of the paracone on the upper first molar therefore much shorter but present. Finally, some Mesophylla and Ectophylla have a rudimentary metacone on the first upper molar yet many individuals lack it completely.

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps detected according to the variation observed on the relative development of metacone on the first upper molar of stenodermatine bats.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 221: Lingual cingulum on the first upper molar.

Cingulum on the occlusal face of first upper molar absent (0), or present, restricted to lingual metacone (1), or present, extends from lingual paracone to posterior edge of metacone (2).

Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines lack cingula on the occlusal face of first upper molar. In contrast, a cingulum is present on the lingual portion of the metacone of the first upper molar in some stenodermatines (e.g. Ardops, Vampyressa thyone). A third condition observed in many stenodermatines (e.g. Platyrrhinus helleri, Vampyressa bidens) is the occurrence of a lingual cingulum extending from lingual paracone to posterior edge of lingual metacone of upper first molar.

Phyllostomus hastatus, which has w-shaped ectolophs on the upper first molar (see character 216) was conservatively scored "-" for this character as it was difficult to trace hypothesis of homology of structures such as internal cingula by comparison between its molars and those of stenodermatines.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Velazco (2005: character 37) used a similar character to describe a sulcus on the posterior face of the paracone when there is a cingulum extending to this cusp in its internal face. Although I focused on the occurrence and extension of the cingulum, the present character and scoring (for species in common in his and the present study) is similar to those of Velazco (2005).

Character 222: Presence of a mesostyle on the first upper molar.

Mesostyle on the upper first molar absent (0), or present (1).

There is no mesostyle on the upper first molar of Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and several stenodermatines (e.g. Chiroderma villosum, Vampyressa brocki). In contrast, a mesostyle is present on the upper first molar in some stenodermatines (e.g. Platyrrhinus helleri and in Vampyrodes.

Phyllostomus hastatus, which has w-shaped ectolophs on the upper first molar (see character 216) was conservatively scored "-" for this character as it was difficult to trace hypothesis of homology of structures such as internal cingula by comparison between its molars and those of stenodermatines.

Velazco (2005: character 33) first used this character in a phylogenetic analysis.

Character 223: Hypoconal basin on second upper molar.

Hypoconal basin developed on the second upper molar (0), or rudimentary but present (1), or completely lacking (2).

A hypoconal basin is present on the second upper molar of Phyllostomus hastatus and Vampyressa melissa. In contrast, a hypoconal basin is rudimentary on the second upper molar of several stenodermatines (e.g. Centurio, Phyllops falcatus). Finally, a hypoconal basin is completely lacking from the second upper molar of Carollia brevicauda and in many other stenodermatines (e.g. Sturnira lilium, Chiroderma villosum, Mesophylla, Vampyressa bidens) (see fig. 8).

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the variation on the relative development of a hypoconal basin on the second upper molar of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 224: Protocone on second upper molar.

Protocone present on second upper molar (0), or absent (1).

A protocone is present in the second upper molar of Phyllostomus hastatus and several stenodermatines (e.g. Stenoderma, Vampyressa melissa). In contrast, a protocone is lacking from the second upper molar of Carollia brevicauda, Rhinophylla pumilio, and many other stenodermatines (e.g. Pygoderma, Ectophylla, Vampyressa thyone). I found it unwise to split states within the "protocone present" condition based on relative size of this cusp on second upper molar, although I observed differences in its development, because the variation was not easily split into clearly discrete categories.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 225: Metacone on second upper molar.

Metacone well-developed on second upper molar (0), or either rudimentary or absent (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Sturnira lilium, Platyrrhinus helleri) have a relatively well-defined metacone on second upper molar. In contrast, the second upper molar of several other stenodermatines has either a very rudimentary metacone, so reduced that the tooth is irregularly piriform in outline (with the narrower portion, the paracone, sitting labially), or the metacone is completely absent (e.g. Vampyrodes, Vampyressa pusilla).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 226: Median ridge on second upper molar when tooth lacks lingual cusps.

Second upper molar lacking lingual cusps with a median ridge present (0), or absent (1).

Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and most stenodermatines without internal (lingual) cusps developed on second upper molar lack a median ridge (e.g. Pygoderma, Mesophylla, Vampyressa bidens, see fig. 8). In contrast, the second upper molar of Ectophylla has a median ridge.

A median ridge is also present on the second lower molar of Ectophylla and it appears correlated with the presence of this ridge on the second upper molar. Therefore it will not be described as a separate character in the lower molar section.

Species that have lingual cusps on second upper molar were scored "-" for this character.

This is the first use of this character a chiropteran phylogenetic analysis.

Character 227: Heel development on second upper molar when lingual cusps are lacking.

Upper second molar lacking lingual cusps but with a thick, swollen base in the lingual side (0), or without swollen base (1).

Carollia brevicauda, Sturnira lilium, and some bats without lingual cusps on second upper molar (e.g. Chiroderma villosum) have a thick, swollen base on the lingual side of second upper molar. This development is greatest in Chiroderma villosum. In contrast, most stenodermatines without lingual cusps do not have a swollen base on the second upper molar (e.g. Ectophylla, Vampyressa nymphaea).

Nogueira et al. (2005) related the largely swollen base of lingual second upper molar of Chiroderma species to the durophagous habits of species of this genus (Nogueira & Peracchi, 2002, 2003).

Species that have lingual cusps on second upper molar were scored "-" for this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 228: Third upper molar.

Third upper molar present (0), or absent (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium and some stenodermatines (e.g. Platyrrhinus helleri) have a third upper molar. In contrast, several other stenodermatines have only two upper molars and consistently lack a third upper molar (e.g. Chiroderma villosum, Mesophylla).

This character has been used previously used by many researchers in phylogenetic analyses, e.g. Owen (1987: character 15, 1991: character 34), Marques-Aguiar (1994: character 29), and Wetterer et al. (2000: character 63). My observations are in accordance with most observations of those previous authors.

Character 229: Development of the third upper molar.

Third upper molar relatively well developed (0), or poorly developed, peg-like (1).

Phyllostomus hastatus, Carollia brevicauda and Rhinophylla pumilio have a relatively well developed third upper molar, with remnants of the paraconal and protoconal basins. In contrast, when a third upper molar is present in stenodermatines, it is generally peg-like, and poorly developed, lacking evidence of basins or shearing ridges.

All species lacking a third upper molar were scored “-” for this character.

Owen (1987: character 15) and Marques-Aguiar (1994: character 29) used size of third upper molar in their character concerning variation of this tooth. However I agree with Wetterer et al. (2000) that size is too variable to be understood under a discrete categorization and so circumscribed the present description to the relative development (e.g. traces of cusps and basins) of this tooth.

Lower molars

Character 230: Shape of the first lower molar in occlusal view.

First lower molar rectangular and narrowed anteriorly (0), or quadrate and narrowed anteriorly (1), or rectangular and not narrowed anteriorly (2).

The first lower molar of Phyllostomus hastatus, Rhinophylla pumilio and Sturnira lilium and of some stenodermatines (e.g. Ectophylla) is roughly rectangular with a narrowed anterior portion when seen in occlusal view. In contrast, the first lower molar is roughly quadrate in shape with a narrowed anterior portion in other taxa (e.g. Chiroderma villosum, Vampyressa bidens). A third condition is presence of rectangular first lower molar that lacks the anterior narrowing seen in other taxa (Carollia brevicauda and Uroderma bilobatum).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 231: Shape of second lower molar in occlusal view.

Second lower molar rectangular without posterior narrowing (0), or rectangular but narrowed posteriorly (1), or quadrate and narrowed posteriorly (2), or subovoide (3), or circular with a diameter greater than breadth of mandibular ramus (4).

The second lower molar of Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, and some stenodermatines (e.g. Artibeus concolor, Vampyrodes) is roughly rectangular and not narrowed posteriorly. In contrast, the second lower molar is rectangular but narrowed posteriorly in several stenodermatines (e.g. Uroderma bilobatum, Vampyressa melissa). A third condition is found in some other stenodermatines (e.g. Platyrrhinus helleri), which have a roughly quadrate second lower molar that is narrowed posteriorly. The shape of second lower molar in occlusal outline in Mesophylla and Ectophylla seems to represent two distinct conditions, each of them unique (i.e. autapomorphic for each genus) herein described as two separate states: Mesophylla has a subovoide second lower molar, and Ectophylla has a circular second lower molar that is greater in diameter than the breadth of mandibular ramus.

This character has been ordered 0⇔1⇔2⇔3⇔4 to reflect a series of logically intermediate steps detected according to the variation on the relative antero-postero and labio-lingual lengths with consequent shifts in shape of the second lower molar of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 232: Level of base of crowns of first lower molar and fourth lower premolar.

First lower molar and fourth lower premolar with base of crowns situated in the same level in the mandible (0), or anterior part of first lower molar located above posterior part of fourth lower premolar (1).

The crowns of first lower molar and fourth lower premolar of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Ectophylla, Vampyressa melissa) are situated at a same level in the mandible and do not overlap. In contrast, some stenodermatines have the anterior lower molar (= first) situated above distal lower premolar (= fourth) (e.g. Vampyrodes caracciolli) (see fig. 13).

There is variation in this character within Vampyressa brocki and V. bidens, which were scored 0/1 in this study.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 233: Paraconid on first lower molar.

Paraconid present on first lower molar (0), or absent (1).

A paraconid is present on the first lower molar of Phyllostomus hastatus and Carollia brevicauda. In contrast, a paraconid is absent on the on the first lower molar of all stenodermatines (e.g. Chiroderma villosum, Ametrida, Vampyressa melissa).

Although Wetterer et al. (2000) reported to have found individuals of Platyrrhinus helleri and Vampyrodes caracciolli with a paraconid on on the first lower molar, I did not observe this in these species. In this respect, my scoring for Platyrrhinus helleri and Vampyrodes agree with that of Velazco (2005).

This character has appeared in the phylogenetic analyses of Lim (1993: character 9), Wetterer et al. (2000: character 68) and Velazco (2005: character 52).

Character 234: Relative size of protoconid on first lower molar.

Height of protoconid on first lower molar minimally two-thirds the height of the fourth lower premolar (0), or height of protoconid on first lower molar roughly half the height of the fourth premolar (1), or height of protoconid on first lower molar clearly less than a half of fourth lower premolar height (2).

The protoconid on first lower molar of Phyllostomus hastatus, Carollia brevicauda, and many stenodermatines (e.g. Ariteus, individuals of Mesophylla, Vampyressa bidens) is just a little smaller than the height of fourth lower premolar, minimally 2/3 of the height of that tooth. In contrast, the protoconid on first lower molar is half the height of fourth lower premolar in many stenodermatines (e.g. Sturnira lilium, Centurio, Phyllops falcatus, Vampyressa nymphaea). Finally, the protoconid on first lower molar is less than half the size of fourth lower premolar in some other stenodermatines (e.g. Sphaeronycteris).

There is variation on relative size of protoconid on first lower molar in Mesophylla and this taxon was scored 0/1 in the data matrix for this character.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a phylogenetic analysis.

Character 235: Metaconid on the first lower molar.

Metaconid present on first lower molar (0), or absent (1).

A metaconid is present on first lower molar of Phyllostomus hastatus, Carollia brevicauda, and some stenodermatines (e.g. Artibeus jamaicensis, Ametrida). In contrast, a metaconid is lacking on first lower molar of several stenodermatines (e.g. Chiroderma villosum, Ardops, Vampyressa nymphaea).

This character appeared in the phylogenetic analyses of Lim (1993: character 9), Wetterer et al. (2000: character 69), and Velazco (2005: character 55). My scoring is similar to that of these authors but I agree with Velazco (2005) that no metaconid is present on first lower molar, and disagree with Wetterer et al. (2000) that found a metaconid on the first lower molar of Vampyrodes.

Character 236: Entoconid on first lower molar.

Entoconid present on first lower molar (0), or absent (1).

An entoconid is present on first lower molar of Phyllostomus hastatus, Carollia brevicauda, Sturnira lilium, and several stenodermatines (e.g. Uroderma bilobatum). In contrast, an entoconid is lacking on the first lower molar of many stenodermatines (e.g. Chiroderma villosum, Ectophylla, Vampyressa).

This character first appeared in a phylogenetic analysis of the genus Sturnira (Pacheco and Patterson, 1991: character 14) and subsequently in the analyses of Lim (1993: character 9), and Wetterer et al. (2000: character 70).

Character 237: Relative size of the metaconid on second lower molar.

Metaconid on second lower molar slightly smaller than protoconid on second lower molar, no less than two third the height of it (0), or about the same height (1), or twice the height of protoconid (2).

The metaconid on the second lower molar of Carollia brevicauda, Sturnira lilium, and some stenodermatines (e.g. Ardops) is a little smaller than the protoconid on the same tooth, roughly two-thirds the size of the protoconid or more. In contrast, several stenodermatines have a metaconid and a protoconid on second lower molar that are subequal in height (e.g. Sturnira lilium, Ametrida, Vampyressa bidens). A third condition is found in Vampyressa melissa, V. pusilla, and V. thyone, in which the much larger metaconid on second lower molar is roughly twice the height of the protoconid.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the variation on the metaconid development onto the second lower molar within stenodermatine bats.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 238: Direction of metaconid on second lower molar.

Metaconid on second lower molar is directed vertically (0), or is directed horizontally in an anteromedial direction, sometimes extending over the entoconid basin of first lower molar (1).

The metaconid of the second lower molar is directed vertically in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Ectophylla, Vampyressa nymphaea). In contrast, the metaconid of the second lower molar in Vampyressa bidens and V. brocki is oriented somewhat horizontally in an anteromedial direction, often extending over the entoconid basin of the first lower molar.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 239: Hypoconid on second lower molar.

Hypoconid on second lower molar present (0), or absent (1).

Phyllostomus hastatus, Carollia brevicauda and Chiroderma villosum have a hypoconid on the second lower molar. In contrast, most stenodermatines lack a hypoconid on this tooth (e.g. Vampyrodes, Vampyressa brocki).

Velazco (2005: character 56) first used this character in his phylogenetic analysis of Platyrrhinus. He detected intraspecific variation in Platyrrhinus helleri, which I may have not detected due to the smaller sample analyzed. I accordingly scored P. helleri with 0/1 following Velazco (2005).

Character 240: Entoconid on second lower molar.

Entoconid on second lower molar absent (0), or present (1).

An entoconid is lacking from the second lower molar of Phyllostomus hastatus, Carollia brevicauda and many stenodermatines (e.g. Platyrrhinus helleri, Ectophylla, Mesophylla). In contrast, an entoconid is present on the second lower molar of several other stenodermatines (e.g. Ametrida, Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 241: Shape of the entoconid on second lower molar.

Entoconid on second lower molar rounded and small (0), or moderately developed, lower than metaconid (1), or very large, forms a quadrate-shaped crest, subequal or larger than metaconid (2).

Some stenodermatines have a small, rounded entoconid on the second lower molar (e.g. Ectophylla, Vampyressa nymphaea). In contrast, some stenodermatines have a moderately well-developed entoconid that is lower than the metaconid (e.g. Centurio, Vampyressa bidens). A third condition is found in some Vampyressa (s. s.), in which the entoconid is enormous (subequal to or larger than the metaconid), forms a quadrate-shaped crest, and directed vertically (e.g. Vampyressa melissa, V. pusilla).

It is possible that the “quadrate entoconid” that I describe here for some Vampyressa is the fusion of more than one cusp. Until this hypothesis has been tested, I describe it as a single, very well-developed crest-like cusp.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the variation in size and shape of the entoconid on the second lower molar within stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 242: Hypoconulid on second lower molar.

Hypoconulid absent on second lower molar (0), or present (1).

A hypoconulid is absent from the second lower molar of Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines (e.g. Mesophylla, Vampyressa nymphaea). In contrast, a hypoconulid is present in Chiroderma villosum.

The occlusion of the thick base of the second upper molar (M2) (see character 227) with the crest and cusps of the second lower molar (m2) appears to work like a “nut-cracker” for C. villosum and bears much of the conclusions taken by Nogueira et al. (2005) about the durophagy-related morphology of cheek teeth in Chiroderma.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 243: Third lower molar.

Third lower molar always present (0), or sometimes present (1), or absent (2).

The third lower molar is always present in Phyllostomus hastatus, Carollia brevicauda, Sturnira lilium, and some stenodermatines (e.g. Uroderma bilobatum). In contrast, this tooth is variably present in Vampyressa bidens. A third condition observed in several other stenodermatines (e.g. Chiroderma villosum, Ectophylla, Vampyressa pusilla) that consistently lack a third lower molar.

In his original description of Vampyressa melissa Thomas (1926) commented that the presence of the third lower molar in the holotype would probably prove to be inconsistent within this species, but in fact I found a minute third molar in all specimens of V. melissa examined.

This character has been ordered 0⇔1⇔2 to reflect a series of logically intermediate steps detected according to the hypothesis of a progressive evolution in the lost of a third upper molar within stenodermatines.

This character has been used in the phylogenetic analyses of Owen (1987: character 22, 1991: character 46), Pacheco and Patterson (1991:

character 9), Marques-Aguiar (1994: character 29), and Wetterer et al. 2000: character 66). My scoring is different from that of Wetterer et al. (2000) because I created a separate state for bats that consistently lack the third lower molar.

Character 244: Development of third lower molar.

Third lower molar relatively well developed, one-third or more the size of the second lower molar in occlusal view (0), or poorly developed, peg-like, less than one-third the size of second lower molar (1).

Phyllostomus hastatus, Carollia brevicauda, and several stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum, Phyllops falcatus, have a relatively well-developed third lower molar that is about one-third or more the size of second lower molar in occlusal view. In contrast, several other stenodermatines possessing third lower molar have a poorly developed, peg-like third lower molar that is less than one-third the size of second lower molar (e.g. Vampyressa bidens, Vampyressa melissa).

This is the first use of this character in a chiropteran phylogenetic analysis.

Diastemata

Lim (1993: 164, character 11) originally used the occurrence of diastemata between cheek teeth in his analysis of phylogenetic relationships of stenodermatine bats. He hypothesized a progressive increase in the diastema between premolars and molars and treated these in a single character. Wetterer et al. (2000: p. 86-87, characters 71, 72, and 73) split Lim's (1993) character into three distinct characters. In this section, I split these further to account for gaps occurring between each pair of adjacent teeth from incisors to molars. I also created a separate character to describe the relative size of the gaps in the lower dentition of stenodermatine bats.

Upper dentition diastemata

Character 245: Upper inner incisors contact.

Right and left upper inner incisors adjacent with no diastema between them (0), or separated by a narrow diastema (1), or separated by a wide diastema (2).

The right and left upper inner incisors of Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines are directely adjacent to each other with virtually no space between them (e.g. some Vampyrodes, Chiroderma villosum). In contrast, the upper inner incisors of several stenodermatines are separated by a relatively narrow gap (e.g. Ectophylla). Finally, other stenodermatines have a wide diastema between the right and left upper inner incisors (e.g. Vampyressa melissa).

Some species exhibit intraspecific variation in this character: Platyrrhinus helleri and Vampyressa thyone have either a narrow or wide diastema between the right and left upper inner incisors, and Vampyrodes has either virtually no diastema or a narrow diastema between those teeth. I scored all such cases with the two correspondent states.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Velazco (2005: character 24) described a character to account for the variation in the contact between upper inner incisors. The difference between his character and the present is that I described in this character only the occurrence or not of a diastema (i.e. a space between two tooth bases) between the upper inner incisors. May the teeth partially touch the extent of this contact is described in the next separate character (character 246).

Character 246: Upper inner incisors extent of contact when right and left teeth are in contact.

Right and left upper inner incisors in contact from base to medial section (0), or from medial section to tip (0).

In some stenodermatines, when the right and left upper inner incisors of are in contact, the zone of contact extends from the tooth base to roughly the medial section of the tooth (e.g. Sturnira). In contrast, the upper inner incisors are in contact (when those teeth touch) more distally in most stenodermatines (e.g. Platyrrhinus helleri, Vampyressa nymphaea, see fig. 5). In these forms, the right and left upper inner incisors contact each other from roughly the midpoint of the tooth to its tip.

Species with polymorphism concerning to upper incisors contact (e.g. Ectophylla) were accordingly scored to account for instances when the teeth are directly adjacent, and those that always have a diastema between upper inner incisors were logically scored “-“ for this character.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 247: Upper inner and outer incisors' contact.

Inner and upper outer incisors in contact with each other (0), or separated by diastema (1).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Vampyrodes) the inner and upper outer incisors are in close contact with each other. In contrast, the upper incisors are separated by a small diastema in several other stenodermatines (e.g. Vampyressa bidens, V. nymphaea).

Vampyressa thyone was polymorphic for this character and accordingly scored "0/1" in the data matrix.

This is the first use of this character in a phylogenetic analysis.

Character 248: Upper outer incisor and upper canine contact.

Upper outer incisor and the upper canine in contact with each other (0), or separated by a diastema (1).

The upper outer incisor is in close contact with the canine in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Uroderma bilobatum, Vampyressa pusilla). In contrast, several other stenodermatines have a diastema between their upper outer incisors and upper canines (e.g. Chiroderma villosum, Ectophylla).

Mesophylla and Vampyressa nymphaea have sometimes a gap between their upper outer incisors and their upper canines, and I scored these two taxa with the two conditions accordingly. Whether or not these conditions signify consistent characters of taxonomic value rather than individual variation within each of those two taxa will be explored further elsewhere.

This character has appeared in the phylogenetic analysis of Simmons and Conway (2001: character 32).

Character 249: Upper canine and third upper premolar contact.

Upper canine always in tight contact with third upper premolar (0), or sometimes separated by a diastema (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines (e.g. Uroderma bilobatum, Vampyressa brocki) have the upper canine and the third upper premolar positioned tightly together. In contrast, several stenodermatines have the upper canine and the third upper premolar sometimes separated by a small gap (e.g. Ectophylla).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 250: Third upper premolar and fourth upper premolar contact.

Third upper premolar in contact with fourth upper premolar (0), or teeth separated by diastema (1).

In Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and Vampyrodes, the third upper premolar is in close contact with the fourth upper premolar. In contrast, the anterior (third) premolar and the posterior (fourth) upper premolar are separated by a diastema in several other stenodermatines (e.g. Platyrrhinus helleri, Ectophylla, Vampyressa bidens).

Pacheco and Patterson (1991: character 11) first used this character in a phylogenetic analysis in their study of the genus Sturnira. Subsequently Wetterer et al. (2000: character 71) used it in their phylogeny of the family Phyllostomidae, and Simmons and Conway (2001: character 38) in their study of the Moormopidae.

Character 251: Fourth upper premolar and first upper molar contact.

Fourth upper premolar in contact with first upper molar (0), or teeth often or always separated by diastema (1).

The fourth upper premolar is in contact with first upper molar in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and in several stenodermatines (e.g. Vampyrodes, V. brocki). In contrast, the first upper molar is often separated from the fourth upper premolar by a diastema in other stenodermatines (e.g. Ectophylla, Mesophylla, Vampyressa thyone).

Lim (1993: character 11) scored V. bidens as lacking diastema between fourth upper premolar and first upper molar, whereas Wetterer et al. (2000) scored V. bidens as having it. These conflicting scorings are due to the intrapopulational variation for this character within Vampyressa species. According to my observations, *V.* brocki is the only Vampyressa species (s. l.) that appear to consistently lack a diastema between fourth upper premolar and first upper molar.

Pacheco and Patterson (1991: character 7) first used this character in a chiropteran phylogenetic analysis, and subsequently Lim (1993: character 11), and Wetterer et al. (2000: character 72).

Character 252: First upper molar and second upper molar contact.

First upper molar in contact with second upper molar (0), or teeth sometimes separated by diastema (1), or teeth always separated by a diastema (2).

The first upper molar is in contact with the second upper molar in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Mesophylla, Vampyressa brocki). In contrast, the anterior upper molar (M1) is sometimes separated from the posterior upper molar (M2) by a small diastema in some stenodermatines (e.g. Vampyressa bidens, V. thyone). A third condition, seen only in Ectophylla, is the first upper molar always separated from the second upper molar by a diastema.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This character has appeared in the phylogenetic analysis of Pacheco and Patterson (1991: character 7) and Wetterer et al. (2000: character 73). I have created a third state to accommodate the unique condition found in Ectophylla.

Lower dentition diastemata

Character 253: Right and left lower inner incisors contact.

Right and left lower inner incisors adjacent (0), or sometimes separated by diastema (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Vampyressa melissa) have right and left lower inner incisors in contact. In contrast, some stenodermatines (e.g. Platyrrhinus helleri, Vampyressa bidens, V. brocki) sometimes have a diastema between the right and left lower inner incisors (see fig. 14).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 254: Lower inner incisor, lower outer incisor, and lower canine contact.

Lower inner incisor, lower outer incisor and lower canine always adjacent (0), or sometimes separated by a diastema (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Chiroderma villosum, Vampyressa melissa) have the lower inner and outer incisors and canine always completely in contact. In contrast, Platyrrhinus helleri frequently have diastema separating these teeth (see fig. 14). Variation in diastema patterns between the lower inner and outer incisors and canine appears to not be independent as in the case of other diastema described in previous characters in this study, and were consequently treated in conjuction in the present character.

Vampyressa bidens that generally have only one lower incisor was scored "-" for this character in the data matrix.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 255: Lower canine and second lower premolar contact.

Lower canine adjacent to second lower premolar (0), or separated by diastema (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Chiroderma villosum, Vampyressa bidens) have the lower canine and the second lower premolar in contact. In contrast, some stenodermatines (e.g. Ectophylla, Vampyressa melissa) have a diastema between the lower canine and the second lower premolar (see fig. 14).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 256: Second lower premolar and fourth lower premolar contact. Second lower premolar adjacent to fourth lower premolar (0), or separated by a diastema (1).

Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Platyrrhinus helleri, Uroderma bilobatum) have their two lower premolars in contact. In contrast, most stenodermatines (e.g. Chiroderma villosum, Mesophylla, Vampyressa nymphaea) have a diastema between these teeth (see fig. 14).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 257: Fourth lower premolar and first lower molar contact. Fourth lower premolar in contact with first lower molar (0), or teeth separated by diastema (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and most stenodermatines (e.g. Uroderma bilobatum, Vampyressa nymphaea) have their fourth lower premolar and their first lower molar in contact. In contrast, some other stenodermatines (e.g. Ectophylla, Mesophylla) have a diastema between the fourth lower premolar and the first lower molar (see fig.14).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 258: First lower molar and second lower molar contact.

First lower molar in contact with second lower molar (0), or teeth separated by diastema (1).

The first lower molar is in contact with the second lower molar in Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines (e.g. Vampyrodes, Vampyressa brocki). In contrast, the first lower molar is sometimes separated from the second lower molar by a small diastema in Ectophylla and Vampyressa nymphaea.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 259: Relative size of diastemata, from smallest to largest.

Gap size varying according to the formula c / p2 = m1 / m2 < p4 / m1 < p2 / p4 (0), or c / p2 < p2 / p4 (1), or p4 / m1 < p2 / p4 (2), or p4 / m1 < p2 / p4 = c / p2 (3).

The relative size of the diastemata occurring between lower postcanine teeth varies among stenodermatines. To describe this variation, I created a series of gap formulae by sorting gaps between pairs of teeth in an ascending order from smallest to largest. Ectophylla alba has the gap between the lower canine and the second lower premolar approximately equal to the gap between the first and the second lower molar, which are both smaller than the gap found between the fourth lower premolar and the first lower molar, which is further slightly smaller than the gap between the second and the fourth lower premolars. In contrast, Vampyressa bidens has the gap between the lower canine and the second lower premolar smaller to subequal to that between the second and the fourth lower premolars. A third condition observed in Mesophylla conforms to the following formula: gap between fourth lower premolar and first lower molar < gap between second and fourth lower premolars. Vampyressa melissa has a fourth condition, in which gap between fourth lower premolar and first lower molar < gap between second and fourth lower premolars = gap between lower canine and lower second molar (see fig. 14). Finally, Vampyressa pusilla has the gap between fourth lower premolar and first lower molar < gap between lower canine and second lower molar < gap between second and fourth lower premolars.

Individuals of Vampyressa thyone have either the third or the fifth condition (i.e. the taxon was scored with 2 or 4). Whether those differences in the distribution of gaps of the postcanine lower teeth of V. thyone represents consistent signal to define distinct species will be further explored separately in another study.

All species without diastema in the lower dentition, or with a single diastema were scored “-” for this character in the data matrix.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Occlusal patterns

Character 260: Frontal gap between occluded teeth.

Upper inner incisor and lower inner incisor in contact when jaws are in occlusion (0), or separated by a small gap, teeth may occasionally touch when in occlusion

(1), or separated by wide gap and rarely or never touch when jaws are in occlusion (2).

In most phyllostomids, the upper and lower inner incisors contact each other or are only separated by a tiny gap when the jaws are in occlusion (Wetterer et al., 2000). This pattern is observed in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and many stenodermatines (Ectophylla, Vampyressa bidens). Another condition occurs in Chiroderma villosum, Vampyressa melissa, and other undescribed forms of Vampyressa sp. (e.g. from Bocas del Toro), which have a small gap between their incisors when the jaws are in occlusion. In these taxa the gap between the upper and lower teeth is less than a half of the height of upper inner incisors. Finally, Platyrrhinus helleri, Vampyrodes, and Uroderma bilobatum have a wide gap separating the upper and lower incisors when they are in occlusion.

Freeman (1988) has suggested that the wide gap between the occluded incisor teeth of stenodermatine bats would serve as a space for squeezed juice to escape from their mouths while fruits are processed. As noted by Wetterer et al. (2000) Sturnira lilium, Vampyressa and Ectophylla (which includes Mesophylla in their analysis) are the only stenodermatines with a “normal occlusion”, i.e., without a wide frontal gap when their jaws are closed. On the other hand, Ectophylla, Mesophylla, and Vampyressa have a gap displaced laterally (see character 203) that may have a similar function, which remains to be further investigated.

In Vampyressa (s.l.) the wear frequently observed the upper incisor tooth is likely related to the pattern of occlusion of incisors, which are in closer contact in Vampyressa brocki, V. nymphaea, V. bidens, V. thyone, and Mesophylla than in Vampyressa melissa and Vampyressa sp. (from Bocas del Toro).

Finally, in Sturnira lilium there is sometimes a small gap between the two upper inner incisors, which remains when the jaws are closed, but in other species of Sturnira (e.g. S. tildae) this little gap does not appear. The gap in S. lilium appears at first analysis not to be homologous to any of the conditions described in this and the following character. I however scored S. lilium with 0/1 to be conservative, and left unresolved if the condition deserves to be treated as a discrete unit, pending inclusion of more Sturnira species in a phylogenetic analysis including this character.

This character has been ordered 0⇔1⇔2 to reflect a series of logical progressive intermediate transformations in the appearance of a gaped interval between the occluded incisors of stenodermatines.

My description and scoring for this character are similar to a character originally described by Wetterer et al. (2000: character 55), except that I created one intermediate state.

Character 261: Lateral gap between occluded teeth.

When jaws are in occlusion, all spaces filled by occluded tooth series from canine to molars (0), or tiny gaps are formed between teeth in the cheek tooth series (1), or a large lateral gap is formed between the upper third premolar and the lower second premolar when the jaws are in occlusion (2).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines have a completely closed occlusion of their cheek tooth rows with the jaws are in occlusion so that there are no gap between canines, premolars and molars (e.g. Platyrrhinus helleri, Uroderma bilobatum). In contrast, Mesophylla has tiny gaps between cheek teeth when its jaws are closed. Finally, most stenodermatines (e.g. Chiroderma villosum, Ectophylla, and Vampyressa) have a single large lateral gap located in between their upper and lower premolars when their jaws are in occlusion.

The lateral gap is formed by an apparent reduction in size of both first premolars in the upper and lower jaws (upper third and lower second premolars), and reinforced in some cases by the occurrence of a diastema between some teeth (see characters about upper and lower teeth contact). This may have a functional significance in food processing, but this hypothesis has not been yet tested. Although the lateral gap may have similar functions as the frontal gap that appears in other stenodermatines (see character 202), the suggestion of Freeman (1988) may not apply in this case, since juice may not easily escape from the lateral gap unless the mouth of the bat is widely open.

This character has been ordered 0⇔1⇔2 to reflect a series of logical progressive intermediate transformations in the appearance of a gaped intervals between the occluded canine and postcanine teeth of stenodermatines.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 262: First teeth in contact during occlusion.

Molars occlude before the premolars (0), or premolars occlude before or simultaneously with the molars (1).

During the act of biting, the first lower and upper cheek teeth to occlude are the molars in most bats. This pattern of the occlusion has been summarized by Freeman (1998) as being “from the back to the front”, and is observed in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and many stenodermatines (e.g. Uroderma bilobatum, Ectophylla). In contrast, in many other stenodermatines (Platyrrhinus helleri, Vampyressa melissa) the premolars occlude before or simultaneously to the molars at the posterior end (“from the front to the back”, as described by Freeman, 1988). Freeman (1988) originally observed the “front-to-back” pattern of occlusion of mandible/maxilla in the short-faced bats Pygoderma and Centurio. She noticed that the mechanism of biting in these species is highly specialized, suggesting that it may be related to some specialized feeding habits.

This is the first use of this character in a chiropteran phylogenetic analysis.

Poscranium morphology

Character 263: Articulation of the clavicle with scapula.

Distal tip of clavicle articulates with coracoid process of the scapula (0), or is suspended between coracoid and acromion (1).

The distal tip of clavicle articulates with the coracoid process of the scapula in Carollia brevicauda and some stenodermatines (e.g. Mesophylla) In contrast, the clavicle articulates between acromion and coracoid in many stenodermatines (e.g. Chiroderma villosum, Centurio, Vampyressa bidens).

This character has appeared in the phylogenetic analysis of Simmons (1998: character 108), Simmons and Geisler (1998: character 114), Wetterer et al. (2000: character 74), and Simmons and Conway (2001: character 137).

Character 264: Relative length of metacarpals.

Third and fifth metacarpals subequal in length and longer than fourth metacarpal (0), or third metacarpal longer than fourth and fifth (1), or fifth metacarpal longer than third and fourth metacarpal (2).

Carollia brevicauda and several other stenodermatines (e.g. Ectophylla, Vampyressa nymphaea, V. pusilla) have the metacarpals III and V subequal in size and both longer than the IV. In contrast, the metacarpal III is the longest of the metacarpal bones in Phyllostomus hastatus, Platyrrhinus helleri, Ametrida, Centurio, Vampyressa bidens and V. brocki. Finally, the longest metacarpal element is the fifth in Rhinophylla pumilio, Sturnira lilium and several stenodermatines (e.g. Vampyressa melissa).

This character has previously appeared in the phylogenetic analyses of Simmons (1996: character 10), Wetterer et al. (2000: character 84), and Velazco (2005: character 59). The present character states correspond to states 0, 1, and 6 of character 84 in Wetterer et al. (2000: p. 91). My scoring is in disagreement with Wetterer et al. (2000) for Vampyressa bidens, which has the third metacarpal larger than the other two according to my morphometric data (n = 178), and Vampyressa thyone (= V. pusilla in Wetterer et al., 2000), which has the fifth metacarpal longest according to my morphometric data (n = 267). All morphometric data of Vampyressa (s.l.) collect over the course of this study will be published elsewhere in revisions of these taxa. On the other hand, Vampyressa pusilla (as defined in Lim et al., 2004) has the third and the fifth metacarpal subequal and larger than the fourth (n = 19). My scoring is also in disagreement with Wetterer et al. (2000) but coincides with that of Velazco (2005) for Platyrrhinus helleri, who indicated that the third metacarpal is the longer in this species.

Character 265: Relative length of first and second phalanges of digit IV.

First and second phalanx of digit IV subequal (0), or second phalanx of digit IV longer than first phalanx (1), or second phalanx of digit IV smaller than first (2).

The second phalanx of digit IV is subequal in length to first phalanx of digit IV in Carollia brevicauda, Rhinophylla pumilio, Sturnira lilium, and many stenodermatines (e.g. Chiroderma villosum, Vampyressa bidens). In contrast, the second phalanx of digit IV is longer than the first phalanx IV in several stenodermatines (e.g. Ectophylla, Mesophylla, Vampyressa pusilla, and V. thyone. Finally, Centurio and Phyllops falcatus have the second phalanx of digit IV is shorter than the first phalanx IV.

Simmons (1996: character 10) originally described this character in her analysis of phylogenetic relationships among bats of the genus Micronycteris, and it subsequently also appeared in the phylogenetic analyses of Wetterer et al. (2000: character 86) and Simmons and Conway (2001).

Character 266: Neural process on first thoracic vertebra.

Neural process absent or poorly developed on the first thoracic vertebra (0), or well developed (1).

The neural process on the first thoracic vertebra is absent or replaced by a small ridge in Carollia brevicauda and in many stenodermatines (e.g. Sturnira lilium, Mesophylla, Ectophylla, Vampyressa thyone). In contrast, a conspicuous neural process is present on the first thoracic vertebrae in some other stenodermatines (e.g. Artibeus [Dermanura] cinereus, Sphaeronycteris. The neural process seems to vary in development among sexes in Pygoderma, being less developed in males of the species or reduced to a tuberosity, and more developed in females. Pending the analysis of a larger number of samples of skeletons of Pygoderma, I did not score a separate state for this species, which was coded with “1” in the data matrix.

Simmons and Conway (2001: character 120) described a character to account for the development of neural spines in the first four thoracic vertebrae.

Character 267: Relative development of neural spines on lumbar vertebrae.

Neural spines poorly developed on lumbar vertebrae (0), or developed, maximum height about 1/4 of height of lumbar vertebra body, height of spines often approximately subequal from L1 through L4, or sometimes the pairs of spines in L1 and L4, and L2 and L3 are subequal in height (1), or well developed, maximum height 1/3 to 1/2 of the height of lumbar vertebra body, height of spines increases gradually from L1 to L3, and sometimes to L4 (2).

Neural spines in the lumbar vertebrae are poorly developed in Carollia brevicauda and Uroderma bilobatum. In contrast, neural spines are well developed and of a subequal height in many stenodermatines (e.g. Sturnira lilium, Phyllops falcatus, Ectophylla, Ardops). In these forms the spines do not vary much in height, having roughly the same height from L1 to L4, or sometimes L1 and L4 are subequal in size as well as L2 to L3. Finally, neural spines are well developed in many other stenodermatines but increase gradually in height from the first to the third, and sometimes to the fourth lumbar vertebra (e.g. Ametrida, Centurio, Pygoderma, and Sphaeronycteris).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 268: Morphology of anterior face of manubrium (manubrium sterni).

Surface of the anterior face of manubrium simple, rounded with small head (0), or quadrate with large head (1).

In the medial part of anterior face of the manubrium there is a simple crest-like projection rounded in shape in Carollia brevicauda and some stenodermatines (e.g. Ectophylla, and Vampyressa brocki). In contrast, the medial anterior face of the manubrium has a large, quadrate shaped crest in several other stenodermatines (e.g. Platyrrhinus helleri, Mesophylla, Vampyressa bidens).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 269: Angle between the body and ventral process of manubrium.

Angle circumscribed between body and ventral process of manubrium acute (0), or roughly straight (90°) (1), or obtuse (2).

The angle between the body and the ventral manubrium is less than 90° in Phyllostomus hastatus, Carollia brevicauda, and in many stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum, Ectophylla). In contrast, this angle is roughly straight (i.e. roughly 90°) in some stenodermatines (e.g. Chiroderma villosum, Vampyressa brocki). A third condition is found in Ametrida and Sphaeronycteris, which have an obtuse angle between the body and ventral process of manubrium.

This character has appeared in the phylogenetic analyses of Simmons (1998: character 87), Simmons and Geisler (1998: character 92), and Simmons and Conway (2001: character 128).

Character 270: Relative size of lateral process of manubrium.

Lateral process of manubrium narrow, anteroposterior width approximately one half or less of the length of the ramus of lateral process (0), or broad, wider than half length of ramus (1).

The lateral process of manubrium is narrow in most stenodermatines (e.g. Mesophylla, Vampyressa melissa), its width measuring approximately one half or less of the length of the ramus of lateral process of manubrium. In contrast, the process is wide in Ardops, and Sphaeronycteris; larger than the half of the length of the ramus.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 271: Notch in the ventromedial margin of lateral process of manubrium.

Rounded notch or perforation in the ventro-medial margin of lateral process of manubrium absent (0), or present (1).

A rounded notch is absent from the posterior margin of the lateral process of manubrium in Carollia brevicauda and some stenodermatines (e.g. Mesophylla, Vampyressa pusilla). In contrast a notch, which is sometimes enclosed as a perforation, is present in the postero-medial border of the process in some other stenodermatines (e.g. Vampyressa brocki, V. nymphaea, Ardops).

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 272: Keel of mesosternum (corpus sterni, gladiolus).

Keel of mesosternum poorly developed and irregular in shape (0), or well developed and straight or serrated in shape (1), or developed and larger at the mesosternum longitudinal middle point (2).

The keel of mesosternum provides a surface for origin of muscles related to flight in bats and variation in its morphology may imply differences in flight abilities. The keel of the mesosternum is poorly developed in Carollia brevicauda, and some stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum). In contrast, the keel is well developed and of uniform height with a straight or serrated edge in many other stenodermatines (e.g. Centurio, Vampyressa melissa). A third condition occurs in other stenodermatines (e.g. Ardops, Ectophylla), which have a keel with the medial part more developed and higher than the rest of mesosternum.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

This is the first use of this character in a phylogenetic analysis.

Character 273: Morphology of posterior xiphistern (processus xiphoideus). Posterior end of xiphistern with wide lateral flare (0), with little developed or no lateral flare (1).

The posterior end of xiphisternum has a little or no lateral flare in Carollia brevicauda, and many stenodermatines (e.g. Ectophylla, Vampyressa nymphaea). In contrast, several other stenodermatines (e.g. Artibeus concolor, Ariteus, Vampyressa melissa) have a well-developed lateral flare in the distal xiphisternum.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 274: Number of costal cartilages articulating with mesosternum. Five or more costal cartilages posterior to second rib articulate with mesosternum (0), or four coastal cartilages posterior to second rib articulate with mesosternum (1), or three costal cartilages posterior to second rib articulate with the mesosternum; the fourth cartilage articulates with a point medial in the third rib (2).

Five or more costal cartilages posterior to second rib articulates with the mesosternum in individuals of Carollia brevicauda, in Sturnira lilium, Chiroderma villosum, as well as in many stenodermatines (e.g. Mesophylla, Vampyressa melissa and Vampyressa nymphaea. In contrast, four costal cartilages articulate with posterior mesoternum in other individuals of Carollia brevicauda and and in many other stenodermatines (e.g. Vampyressa bidens, V. thyone*)*. A third condition is seen in Ectophylla, Ardops, and Ariteus, in which the fourth rib is attached to the mid-point of the third rib so only three costal cartilages articulate directly with the mesosternum.

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of states.

Simmons and Geisler (1998), and Simmons and Conway (2001: character 134) used similar characters to account for the variation in the number of costal cartilages connecting the mesosternum with the ribs in bats. I have added states 1 and 2 to accommodate the variation I have found within stenodermatines.

Character 275: Relative development of the expanded costal cartilage of the first rib.

Expanded coastal cartilage of first rib relatively narrow, smaller than lateral process of manubrium (0), or well developed, its width roughly equals to that of the lateral process of the manubrium (1).

The costal cartilage attached to the first rib is relatively narrow in some stenodermatines (e.g. Ectophylla, Vampyressa bidens). In contrast, this costal cartilage is well developed in other stenodermatines (e.g. Ariteus, Phyllops falcatus, Centurio), its width being roughly equals to that of the lateral process of the manubrium.

This is the first use of this character in a chiropteran phylogenetic analysis.

Character 276: Tail.

Tail present (0), or absent (1).

Phyllostomus hastatus and Carollia brevicauda have caudal vertebrae and a tail. In contrast, Rhinophylla pumilio and all stenodermatines lack a tail.

This character has been used previously in the phylogenetic analyses of Straney (1980: G1-3) and Wetterer et al. (2000: character 89).

Character 277: Relative size of calcar in relation to foot.

Calcar subequal to foot (0), or shorter than foot (1), or absent (2).

The calcar is usually subequal to the foot in Phyllostomus hastatus. In contrast, the calcar is shorter than the foot in Carollia brevicauda and in all stenodermatines except Sturnira, which lacks a calcar.

This character was used previously by Straney (1980: character G6-8), Simmons (1996: character 11), Simmons (1998: character 157), Simmons and Geisler (1998: character 171), Wetterer et al. (2000: character 87), and Simmons and Conway (2001: 174). Simmons and Conway (2001) recognized more states of proportional size of the calcar and foot in their phylogeny of mormoopid bats.

Soft Tissue Morphology

Brain

Character 278: Inferior colliculi exposure on surface of brain.

Inferior colliculi completely covered by cerebelar vermis (0), or only partially covered, colliculi at least partially visible in dorsal view of brain (1).

The inferior colliculi are completely covered by the cerebelar vermis in Phyllostomus hastatus, Rhinophylla pumilio, Carollia brevicauda, and some stenodermatines for which this information is available (Sturnira lilium, Uroderma bilobatum, Chiroderma villosum, and Vampyressa nymphaea). In contrast, the colliculi are partially covered medially by the cerebelar vermis in some other stenodermatines (e.g. Mesophylla, Vampyressa thyone).

This character has first appeared in the component analyses of Straney (1980: character D1, 2) and subsequently in the phylogenetic analyses of Wetterer et al. (2000: character 136), and Simmons and Conway (2001: character 52).

Hyoid Myology

Character 279: M. mylohyoideus.

M. mylohyoideus divided (0), or undivided (1).

M. mylohyoideus is divided into anterior and posterior parts in Uroderma bilobatum and several stenodermatines (Vampyressa thyone). In contrast, m. mylohyoideus is undivided in Sturnira lilium.

This character has first appeared in the component analyses of Straney (1980: characters E9, E11), and subsequently in the phylogenetic analyses of

Wetterer et al. (2000: character 90), and Simmons and Conway (2001: character 56)

Character 280: Origin of fibers of m. sternohyoideus.

Fibers of m. sternohyoideus originate from clavicle (0), or does not originate from clavicle (1).

The lateral fibers of m. sternohyoideus take origin from the manubrium and the clavicle in Carollia brevicauda, Platyrrhinus helleri, Uroderma bilobatum, and Vampyressa thyone (Griffiths, 1982). In contrast, the fibers do not have a clavicular origin in Sturnira lilium.

This character has appeared in the phylogenetic analyses of Wetterer et al. (2000: character 92).

Character 281: Insertion of m. ceratohyoideus on ceratohyal.

M. ceratohyoideus does not insert on ceratohyal (0), or part of muscle inserts on ceratohyal (1).

M. ceratohyoideus does not insert on the ceratohyal element of the hyoid apparatus in Phyllostomus hastatus. In contrast, part of the m. ceratohyoideus insert into the ceratohyal element of the hyoid apparatus in Carollia brevicauda and several stenodermatines (e.g. Platyrrhinus helleri, Vampyressa thyone).

This character has first appeared in the analysis of Simmons (1998: character 56), subsequently in the analysis of Simmons and Geisler (1998: character 59) and then in the study of Wetterer et al. (2000: character 94).

Character 282: Insertion of m. ceratohyoideus into the stylohyal element.

Part of the m. ceratohyoideus does not insert on stylohyal (0), or inserts (1).

M. ceratohyoideus does not insert on the stylohyal in Carollia brevicauda, and some stenodermatines (e.g. Sturnira lilium, Uroderma bilobatum). In contrast, part of the m. ceratohyoideus inserts on the stylohyal element in Phyllostomus hastatus, Platyrrhinus helleri and Vampyressa thyone.

This character has appeared in the phylogenetic analyses of Simmons (1998: character 58), Simmons and Geisler (1998: character 61), and Wetterer et al. (2000: character 95).

Character 283: Lateral slip of sphincter colli profundus.

Lateral slip of m. sphincter colli profundus present (0), or absent (1).

A lateral slip of m. sphincter colli profundus is present in Phyllostomus hastatus, Carollia brevicauda, and several stenodermatines (e.g. Platyrrhinus helleri, Uroderma bilobatum). In contrast, this slip is absent in Sturnira lilium.

This character has appeared in the phylogenetic analyses of Wetterer et al. (2000: character 104).

Character 284: Direction of lateral slip of sphincter colli profundus.

Lateral slip of m. sphincter colli profundus passes laterally to insert onto cervical region (0), or anterolaterally (1).

The lateral slip of m. sphincter colli profundus departs from the fascia and passes laterally to insert onto the cervical skin of Phyllostomus hastatus and Carollia brevicauda. In contrast, this slip passes anteromedially on the way to its insertion onto the cervical skin in several stenodermatines (e.g. Platyrrhinus helleri, Uroderma bilobatum).

Sturnira lilium, which lacks a lateral slip of m. sphincter colli profundus was scored “-“.

This character has appeared in the phylogenetic analyses of Wetterer et al. (2000: character 105).

Poscranium Myology

Character 285: M. dorsi patagialis.

M. dorsi patagialis present (0), or absent (1).

The m. dorsi patagialis is a muscle unique to bats (Strickler, 1978). This muscle is present in Phyllostomus hastatus and most stenodermatines. In contrast, m. dorsi patagialis is absent in Centurio senex.

This character appeared in the phylogenetic analyses of Simmons (1998: character 111), and Simmons and Geisler (1998: character 116).

Character 286: Distal muscle belly of m. occipitopollicalus.

Distal muscle belly of m. occipitopollicalus absent (0), or present (1).

A distal muscle belly is absent in the m. occipitopollicalis complex of Phyllostomus hastatus, Carollia brevicauda, and some stenodermatines (e.g. Sturnira lilium, Centurio senex) In contrast a distal muscle belly is present in the m. occipitopollicalus complex of Chiroderma villosum (Strickler, 1978).

This character has appeared in the phylogenetic analyses of Straney (1980: characters C1-2), Simmons (1998: character 117), Simmons and Geisler

(1998: character 122), Wetterer et al. (2000: character 75), and Simmons and Conway (2001: character 179).

Character 287: Insertion of caput mediale of. m. triceps.

Caput mediale of m. triceps inserts on elbow sesamoid (0), or on caput laterale tendon (1).

The caput mediale of m. triceps of Phyllostomus hastatus and Carollia brevicauda inserts on the elbow sesamoid (Strickler, 1978). In contrast, the caput mediale of m. triceps inserts on the tendon of the caput laterale in Centurio senex (Strickler, 1978).

This character has appeared in the phylogenetic analysis of Wetterer et al. (2000: character 78).

Tongue

Character 288: Morphology of medial circumvallated papilla.

Papillary bodies of medial circumvallated papilla separate from valla, fossae complete (0), or fused anterolaterally and posteromedially to valla, fossa incomplete (1).

Most phyllostomids have two medial circumvallated papillae on the dorsolateral tongue (Griffiths, 1982, Gimenez, 1993, Gimenez et al., 1996, Wetterer et al., 2000). The fossae of medial circumvallated papillae are complete in Phyllostomus hastatus, Carollia brevicauda, and most stenodermatines. In contrast, the fossa is incomplete in Centurio and Sphaeronycteris.

Wetterer et al. (2000: character 108) originally described this character and used it for the first time in a phylogenetic analysis. My character states and scoring are identical to theirs (see character 108, Wetterer et al., 2000: page 102).

Character 289: Lateral circumvallate papillae.

Lateral circumvallate papillae present (0), or absent (1).

Most phyllostomid bats have a pair of circumvallate papillae on the lateral surface of the tongue (Wetterer et al., 2000). In contrast, Centurio lacks those lateral papillae.

This character has appeared in the phylogenetic analyses of Gimenez (1993: character 3.3.2.2, 3.3.5.3), Gimenez et al. (1996: character 6), Wetterer et al., (2000: character 109), and Simmons and Conway (2001: character 73).

Character 290: Location of lateral circumvallate papillae.

Lateral circumvallate papillae located laterally on tongue (0), or dorsolaterally (1), or dorsally (2).

Most phyllostomids possess a pair of lateral circumvallated papillae on the lateral surfaces of the tongue (Griffiths, 1982, Smith and Hood, 1984, Gimenez, 1993, Gimenez et al., 1996, Wetterer et al., 2000). In contrast, Sturnira lilium and some stenodermatines have the lateral circumvallate papillae located dorsolaterally (e.g. Platyrrhinus helleri, Vampyressa bidens). A third condition is observed in Chiroderma villosum and Ectophylla, which have the lateral circumvallated papillae situated on the dorsal surface of the tongue.

Gimenez (1993: character 3.3.4.2) first used this character in a phylogenetic analysis, and her character state definitions have been followed by Wetterer et al. (2000: character 110) and were adopted in this study as well. Gimenez (1993) however indicated that the papillae were laterally placed in Vampyressa bidens and V. pusilla, which I disagree with. My scoring for those species is in agreement with that of Wetterer et al. (2000: character 110).

Character 291: Papillae on pharyngeal region of the tongue.

Pharyngeal region of tongue completely covered with papillae (0), or covered only laterally (1), or unpapillated (2).

In Phyllostomus hastatus and in some stenodermatines (e.g. Ectophylla, Mesophylla) the entire pharyngeal region of the tongue is covered with papillae. In contrast, Carollia brevicauda, Rhinophylla pumilio, and many stenodermatines have the pharyngeal region of the tongue laterally covered with papillae while the dorsal surface is bare (e.g. Artibeus jamaicensis, Chiroderma villosum). A third condition observed in some other stenodermatines is a completely bare pharyngeal tongue (e.g. Centurio, Pygoderma).

This character appeared first in the phylogenetic analyses of Gimenez (1993: characters 3.3.2.3, 3.3.3.3, 3.3.4.7 - 8), and subsequently in Wetterer et al. (2000: character 111) and Simmons and Conway (2001: character 76). My scoring and definition of states overall follows Wetterer et al. (2000) for this character.

Character 292: Direction of medial-posterior mechanical papillae.

Most medial-posterior mechanical papillae inclined toward the pharyngeal region of the tongue (0), or inclined toward tip of the tongue (1).

Gimenez (1993) and Wetterer et al. (2000) described the medial-posterior mechanical papillae as located mesially in relation to the medial vallate papillae and to the anterior mechanical papillae. Those medial-posterior mechanical papillae vary in their orientation: most medial-posterior mechanical papillae are directed toward the pharyngeal region in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and Sturnira lilium. In contrast, the medial posterior mechanical papillae are directed towards the tip of the tongue in all the remaining stenodermatines.

Gimenez (1993: character 3.3.4.11) first used this character, which was subsequently used by Wetterer et al. (2000: character 116), and Simmons and Conway (2001: character 74). My states 0 and 1 are identical with states 0 and 1 from Wetterer et al. (2000: page 109, character number 116) description.

Character 293: Bifid anterior mechanical papillae.

Bifid anterior mechanical papillae absent (0), or present (1).

Long-tipped, bifid anterior mechanical papillae are absent in Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and some stenodermatines (e.g. Sturnira lilium, Platyrrhinus helleri). In contrast, a band of bifid anterior mechanical papillae occurs in many other stenodermatines (e.g. Mesophylla, Vampyressa nymphaea).

This character first appeared in the phylogenetic analyses of Gimenez (1993: character 3.3.4.10), and subsequently of Wetterer et al. (2000: character

118). I agree with Wetterer et al. (2000) who described found bifid anterior mechanical papillae in stenodermatines other than Mesophylla, Vampyressa bidens, and V. pusilla, the only taxa in which Gimenez (1993) found those papillae.

Character 294: Basketlike medial-posterior mechanical papillae.

Basketlike medial-posterior mechanical papillae present (0), or absent (1).

Phyllostomus hastatus, Carollia brevicauda, Rhinophylla pumilio, and Sturnira lilium have basketlike medial-posterior mechanical papillae, which are defined as papillae with central concavities and cylindrical bases (Wetterer et al., 2000). In contrast, most stenodermatines lack basketlike medial-posterior mechanical papillae (e.g. Mesophylla, Vampyressa nymphaea).

This character first appeared in the phylogenetic analyses of Gimenez (1993: characters 3.3.2.5, 3.3.3.5, 3.3.4.9, 3.3.5.7), and subsequently in the analysis of Gimenez (1996: character 10), Wetterer et al. (2000: character 119), and Simmons and Conway (2001: character 75).

Character 295: Horny papillae pattern.

Single large horny papilla present amid elliptical cluster of smaller horny papillae (0), or two large horny papillae present (1), or no large horny papillae (2).

All phyllostomid bats have elliptical clusters of highly keratinized papillae, horny shaped and located near the tip of the tongue (Gimenez, 1993, Wetterer et al., 2000). In Carollia brevicauda, Sturnira lilium, and many stenodermatines (e.g. Chiroderma villosum, Vampyressa nymphaea) there is a single large papilla on the midsagittal line of the tongue (Wetterer et al., 2000). In contrast, Platyrrhinus helleri, Vampyrodes and Uroderma bilobatum have two large horny papillae amid the cluster of smaller papillae at both sides of the midline of the tongue (Wetterer et al., 2000). Finally, the tongue of Rhinophylla pumilio lacks large horny papillae, with all of the horny papillae being subequal and small in size.

This character has appeared in the phylogenetic analyses of Griffiths (1982: character 16), Gimenez (1993: character 3.3.5.13), Gimenez et al. (1996: character 12), Wetterer et al. (2000: character 124), and Simmons and Conway (2001: character 72).

This multistate character was not ordered since no clear logical transformation pathway could be detected by the observation of horny papillae patterns.

Character 296: Small horny papillae posterior to main (large) papillae.

Two small papillae posterior to main horny papillae (0), or none (1).

Two small horny papillae are located posterior to the main, large horny papillae in Carollia brevicauda, Sturnira lilium, and most stenodermatines (e.g. Vampyressa bidens). In contrast, Uroderma bilobatum lacks small horny papillae posterior to main large horny papillae. Rhinophylla pumilio was scored with (-), “inapplicable”, since all the horny papillae are the same size and it lacks large, main papillae for comparison.

This character has appeared in the phylogenetic analyses of Gimenez et al. (1996: character 12), and Wetterer et al. (2000: 126).

Digestive tract

Character 297: Brunner's glands.

Brunner's glands present (0), or absent (1).

Brunner's glands are present in the gastroduodenal tract of *Phyllostomus hastatus*, and some stenodermatines (*e.g.* *Sturnira lilium*, *Artibeus jamaicensis*). In contrast, Brunner's glands are absent in many stenodermatines (*e.g.* *Vampyrodes*, *Chiroderma villosum*, *Vampyressa nymphaea*).

This character first appeared in the study of Straney (1980: character A1), and subsequently in the phylogenetic analyses of Wetterer *et al*. (2000: character 129). My scoring is the same as that of Wetterer *et al*. (2000). I made no original observations for this character scoring.

Reproductive tract

Character 298: Cornual lumina.

Cornual lumina reduced to tubular intramural cornua (0), or totally fused, without distinct cornual lumina (1).

Phyllostomus hastatus, *Rhinophylla pumilio* and *Carollia brevicauda* have the cornual lumina reduced to tubular intramural uterine cornua (Hood and Smith, 1982, 1983). In contrast, there is no remnant of the cornual lumina in many stenodermatines, such as *Uroderma bilobatum*, *Vampyressa thyone* (Hood and Smith, 1983).

This character has appeared in the phylogenetic analyses of Hood and Smith (1982: character 3), Simmons (1998: character 167), Simmons and Geisler

(1998: character 181), and Wetterer et al. (2000: character 132). I made no original observations for this character scoring.

Character 299: Connection of oviduct to uterus.

Connection of oviduct and uterus is lateral (0), or posterolateral, fundic lateral (1), or fundic medial (2).

The oviduct connects to the lateral aspect of the body of the uterus in Phyllostomus hastatus. In contrast, the oviduct in Rhinophylla pumilio and Carollia brevicauda has a posterolateral, fundic entry to the uterus body. A third condition is observed in many stenodermatines (e.g. Ectophylla), which have a fundic medial connection between oviduct and the body of the uterus.

This character was previously used in a phylogenetic analysis by Hood and Smith (1982: character 5) and subsequently by Wetterer et al. (2000: character 133). I made no original observations for this character scoring.

Character 300: Ovarian ligament.

Ovarian ligament extends from ovary to entry of oviduct (0), or from ovary directly to uterus (1).

The ovarian ligament attaches the ovary to the oviduct in Phyllostomus hastatus. In contrast, in Carollia brevicauda, Rhinophylla pumilio, and several stenodermatines (e.g. Ectophylla, Centurio, Vampyressa thyone), the ovarian ligament attaches the ovary directly to the lateral uterus.

This character appeared in the phylogenetic analyses of Hood and Smith (1982: character 6) and Wetterer et al. (2000: character 134). I made no original observations for this character scoring.

Results and Discussion

Phylogenetic Relationships within Stenodermatinae (Chiroptera, Phyllostomidae): Analyses of partitioned datasets

As briefly explained in the “material and methods” section, my goal in partitioning the data was exclusively analytical. Therefore, I do not intend to discuss results from each partition as phylogenetic alternative hypotheses and I rather use a comparative approach while discussing the positions and interrelationships of taxa in the all-characters combined tree (morphology plus sequence data from cyt-b and RAG2 combined), which is carried out further in this discussion.

The craniodental dataset

The Maximum Parsimony (MP) analysis of the craniodental set of characters for stenodermatines, using the ordered character transformations as explained in the character descriptions, resulted in five most-parsimonious trees that required 770 steps (CI = 0.35, RI = 0.6, table 2, and fig. 15). The resolution of the trees resulting from the MP analysis with the present data set was considerably higher than that provided by a smaller set of craniodental characters analysed in Wetterer et al. (2000, see fig. 15).

Wetterer et al. (2000), using 35 craniodental characters recovered a paraphyletic Stenodermatinae with some stenodermatine genera nesting together with glossophagines, other with desmodontines, glossophagines and carolliines (Wetterer et al., 2000: 129, and see fig. 15). In contrast, monophyly of stenodermatines including and to the exclusion of Sturnira was strongly corroborated by the present craniodental data (table 2, and fig. 15). Other well-supported clades in the present analysis that were not recovered in Wetterer et al. (2000) craniodental tree were a clade formed by Chiroderma, Ectophylla, Mesophylla, and Vampyressa (s.l.); a clade formed by V. bidens, V. brocki and V. nymphaea; a clade formed by Platyrrhinus and Vampyrodes; the short-faced bats clade (subtribe Stenodermatina); and a clade formed by Ardops and Ariteus. Finally, a clade with Vampyressa melissa, V. thyone, and V. pusilla appeared but was little supported by the craniodental data set (fig. 15). A clade formed by Ametrida and Sphaeronycteris was recovered in both, the present and Wetterer et al. (2000) analysis (fig. 15).

Most of the clades recovered in the craniodental tree appeared and several were well supported by the combined analysis (= total evidence), including cyt b, RAG2 and all morphological characters (see further). That makes the craniodental characters a robust source of evidence to reconstruct the phylogeny of stenodermatine bats.

The morphological dataset

The Maximum Parsimony (MP) analysis of the morphological characters for stenodermatines, using the ordered character transformations as described in the character descriptions, resulted in four most-parsimonious trees (fig. 16) of 1238 steps (CI = 0.37, RI = 0.6, table 2).

Morphological data recovered more clades and resolution overall, when compared to the craniodental data set.

Notably more refined information brought about by the analysis of the total of morphological characters when compared to the craniodental subset were the basal position of Uroderma to the P. helleri and Vampyrodes clade; the basal position of the clade formed by Artibeus concolor and A. jamaicensis in relation to a clade formed by Artibeus cinereus and several stenodermatines, and the split of short-faced bats in two clades, separating continental and Antillean forms; and the relationships between Chiroderma villosum, Vampyressa bidens, and the clade formed by Vampyressa brocki and V. nymphaea (successively sister, following this order).

Within the Antillean species clade, Stenoderma (Porto Rico) was basal to the clade with Ardops (Lesser Antilles) and Ariteus (Jamaica). This Antillean clade and Phyllops falcatus (from Cuba) were of uncertain position within short-faced bats. All continental short-faced formed a clade according to the morphological data, being Pygoderma basal to a clade formed by Centurio, Ametrida and Sphaeronycteris. The relationships between the Antillean forms clade, the single Antillean with uncertain position (Phyllops falcatus) and the continental forms clade remained uncertain based on morphology (fig. 16, table 2).

Monophyly of subtribe Vampyressina (sensu Baker et al., 2003) was not supported by the analysis of morphological data; rather, I recovered a clade including all “vampyressines” (sensu Baker et al. 2003) plus Ectophylla. This result is in accordance to those based on a mostly morphological analysis provided by Wetterer et al. (2000, see figs. 3A and 16).

The present analysis has recovered overall different topologies compared to the analysis of Wetterer et al. (2000), although both morphological data sets recovered the clades (1) “short-faced”, (2) Uroderma, Platyrrhinus and Vampyrodes (the two latter sister taxa and Uroderma basal), (3) Stenoderma (basal), Ardops and Ariteus (sister taxa), and finally (4) a basal position of Chiroderma to Vampyressa (s.l.) species (see figs. 3A and 16). Discrepancies of the topologies recovered through morphological based analysis with molecular will be discussed below.

The cytochrome b dataset

The MP analysis of cyt-b resulted in four most parsimonious trees of 2166 steps (CI=0.36; RI=0.6, fig. 17, table 2). Positions of Chiroderma, Uroderma, Ectophylla, Enchisthenes, and Mesophylla and of most clades recovered (e.g. Platyrrhinus helleri + Vampyrodes) were different in each of these four fundamental trees and unresolved by this dataset and analysis.

“Vampyressina” (a name proposed in Baker et al., 2003 to encompass a clade comprising Platyrrhinus, Vampyrodes, Chiroderma, Vampyressa, Vampyriscus and Metavampyressa) was weakly supported by cyt-b data (bootstrap value<< 50, table 2), and this relationships do not appear in the strict consensus tree (fig. 17). Cytochrome b data recovered several clades also recovered by morphology, all occurring in uncertain position in the

Stenodermatinae tree (1) Platyrrhinus with Vampyrodes (2) Vampyressa bidens, V. brocki and V. nymphaea, the latter two sister taxa and (3) the short-faced clade (4) the Artibeus concolor and A. jamaicensis clade.

Short-faced bats (subtribe Stenodermatina) were split into three clades in the analysis of cyt-b data, instead of three as in the case of morphological data analysis: a clade with continental species distributed on the Neotropical mainland (Ametrida, Centurio, Pygoderma and Sphaeronycteris), a clade with the Antillean species Phyllops falcatus (Cuba and Hispaniola) and Stenoderma (Puerto Rico), and a clade formed by the Antillean species Ardops and Ariteus (respectively, Lesser Antilles and Jamaica).

Radically diffent result from cytb from the morphological data analysis was that Ametrida and Pygoderma formed a well supported clade, a relationship that is only repeated in the tree with cytb and RAG2 combined (see further) and that Vampyressa (s.s., V. melissa, V. thyone, and V. pusilla) appeared as sister clade to the Platyrrhinus and Vampyrodes clade.

The RAG2 dataset

The MP analysis of RAG2 resulted in 54 most-parsimonious trees of 349 steps (CI=0.76; RI=0.76). With only 91 parsimony-informative characters, RAG2 appeared little informative for resolving relationships within Stenodermatinae. The RAG2 dataset not strongly disagreed with the morphological tree, and provided a series of relationships in agreement with it (figs. 16 and 18).

The RAG2 data analyses recovered two large clades, one comprising species of “Vampyressina” (sensu Baker *et al.*, 2003) and the other including the short-faced bat species (subtribe Stenodermatina, sensu Wetterer *et al.*, 2000), *Artibeus* (sensu lato), *Ectophylla* and *Enchisthenes*. In contrast, the analysis of morphological data resulted in one clade with *Enchisthenes* and short-faced and another with the remaining stenodermatines (figs. 16 and 18). *Enchisthenes* had uncertain position according to MP analysis of RAG2 and cyt-b data (figs. 17 and 18).

Within the large clade of “vampyressina bats” recovered itn the RAG2 analyses, two clades were found, one including *Vampyressa* (*s.s.*) and the other with *Vampyressa brocki*, *Vampyressa nymphaea* and *Vampyressa bidens.*

This was the only analysis in which the subgenus *Metavampyressa* appears paraphyletic, *i.e.* *Vampyressa (Metavampyressa) nymphaea* is basal to a clade formed by *Vampyressa* (*Metavampyressa brocki)* and *Vampyressa bidens*. The sister relationship of *Vampyressa brocki* and *Vampyressa bidens* was weakly supported by MP (bootstrap = 73, fig. 18). Two other partitions of data (cyt-b and morphology) recovered a monophyletic *Metavampyressa* with a basal *Vampyriscus* (figs. 16 and 17).

In both the MP analysis of RAG2 and cyt b data (as in the MP analysis of cyt-b) the positions of *Uroderma*, *Chiroderma,* *Ectophylla* and *Mesophylla* remained unresolved, which contrasts with the resolved topologies based on morphological data (figs 16, 17 and 18).

According to RAG2 data, Artibeus cinereus was basal to a clade formed by Artibeus concolor and A. jamaicensis, similarly to the results of the analysis of cyt-b data. In contrast, Artibeus was paraphyletic according to morphological data (figs. 16 and 18).

Short-faced bats were split into three clades according to RAG2 data: a clade with continental species distributed on the Neotropical mainland (Ametrida, Centurio, Pygoderma and Sphaeronycteris) as in the results provided by MP analysis of morphological data, a clade with the Antillean species Phyllops falcatus and Stenoderma, basal to all the other short-faced bats (the position occupied by Ardops and Ariteus in the cyt-b tree), and successively sister to a clade formed by the Antillean species Ardops and Ariteus, which was turn successively sister to the continental species (fig. 16). Among the mainland species of short-faced bats, Centurio was basal to a clade formed by Ametrida and Sphaeronycteris, and Pygoderma is basal to this three-taxon clade as in the morphological trees (figs. 16 and 18). Relationships within continental short-faced bats based on RAG2 are in agreement with morphology and differ from cyt b (figs. 16, 17, and 18).

The RAG2 and cytochrome b combined dataset

I tested for compatibility between the two genes using the IDL test, and the two gene matrices were shown to be compatible according to this estimator ($p = 0.56$, both genes were incongruent with morphology according to this estimator; p

= 0.01). I subsequently combined the two genes and analyzed them with unweighted maximum parsimony.

The consistent relationships found in trees recovered (fig. 19) were:

(1) a clade formed by subgenus Metavampyressa (V. brocki and V. nymphaea) with Vampyressa bidens as sister,

(2) a clade formed by Vampyrodes and Platyrrhinus helleri,

(3) a clade formed by Ectophylla and Enchisthenes,

(4) a clade formed by Phyllops falcatus and Stenoderma,

(5) a clade formed by Ardops and Ariteus,

(6) a clade formed by successively sister Sphaeronycteris, Centurio, Ametrida and Pygoderma, and

(7) a clade formed by Artibeus concolor and A. jamaicensis, with Artibeus (Dermanura) cinereus as basal.

Clade (1) was the only clade only not recovered previously in the RAG2 analyses (figs. 18 and 19). Clades (2) and (5) were recovered by all three sets of characters (morphology, RAG2, and cyt-b; respectively figs. 16, 17, 18, and 19); clades (3) and (6) were novel, i.e., exclusive to the combined matrix with the two genes (fig. 19); and clades (4) and (7) were recovered in each of the analyses of the two genes separately (figs. 17, 18, and 19).

Phylogenetic Relationships within Stenodermatinae (Chiroptera, Phyllostomidae): Total evidence

The heuristic search (Maximum Parsimony) of combined 2803 RAG2, cyt-b and morphological characters for stenodermatines resulted in a total number of 105148 rearrangements tried, and in the recovery of two most-parsimonious trees with 3759 steps (CI = 0.38, RI = 0.42, table 3, fig. 20). Of 2803 characters included in the analysis, 737 characters were parsimony-informative. Trees and measurements of support recovered by MP analyses of all-characters combined are shown in fig. 20, and table 3. The discussion of relationships found in the all-characters combined analyses is provided as follows, clade by clade, and contrasted with the results from other analyses.

Phylogeny of Stenodermatinae

Redefinition of Vampyressa

Paraphyly of Vampyressa (s.l.) has long been suspected based on previous analyses of both morphological and molecular data (e.g. Wetterer et al., 2000, Porter and Baker, 2004), the only study including all species Vampyressa (s.l.) prior to this one was the recent molecular-only analysis of Hoofer and Baker (2006). Paraphyly of Vampyressa (s. l. Simmons, 2005) was fully confirmed by the data presented here.

On the other hand, monophyly of Vampyressa to include the species Vampyressa melissa, V. thyone and V. pusilla was strongly supported by the total evidence analysis. This finding is congruent with results of previous molecular analysed (Porter and Baker, 2004, Hoofer and Baker, 2006) which showed clearly that Vampyressa bidens, V. brocki and V. nymphaea do not belong in the same clade with Vampyressa melissa, V. pusilla, and V. thyone. Most analyses of data partitions in the present study reinforced these conclusions, and even those cases in which paraphyly of Vampyressa (s.l.) was not markedly demonstrated (because of low support) it was never contradicted.

Vampyressa must therefore be redefined to include only those taxa that form a clade with the nominate species, in this case three taxa: Vampyressa melissa, V. pusilla (the nominate form), and V. thyone. This clade was well defined by the present analysis with high support including most partitions of data (table 3, figs. 16 to 20). Two unambiguous changes, three ACCTRAN changes, and three DELTRAN changes at this node resulted from the optimizations tried (table 4). Because this clade has not been explicitly diagnosed up to now, I provide an emended diagnosis below based on characters supporting that node in the total evidence tree, using all optimizations (unambiguous, ACCTRAN and DELTRAN; for a summary of characters diagnosed through those optimizations see table 4) that in combination may define those taxa. A discussion of the relationships of Vampyressa bidens, V. brocki and V. nymphaea and their taxonomic status is provided in the next section, in the same fashion.

Emended diagnosis of the genus Vampyressa Thomas, 1900

Type species Vampyressa pusilla (Wagner, 1843)

Pelage medium to pale brown; dorsal fur tricolored; ventral fur predominantly unicolored; facial stripes present, subequal in breadth and faint, moderately or relatively well-marked; anterior tip begins close to the mouth and posterior tip of dorsal facial stripe reaches maximally as far as anteromedial pinna insertion; dorsal stripe completely lacking; propatagium furred; fur on the ventral uropatagium either scarce or somewhat more concentrated in the middle; ears short and rounded; ventral edge of the external narial opening narrow, its lateral border limited to the level of posterior face of the upper outer incisor, either v-shaped or a short straight bar; anterior nasal ending before anterodorsal maxilla and creating a recess between those bones; nasal and maxilla do not forming a continuous edge; lateral maxilla not compressed or only slightly compressed at the level of premolars; anterodorsal, laterodorsal, and sometimes postorbital region of the rostral skull slightly inflated; bucal ceiling continuously arching anteroposteriorly; small medial part of the postglenoid process present, bends over the articular surface of the glenoid fossa; anteriormost tip of the orbital rim variably located between posterior fourth upper premolar (P4) and first upper molar (M1); breadth of shaft of upper inner incisors unequal; inner upper incisor (I1) bilobed but bilobation may often be obscured by wear in species in which this tooth is shallowly notched on the anterior face; third upper premolar (P3) styliform and with a straight base; third upper premolar (P3) implanted in horizontal alveolar surface, roughly in the same plane as fourth upper premolar (P4); one postero-lateral cusp arising from the cingulum of the fourth upper premolar (P4) reaching from 1/3 to a little less than 1/2 the height of fourth upper premolar (P4); metaconid about twice the size of protoconid on second lower molar (m2); well-developed entoconid on second lower molar forming a quadrate-shaped crest, entoconid very large, subequal to metacone in height and directed vertically; no diastema between outer upper incisor (I2) and upper canine (C); diastema present between fourth upper premolar (P4) and first upper molar (M1) in upper dention; diastema present between lower canine (c) and second lower premolar (p2); larger gap (diastema) between lower tooth situated either between lower canine and second lower premolar (p2) or between second lower premolar (p2) and fourth lower premolar (p4); neural processes on lumbar vertebrae subequal (data presently available only for thyone and melissa); keel of mesosternum serrated.

Relationships within Vampyressa (s.s.)

Relationships among the three taxa of Vampyressa there so restricted (encompassing V. melissa, V. pusilla, and V. thyone) were unresolved by partitioned data alone; a clade formed by Vampyressa melissa + V. pusilla appears in some analyses and a clade formed by Vampyressa pusilla and V. thyone appears in others (e.g. morphology; fig. 16, table 3), and a politomy with the three species appeared in each of the separated analyses of cyt b and RAG2 matrices (figs. 17 and 18).

A novel relationship recovered by the two genes combined and by the total-evidence analysis was the placement of Vampyressa thyone as sister to a clade formed by V. melissa and V. pusilla. Vampyressa thyone was for decades thought to be a junior synonymous of V. pusilla, and the current analysis confims the recognition of the differences between these taxa, in agreement with molecular data of Lim et al. (2003), Porter and Baker (2004), Hoofer and Baker (2006).

The clade with Vampyressa melissa and V. pusilla was however poorly supported (table 3) though sustained by three characters optimized through ACCTRAN transformations (table 4). There was no unambiguous change for this node, and a large number of homoplasies lie at it. These results indicate that relationships within Vampyressa are still uncertain. I presume that data from yet unrecognized forms of Vampyressa (to be described elsewhere) are necessary to resolve relationships within Vampyressa (as herein restricted).

Redefinition of Vampyressa (subgenera Metavampyressa and Vampyriscus)

Relationships between Vampyressa bidens, V. brocki, and V. nymphaea have been discussed by Peterson's (1968) when he named three distinct evolutionary lines for Vampyressa (s.l.) represented by the subgenera Vampyressa, Metavampyressa, and Vampyriscus. This arrangement was recognized in the classificatory schemes of Koopman (1994), but was not subsequently tested within a phylogenetic framework.

Davis (1975) suggested the recognition of Vampyriscus to include V. bidens, V. brocki, and V. nymphaea, and Vampyressa to include V. pusilla (and as recognized today, V. thyone) and V. melissa. He based his conclusions on his observations of individual variation in some characters for V. bidens while netting bats in the Iquitos region, Peru where he had the chance of collecting unusually large numbers of specimens of this taxon. According to Davis (1975), diagnostic characters including number of incisors and molars provided the principal support for Peterson's (1968) decisions to split Vampyressa (s.l.) in three subgenera, and those characters did not hold consistently within his Iquitos' material. These observations were cited in the classificatory revision of Baker et al. (2003), and in the study of Hoofer and Baker (2006), both of which were based on molecular data, and both of which suggesting that Vampyriscus should be elevated to genus to encompass Vampyressa bidens, V. brocki, and V. nymphaea.

The data analyzed in the present study may support a monophyletic Vampyriscus encompassing V. bidens, V. brocki, V. nymphaea. Nevertheless this clade is not supported unambiguously morphologically (table 3). On the contrary, there was strong evidence to support for a monophyletic V. brocki + V. nymphaea, with V. bidens being the sister taxon to that clade; an arrangement supported by several morphological synapomorphies (table 4), and fully supported by the combined dataset and most partitions (figs. 16 to 20; and table 3).

Finally, Chiroderma villosum was basal to the clade uniting V. bidens, V. brocki, and V. nymphaea. This larger clade was only moderately to low supported, but shared three unambiguous morphological sinapomorphies (table 4). A basal Chiroderma sister to V. bidens, subsequently sister to a clade with V. bidens and V. brocki was also recovered in the molecular analyses of Lim et al. (2003) and Hoofer and Baker (2006), and sister relationships between Chiroderma and V. bidens and V. brocki were also recovered in some of the molecular analyses of Baker et al. (2003).

Affinitties between Chiroderma and Vampyressa have been early recognized as V. bidens was initially placed in Chiroderma. Dobson (1878) described Chiroderma bidens (= Vampyressa bidens) from Santa Cruz, Peru pertaining, according to his classificatory scheme to the “Subfamily Lobostomidae, Group (…) Stenodermata” (family Phyllostomidae). Dobson (1878) suggested a close relationship of the newly described species with Vampyrops (= Platyrrhinus). Dobson (1878) included in his catalogue C. villosum Peters, “C. pusillum” Wagner and “C. bidens” Dobson, and described another new species: C. salvini. Dobson (1878) was able to compare ‘Chiroderma bidens’ with 'C. pusilum' (=Vampyressa pusilla) and emphasized many similarities between these two species, but did not suggest at any point that these taxa could be set apart from other species of Chiroderma.

Thomas (1889) formalized Dobson's (1878) conclusions about the close relationship between Vampyrops (= Platyrrhinus) and some species of "Chiroderma" (at that point including Vampyressa bidens and Vampyressa pusilla), shifting Chiroderma pusillum (= Vampyressa pusilla) to the genus Vampyrops on account of its dental formula, as this form lacks a third lower molar. Later, Thomas (1900) described a new species of Vampyrops (V. dorsalis) and rearranged the genus into four subgenera according to the number of molara and incisors: V. (Vampyrops), I 2/2, M 3/3; V. (Vampyrodes) I 2/1, M 2/3; V. (Vampyriscus) I 2/1, M 2/3; and V. (Vampyressa) I 2/2, M 2/2. Vampyressa was then a new subgenus name in Thomas (1900), only later elevated to generic rank by Miller (1907). Thomas (1900) however emphasizes his belief that for the "Vampyrops group" the number of molars should not be of generic importance.

In the benchmark work of G. S. Miller (1907), the subgenera of Vampyrops (=Platyrrhinus) as defined by Thomas (1900) -- i.e., Vampyrops, Vampyrodes, Vampyressa, and Vampyriscus -- were elevated to generic status largely based on the dental characters identified primarily by Thomas (1900). The placement of Vampyressa bidens in a separate genus (Vampyriscus Thomas) by Miller (1907) was chiefly based on the occurrence of a single lower incisor on each side of the lower jaw. Miller (1907) erroneously indicated that V.bidens has 2/2 molars. Vampyressa and Vampyriscus each remained monotypic until 1909, when

Thomas described two additional species. Up until that time studies on Vampyressa (s.l. Simmons, 2005) were therefore largely based on affinities in dental formulae and gross superficial similarities in external morphology.

Almost 50 years after the description of Phyllostoma pusillum and after the elevation of the subgenus Vampyressa to generic rank, Thomas (1909) described V. nymphaea and V. thyone based on the six specimens from the Western Andes that were deposited at the British museum. Thomas (1909) remarked on the different shape of the upper premolars, and shape and proportions of the molars of V. nymphaea. Although Thomas (1909) described V. nymphaea as a new species of Vampyressa he expressed some doubts about his generic designation.

> "This species is so different from V. pusilla in the shape of its teeth as to induce doubt as to whether it is rightly referred to this genus." (Thomas, 1909: 231)

The observations of Thomas (1909) were the first to draw attention to more detailed comparisons between Vampyressa (s.l.) and related taxa, particularly Chiroderma and Vampyrops.

The most recent revision of Vampyressa was that of Peterson (1968). This work included a description of a new species, V.brocki, from French Guiana, with some discussion of the relationships of Vampyressa (s.l. Simmons, 2005). Peterson (1968) regarded Vampyriscus as a subgenus of Vampyressa, and proposed a new subgenus (Metavampyressa) to include V. nymphaea and V.

brocki. Peterson (1968) also remarked on the similarities between V. bidens, V. nymphaea, and V. brocki:

> (…) the post-canine teeth of brocki, nymphaea, and bidens show an obvious derivation from the Vampyrops line, with bidens having evolved (…) further with the loss of one pair of lower incisors. The similarity in the shape of the tragus and of the noseleaf (…) the presence of a dorsal stripe provide further evidence of a close affinity (…)
>
> (Peterson, 1968: 11)

Peterson (1968: 11) considered V. pusilla and V. melissa as “deviations” of what he called the “Vampyrops-line”, forming an “independent line of evolution”. He based his conclusions on characters solely related to the evolution of molar teeth. In a later paper, Peterson (1972) provided additional evidence from structure of the soft palate for the close relationship between V. brocki and V. bidens.

After the the “brief systematic revision” of Vampyressa (s.l.) provided by Peterson (1968), only scattered discussions appeared in the literature about the systematics of the genus and its evolutionary relationships with other related genera. Subsequently, Davis (1975) studied variation in a large series of V. bidens obtained in Peru and found eight specimens with previously undescribed variations in dental characters. The principal characters used to diagnose V. bidens, and those that Peterson (1968) used to characterize this species (and the subgenus Vampyriscus), were the presence of a single incisor and the retention of a small third molar in each side of the lower jaw. Davis (1975) dismissed these characters because he found variation in the dental formulae of specimens within his Peruvian series:

> “(…) characters other than dental formula should be emphasized in differentiating the various species of Vampyressa (…), the allocation of V. bidens (…) to one subgenus (Vampyriscus) and V. nymphaea and V. brocki to another (Metavampyressa) is undesirable; the similarity of these two species (…) justify the expansion of the subgenus Vampyriscus to include them, a taxonomic review of V. brocki, V. bidens and V. nymphaea is needed” (Davis, 1975: 264)

Davis (1975) further discussed the close relationship between V. brocki and V. bidens. Davis (1975) suggested relying solely on non-overlapping skull measurements to differentiate these two species of Vampyressa, and suggested that the subgenus Metavampyressa Peterson should be considered a junior synonym of Vampyriscus.

A significant contribution of Davis (1975) was his critique of the reliance on only dental formulae to define species or genera within Vampyressa (s.l.). My observations though suggest that there are three consistent patterns within Vampyressa species (s.l.) and Mesophylla in terms of dental formulae, namely the single lower incisor in V. bidens, the third lower molar in V. melissa and in

Mesophylla, and one variable dental formulae pattern, which is the presence of a third lower molar in *V. bidens*.

As mentioned above, recognition that *Vampyressa* (as here restricted) does not form a clade with *Vampyressa bidens*, *V. brocki* and *V. nymphaea* (as here defined) has also been proposed based on recent analysis of molecular data (*e.g.* Baker *et al*., 2003; Hoofer and Baker, 2006) although *Metavampyressa*, a subgenus as defined by Peterson (1967) to encompass *V. brocki* and *V. nymphaea*, was not recognized by those authors.

According to the present analysis, the clade consisting of *Vampyressa brocki* and *V. nymphaea* (both from subgenus *Metavampyressa* according to Peterson, 1968) was strongly supported (table 3 and figs. 16, 17, 19, 20), and united by five unambiguous synapomorphies plus two characters diagnosed through accelerated optimization (ACCTRAN) and one character diagnosed through delayed optimization (DELTRAN) (see table 4). In contrast, while supported overall by the measures of support tools used (table 3 and figs. 16 to 20) the clade consisting of *Vampyressa bidens*, *V. brocki* and *V. nymphaea* was not unambiguously supported by any character (table 4), although it was recovered by three characters when I used accelerated transformation (ACCTRAN) for optimization, and by two characters, when I used delayed transformation (DELTRAN). Finally, the clade encompassing *Chiroderma villosum*, *Vampyressa bidens*, *V. brocki* and *V. nymphaea* was supported by three unambiguous characters (table 4) and received moderate support values from the morphological partition (see table 3, figs. 16).

The current analysis supports therefore sister relationships between Chiroderma and Vampyressa bidens, V. brocki and V. nymphaea, which is in agreement with mitochondrial and nuclear DNA sequence data (Baker et al., 2000, 2003). Hoofer and Baker (2006: figs. 3-5, pags. 429-31) based on molecular data found the same relationships for the four taxa with similar levels of support. Curiously, results from molecular analyses of cyt-b (Porter and Baker, 2004) and indirect surveys of mitochondrial DNA by mapping restriction-sites within the ND3–ND4 region (Lim et al., 2004) did not provide support to the recognition of Vampyriscus as a genus distinct from Vampyressa.

In summary, Hoofer and Baker (2006) suggested (as also suggested by Baker et al., 2003, and earlier, by Davis, 1975) the recognition of Vampyriscus as distinct genus to encompass bidens, brocki, and nymphaea apart from Vampyressa, with bidens as the basal lineage. Based on the present data, I do not prefer this alternative, however, (1) because it does not acknowledge the morphological differences that have I found between bidens and brocki + nymphae, and (2) because it does not acknowlege the monophyly of Metavampyressa, as repeatedly recovered in my analysis. Another alternative would be relegating bidens, brocki and nymphaea to subgenera within Chiroderma as these four taxa form a clade. Once again, this second alternative is in disagreement with the morphological distinctiveness between these taxa, and it also would lead to confusion regarding use of the name Chiroderma, which has been stable for years.

Based on these observations I suggest a novel arrangement with the use of Metavampyressa Peterson elevated to genus level, the retention of a monophyletic Chiroderma as traditionally defined, and the use of Vampyriscus only for Vampyriscus bidens. I comment further on the status of Chiroderma in a separate section.

Peterson (1968) proposed the designation of subgenera of Vampyressa (s.l.) as follows:

> “Of the various alternatives available, the existing evidence suggests that the genus Vampyressa should be retained to include the above, and that the three lines of evolution within it would best be expressed by designating them as subgenera. Vampyriscus is available for the subgenus represented by bidens as the type species. Vampyressa could again be used as a subgenus containing V. melissa and pusilla as the type species. It is necessary to create a third subgenus, which I propose to be known as Metavampyressa subgen. n. with Vampyressa nymphaea as the type species and to include V. brocki.” (Peterson, 1968: 13)

Because Peterson (1968) did not fully diagnosed subgenus Metavampyressa and this is the first proposal of recognition of this taxon as distinct at the genus level, I provide an emended diagnosis below. Additionally, I provide an emended diagnosis of the genus Vampyriscus as hereby restricted to the monotypic V. bidens. Additionally I provide some references of studies that have ecological information for these taxa.

Emended diagnosis of Metavampyressa Peterson, 1968

Type species Metavampyressa nymphaea Thomas, 1909

Dorsal pelage medium brown; fur tricolored and ventral fur predominantly bicolored; facial stripes present, bright white, unequal in breadth; dorsal facial stripes depart from behind noseleaf where they often meet to form a dense white spot of fur; posterior tip of dorsal facial stripes extends up to the level of medial external pinna of ear; stripe in the back very faint but present; anterior tip of dorsal stripe begins posterior to neck; dorsal forearm covered with hair up to a half of its extension; propatagium haired with unconspicuous hairs; dorsal uropatagium hairless; ventral uropatagium sparsely haired, with hair concentrated in the middle; one or two genal vibrissae present on the cheek; ear with pale border, yellowish, stripe of color often interrupted at tip; folds of internal surface of pinna poorly marked; tragus finely serrated; anterodorsal portion of skull slightly inflated; lateral maxilla compressed at level of premolars; external nares mostly directed dorsally; height of zygoma uneven along its axis; upper inner incisors sometimes unequally bilobed with a shallow notch, with internal lobe much larger than external; hypoconal fossa on P4 relatively deep; P4 curved in lateral aspect; mesosternum not notched.

Ecological traits

Little is know about the species Metavampyressa brocki and M. nymphaea. Metavampyressa nymphaea have been found roosting in Araceae (Anthurium), Cecropiaceae (Cecropia), Rubiaceae (Pentagonia) roosts in apical, and palmate tents, and males of V. nymphaea appear to build harens (Timm, 1984, Koepcke, 1984, Charles-Dominique, 1993, López and Vaughan, 2004, Kunz et al., 1994, Rodríguez-H. et al., 2001, Rodríguez-H. and Tschapka, 2005).

Emended diagnosis of Vampyriscus (Thomas, 1900)

Type species Vampyriscus bidens (Dobson, 1878)

Dorsal pelage medium brown to greyish; dorsal fur tricolored and ventral fur predominantly bicolored; facial stripes bright white, virtually equal in breadth along their extension, fine and well-marked; posterior tip of dorsal facial stripe lengthy, extends up to the level of the posterior pinna insertion; stripe in the back brightly white-marked; anterior tip of the dorsal stripe begins roughly where the dorsal facial stripes terminate; dorsal uropatagium hairless; ventral uropatagium scarcely haired; two genal vibrissae present on the cheek; ear with border and internal shell pale, yellow border stripe either interrupted or continuous; developed and colored basal lobe in lateral pinna; folds of internal ear pavilion well marked; tragus irregularly toothed; tragus has a developed swollen and often hirsute lateral attachment to the internal ear pavilion; notch in the uropatagium v-shaped; sexual dimorphism in size with males slightly larger than females; mesopterygoid fossa shorter than wider; upper outer incisor peg-like with a minute medial tip; one single lower incisor is present in most cases, and the occurrence of more than one in one ramus is an exception; relatively deep groove in the lower incisors. This appears to be the only taxon among "long-faced" stenodermatines (i.e. non short-faced, Stenodermatina s. Wetterer et al. 2000 and Simmmons, 2005) in which the m3 may or may not be present.

Ecological traits

Some evidence indicate that Vampyriscus bidens is a stratified generalist; that prefers Ficus and Cecropia; the species is certainly widespread but captured at generally low frequencies (Handley, 1967, Bernard, 2001, Kalko and Handley, 2001, Lim and Engstrom, 2001a and b, Sampaio et al. 2003, and my own personal observations from the Amazonian Brazil from several localities at the Pará state).

Relationships between Chiroderma and Vampyriscus

As commented above, relationships between Chiroderma and Vampyricus (Vampyriscus as here redefined to be restrict to Vampyriscus bidens) have been acknowledged since the description of V. bidens, originally described as Chiroderma bidens by Dobson (1878). Karyological data have also provided evidence for this relationship and a close relationship between V. brocki and V. nymphaea and these taxa (Greenbaum et al., 1975) despite the fact that each of these genera appeared "dentally and cranially very unique" (Greenbaum et al., 1975: 159).

There are several taxonomic alternatives for describing those relationships: (1) to place Chiroderma, Vampyriscus, and Metavampyressa in a single genus (e.g. relegating bidens, brocki, nymphaea to subgenera as mentioned on the section above about those taxa); (2) to name a subtribe to acknowledge those relationships (e.g. “Chirodermina”); (3) to recognize the three distinct generic names to preserve their unique identities, but without creating a “subset” name to accommodate them. As suggested in the reappraisal of Vampyressa (s.l.) in the precedent sections, the alternative (1) does not acknowledge the morphological distinctiveness described between these taxa, and it does not take into account the stability of the name Chiroderma. In resume, I prefer the third alternative that will not inflate with unnecessary names the already confused taxonomic history of stenodermatines (e.g. in the case of alternative 2) but will contribute to a solid definition of genus identity within the Stenodermatinae clade.

Following this rationale, I report below a brief emended diagnosis of the genus Chiroderma based on my data for Chiroderma villosum to help in differentiating this genus in the grounds of the generic rearrangements of stendenodermatines proposed in this study. This is not a complete diagnosis since Chiroderma was not the focus of my analysis and it is a speciose genus in need of revision, particularly in the case of the eastern South American forms (Tavares et al., 2008). Tables 3 and 4 and figs. 16 to 20 summarize the information used to erect my taxonomic decisions.

Emended diagnosis of Chiroderma Peters, 1860, based on the type species Chiroderma villosum Peters, 1860

Guard hairs present; forearm mostly hairy; dorsal fur bicolored; ventral chiropatagium hairy extending back to postero-medial arm-wing; dorsal uropatagium hairy; eyes large and greatly exposed out of orbits; iris gray olivaceous or brown; noseleaf broad-ovate; noseleaf unicolor or with unsplit gradation; nasal very shortened; sagital crest developed in a raised surface; posterior border of the skull triangular and with a triangular protuberance; lingual cingulum present on I1; stylar cusps on P4 absent; M2 with swollen base; hypoconulid present on m2.

Ecological traits

The ecology of Chiroderma species is poorly known as in the case of Vampyressa (s.l.). Chiroderma are frugivorous bats, foraging preferentially in the middle to upper canopy in forests with high strata, and preferring figs and Cecropia fruits (e.g. Gardner, 1977b, Kalko and Handley, 2001, Tavares et al., 2007, and my own observations on ongoing studies in the Pará state, Amazonian Brazil), but have also been reported to feed both on fruits and seeds, the latter being a just recently known feeding habit among bats (Nogueira and Peracchi, 2002, 2003).

Relationships between Ectophylla and Mesophylla and redefinition of those genera

Resolving relationships between Mesophylla, Ectophylla, and other stenodermatines remained for decades one of the most contentious issues in phyllostomid systematics. As pointed out by Hoofer and Baker (2006) most analyses of morphological data suggest a sister relationship between Ectophylla and Mesophylla (e.g. Lim, 1993, Wetterer et al., 2000), whereas most molecular data suggest paraphyly, and even distant relationships between these two taxa and a sister relationship between Vampyressa (Vampyressa) and Mesophylla (Baker et al., 2003, Porter and Baker, 2004, Hoofer and Baker, 2006).

Exceptions to these “standard” divergences between molecular and morphological results are:

(1) the phylogenetic analyses of molecular data (indirect surveys of mitochondrial DNA by mapping restriction-sites within the ND3–ND4 region) of Lim et al., (2003), which recovered a sister relationship between Ectophylla and Mesophylla, therefore agreeing with morphological data;

(2) the comments of Starrett and Casebeer (1968), whom acknowledged close relationships between Vampyressa and Mesophylla based on their observation of skull and tooth, therefore agreeing with most molecular data.

The study of Starret and Casebeer (1968) have been claimed several times to support with morphological data recent results from analyses of molecular data, which have recovered Vampyressa + Mesophylla clades and others, to the exclusion of Ectophylla. However, Starret and Casebeer (1968) made the following comment, based on their observations:

> “The genera Ectophylla, Mesophylla, and Vampyressa Thomas form a well-defined group within the Stenoderminae, sharing cranial, dental and external

> characters, and showing varying degrees of modification of a similar dentitional pattern."

To my understanding this comment of Starret and Casebeer (1968) demonstrates that they considered Ectophylla, Mesophylla and Vampyressa as three much related taxa. Since they were discussing the hypothesis of considering Mesophylla congeneric with the senior Ectophylla they went further in saying:

> "The skull of Vampyressa pusilla thyone shows more similarity to that of Mesophylla than does the skull of Ectophylla, and exhibits dental features seen in both the other genera. Ectophylla, with its shortened rostrum, raised nasals, and exaggerated circular and flattened last lower molar, appears to be the most highly modified (…) and we see no justification for making it congeneric with Mesophylla"

According to the results of the MP analysis of the present comprehensive morphological set of data with representatives of all genera and most subgenera of stenodermatines, there appears a moderately supported a clade consisting of Ectophylla and Mesophylla, sister to Vampyressa (Vampyressa) (i.e. Vampyressa melissa + V. pusilla + V. thyone), a clade previously recovered by the mostly-morphological analysis of Wetterer et al. (2000) as well (see fig. 3A). Being Ectophylla and Mesophylla part of a such well-defined clade based on the results of my analysis of morphological data, should I also suggest they should be synonymous as already been suggested by those just cited authors?

Most authors have retained Ectophylla, Mesophylla, and Vampyressa as distinct genera (e.g., Koopman, 1993; 1994), while Owen (1987) considered Mesophylla to be a junior synonym of Vampyressa based on a sister relationship of this taxon with V. nymphaea recovered by his analysis (see fig. 1A) as opposed to several other authors that suggested the synonymy of Ectophylla and Mesophylla (e.g., Simpson, 1945; Goodwin and Greenhall, 1962; Simmons and Voss, 1998; Wetterer et al., 2000; see fig. 3A). Results of Owen (1987) were however based on a mixture of discrete and quantitative data analyzed under controversial methods and must be taken with caution and they may not be directly comparable to the methods used in cladistic analyses. Owen’s (1987) methods and results have been criticized in detail by Lim (1993: 149).

One hypothesis to explain it is that many morphological characters are convergent and the data set thus contains considerable homoplasy. For a measure of homoplasy, the morphological tree was calculated to have an elevated index of homoplasy (HI = 0.63), which also appeared in the total evidence tree (HI = 0.62) but may have been overcome for the information that was provided by the molecular characters. “Morphological similarity” has long been noted between Ectophylla and Mesophylla (e.g. Laurie, 1955; Goodwin and Greenhall, 1961; Baker, 1973). Hoofer and Baker (2006) once referred to characters reported by Lim et al. (2003) as supporting an Ectophylla-Mesophylla clade as actually being symplesiomorphies. I partially agree with that statement, which aimed to explain why those taxa often appear closely related but suggest that character evolution among them and their relatives was a little more complex with no straightforward explanation.

According to the present analysis, from the eighteen characters uniting Ectophylla and Mesophylla in a clade, fourteen are parallelisms and four are synapomorphies (see tables 3 and 4). Among these synapomorphies at least two seem to be related to behavior: having a bright yellow ear, with such coloration correlated to other yellow body parts of both species (see fig. 4), and having a transparent dactylopatagium minus. The yellow color of ears, noseleaves, and mouth papillae of these species (see fig. 4) may be related to aposematic and display, or to concealment behaviors. Lim et al. (2003) found two synapomorphies with his analysis of restriction sites.

About relationships between Ectophylla and Mesophylla, Lim et al. (2003) commented:

> “Although we agree with Wetterer et al. (2000) that M. macconnelli and E. alba are sister taxa well supported by several morphological and molecular synapomorphies, there are still obvious differences suggesting that these species are divergent and should retain their generic ranks (…) morphologically, there are several differences in the cranium and dentition between the two taxa suggesting that E. alba is the most modified (…) restriction site data also

> identified eight autapomorphies that defined E. alba and five for M. macconnelli. The karyological, morphological, and molecular differences are substantial for retaining the traditional generic distinctions for E. alba and M. macconnelli."
>
> (Lim et al., 2003: 23-24)

I agree with Lim et al. (2003) and suggest the retention of Ectophylla and Mesophylla as full genera based on those distinct characters already described as unique for each genera described by several authors (e.g. Starret and Casebeer, 1968, for an example on morphology; Greenbaum et al., 1975, for an example on karyotype; Hoofer and Baker, 2006, for an example on molecular) and based in the numerous morphological characters differentiating those species that I found on account of the present investigation.

I provide a list of unique characters for the genera Ectophylla and Mesophylla in the table 5, and an emended diagnosis for each of these genera below, which I recommend to be kept recognized as separate full genus, based on the results of the total evidence analysis. Those diagnoses demonstrate that each of these two genera has a set of unique combinations of characters that justify the retention of generic status to each of them. Also, throughout diagnoses for these genera indicate that Mesophylla and Ectophylla share characters with other species of stenodermatines that have been poorly defined for decades, which may have lead to confusing statements of monophyly involving them all, or some of them separately, making it difficult to place them in any one genus -

those are species that had been included in the Vampyressa s.l. complex (s.l., Simmons, 2005) and were all temptatively redefined in the present study above.

Emended diagnosis of Mesophylla Thomas, 1901

Mesophylla macconnelli Thomas, 1901

Dorsal and ventral fur pale buff, yellowish; dorsal hairs tricolored and ventral hairs predominantly unicolored; rudimentary white spots sometimes present on face or face fully yellowish to pale buff; leaflet behind spear; lateral border of the horseshoe rough edged; external nares oriented mostly dorsally; dorsal edge of narial opening displaced to the level of anterior P4; postorbital constriction with roughly the same breadth as the interorbital constriction; upper tooth series diverges posteriorly as far as premolars but last molar shifted medially, towards the bucal cavity; middle point of the posterior palate displaced posteriorly, terminating in the posterior half of the interorbital region; postglenoid process poorly developed and articular surface of glenoid fossa directed primarily towards ventral plane; maxillary aperture of infraorbital canal located at dorsal to P4 and M1, posterior aperture of canal in the interorbit dorsal to M1; ventral surface of the mandibular ramus located above a plane passing through the ventral surface of the mandibular body; P3 roughly as high as it is long; P3 roughly half or less the size of the P4; protocone absent on M1; m3 present; tiny gaps formed when lateral jaws occlude.

Ecological traits

There is a considerable amount of roost descriptions for Mesophylla in the literature. Mesophylla have been reported roosting in plants of the Araceae family (aroids) (Timm, 1984, Koepcke, 1984, Charles-Dominique, 1993, López and Vaughan, 2004, Kunz et al., 1994) including modified leaves (tents) made of Anthurium spp. leaves (Kunz et al., 1994, López and Vaughan, 2004) and Xanthosoma spp. (Koepcke, 1984; Kunz et al., 1994), and have also been found using leaves of Palmae modified into tents (Koepcke, 1984; Timm, 1987; Foster, 1992, Charles-Dominique, 1993; Kunz et al., 1994; Kunz and McCracken, 1994), such as modified leaves of Astrocarium spp. (e.g. Astrocarium macrocalyx, Foster, 1992; Astrocaryum sciophilum, Charles-Dominique, 1993), and in tents made of leaves of species of the dwarf palms from the genus Geonoma (Koepcke, 1984; Boinski and Timm, 1985; Timm, 1987; Choe and Timm, 1987; Kunz et al., 1994). Mesophylla have been reported roosting in apical tents (as defined in Kunz et al., 1994 and recorded by Brooke, 1990; Charles-Dominique, 1993; Koepcke, 1984; Timm, 1984; Kunz et al., 1994), and in bifid tents (as defined in Kunz et al., 1994, and recorded by Barbour, 1932; Koepcke, 1984; Foster, 1992; Charles-Dominique, 1993; Kunz et al., 1994) and in paradox tents (Timm and Lewis, 1991; Kunz et al., 1994). Mesophylla is relatively widespread geographically and rare locally, and generally few individuals of those species are captured even in exhaustive inventories (e.g. Simmons and Voss, 1998; Lim and Engstrom, 2001a and b).

Emended diagnosis of Ectophylla H. Allen, 1892

Type species Ectophylla alba H. Allen, 1892

Dorsal fur predominantly white with grayish-white parts particularly in posterior back, ventral fur white; dorsal hairs bicolored and ventral hairs unicolored; scales on individual hair entire; facial stripes absent; noseleaf, ears, and thumb bright yellow; short hairs in the base of ear pinna; notch in lateral edge of tragus absent; lateral attachment of tragus simple, undeveloped; dorsal forearm naked; dorsal chiropatagium hairless; premaxilla oriented vertical, perpendicular to a plane passing through the palate; dorsal edge of external nare located at the level of anterior P3; nasals arched and located above maxilla; posterior region of the maxilla slightly inflated; postorbital constriction narrow; rostrum shortened; posterior dorsal skull without protuberance; porterior border of extended palate v-shaped; basisphenoid pits wide and deep; post glenoid process largely bending; cochlea phanerocochlear; zygomatic enlarged; paraoccipital bone well developed; sutura squamosa prominent; posterior mental foramen located at level between p2 and p4; upper inner incisors triangular shaped; upper inner incisors do not converge medially; upper outer incisors are more than one-third the size of inner; no grooving in the lower incisors, blunt cone shaped; outer lower incisors are not hidden by lower canines when viewed from posterior aspect; upper canines diverge lateral; secondary tip onto upper canine displaced bucal, seen in frontal view; lower canine more than twice p3; lower canines straight anteroposteriorly and diverge outward; one post-labial cone sometimes present onto p4; medial ridge present onto M2; lower second molar (m2) circular in shape; protoconid onto m1 about two-thirds of p4; first upper molar and M2 separated by diastema; first lower molar and m2 sometimes separated by diastema; quill of manubrium simple and rounded; angle between body and ventral manubrium less than 90°, acute; lateral circumvallate papillae located dorsal; bifid anterior mechanical papillae absent.

Ecological traits

Ectophylla alba appears to mostly, if not exclusively rely on Heliconia plants for roosting, and always roosts in boat-like tents (Brooke, 1990; Timm, 1982; Timm and Mortimer, 1976, Kunz et al., 1994). This is the only tent-user stenodermatine observed while actively constructed a tent (Rodriguez-Herrera et al., 2006).

Relationships at higher hierarchical levels

Monophyly of Stenodermatinae

The monophyly of Stenodermatinae, corroborated with high support according to the "all-characters" matrix (fig. 20) have long been confirmed by different sets of data (e.g. morphology, Miller, 1907, Lim, 1993, Wetterer et al., 2000; karyology, Baker, 1973; Gardner, 1977a; restriction-site data, Van den Bussche, 1992; 1993; gene sequence data, Baker et al., 2000; Baker et al., 2003).

According to the present study, a total of six unambiguous morphological characters supported the Stenodermatinae clade. Monophyly of Stenodermatinae also appeared in all trees from all analyses of partitions as well, being overall strongly supported, including the analyses of the two genes separately and in combination (figs. 17, 18, and 19).

Remarkably was however the fact that all analyses performed recovered well-supported clades assembling stenodermatines whether including Sturnira or not.

Position of Sturnira

Although there was practically no evidence of a paraphyletic Stenodermatinae, monophyly of Stenodermatinae to the exclusion of Sturnira was equally well-supported by the total evidence tree and most subsets (see table 3). As in the case for the subfamily Stenodermatinae, a total of six unambiguous morphological characters supported a “Stenodermatinae” clade – without Sturnira (characters 44, 180, 219, 284, 292, 294).

In all instances, Sturnira was basal to the remaining stenodermatines and support for stenodermatines with this taxon included was overall higher than without it (table 3, and figs. 16 to 20). The evidence at hand reinforced the “primitive”, i.e., basal position of Sturnira in relation to the other stenodermatines. This position for Sturnira within stenodermatines has been suggested by several authors based on different systems of characters (e.g. Slaughter, 1970; Baker, 1973; Owen, 1987; Gimenez, 1993; Lim, 1993; Wetterer et al., 2000, Baker et al., 2000; Baker et al., 2003).

In classifications, Sturnira has frequently been placed in its own, separate hierarchical category (subfamily, tribe, subtribe, ets.) to reflect the uniqueness of this genus in many characters (e.g. Miller, 1907; Simpson, 1945; Slaughter, 1970; Koopman and Jones, 1970; McKenna and Bell, 1997). Among others, Miller (1907), Simpson (1945), placed Sturnira in its own subfamily [Sturnirinae]. On the other hand, McKenna and Bell (1997) placed Sturnira in the subtribe Sturnirina [within Stenodermatini] in recognition of the many features Sturnira shares with other stenodermatines, as also noted by many previous authors (e.g. Baker, 1967; Gerber and Leone, 1971; Gardner, 1977a). Lastly, a smaller number of alternative arrangements for Sturnira have been suggested, such as the inclusion of Sturnira within carollines based on postcranial characters (e.g., Walton and Walton, 1968).

I concur with recognition of Sturnirini [tribe] as suggested by previous authors (Koopman and Jones, 1970; Koopman, 1994; Wetterer et al., 2000) to acknowledge both the uniqueness of Sturnira and its shared affinities with stenodermatines (also see section on taxonomic considerations). On the other hand I recognize that a fine-grained revision of the position of Sturnira in the broader context of phyllostomids (Chiroptera: Phyllostomidae) is needed because of its uniqueness, and the possibility that this genus could perhaps alternatively fall out of stenodermatines in such higher-level examination. In other words, my results may be interpreted as to question monophyly of Stenodermatinae.

Relationships between Chiroderma, Ectophylla, Mesophylla, Metavampyressa, Platyrrhinus, Uroderma, Vampyressa, Vampyriscus, Vampyrodes

A clade uniting Chiroderma, Ectophylla, Mesophylla, Metavampyressa, Platyrrhinus, Uroderma, Vampyressa, Vampyriscus, and Vampyrodes, i.e. part of subtribe Ectophylina (sensu Wetterer et al., 2000 but excluding Artibeus) was moderately supported by the MP analysis of all morphological characters (fig. 16). This clade did not appear in the total evidence tree or in any of the other analyses. Rather it consistently appeared a clade with all those taxa to the exclusion of Ectophylla, in the total evidence tree, and in the separate and combined genes analyses indepently of the morphological character optimizations tried (Unambiguous, ACCTRAN and DELTRAN) were unable to detect many morphological diagnostic characters for it (table 4). To this clade, previously recovered in molecular phylogenies (Baker et al., 2003 and Hoofer and Baker, 2006) it has been suggested the name of Vampyressina (Baker et al., 2003). Taxonomy, and therefore considerations about the infranames for stenodermatines (Vampyressina and Ectophyllina) and hierarchical categorizations for this clade and others within Stenodermatinae are discussed in a separate section further, in this study.

Relationships between Chiroderma, Ectophylla, Mesophylla, Metavampyressa, Vampyressa and Vampyriscus

A clade uniting Chiroderma, Ectophylla, Mesophylla, Metavampyressa, Vampyressa and Vampyriscus was well supported by the analysis of morphological data and already appeared well supported in the craniodental subset (figs. 15 and 16, and table 3). This clade did not appear in any other analyses, including the total evidence tree (figs. 17 to 20 and table 2). Instead it appeared a weakly supported clade of those taxa to the exclusion of Ectophylla in the total evidence analysis (fig. 20, table 2). I do not recognize any of these hypothetical clade configurations, on the grounds of the weak evidence recovered, and consequently they were not included in the taxonomic considerations below.

Relationships between Platyrrhinus, Uroderma, and Vampyrodes

A source of considerable dispute in taxonomic history of stenodermatines has been the position of Uroderma. Burt and Stirton (1961) suggested without substantial evidence that *Uroderma* should be synonymized with *Artibeus,* becoming a subgenus of the latter. Over the last decades, *Uroderma* appeared as sister to *Artibeus* (*s.l.* Simmons, 2005) in a number of analyses of various morphological systems (*e.g*. Lim, 1993; Gimenez, 1993). On the other hand, karyological data have rejected the suggestion that *Uroderma* and *Artibeus* should be synonymized, as *Uroderma* has a unique karyotype unlike any other stenodermatine bat (Baker, 1967, 1973; Greenbaum *et al.*, 1975). Other authors have treated *Uroderma* as a separate, single offshoot or lineage (*e.g.* Baker, 1973 based on karyological information) or simply as a taxon of uncertain position (*e.g.* Gardner, 1977). Smith (1976) proposed sister relationships between *Uroderma*, *Vampyressa*, *Vampyrodes* and *Platyrrhinus* but did not present any data supporting this relationship. Based on restriction sites, Van den Bussche (1992) recovered a close relationship between *Vampyrodes*, *Uroderma,* and *Platyrrhinus*, something corroborated by my morphological data with relatively high support (fig. 16), but diagnosed by only two unambiguous synapomorphies (table 4) and by the total evidence tree with low support, but not by any of the molecular data sets as analysed in the present study (figs. 17 to 19). Based on these results, the position of *Uroderma* remains somewhat uncertain but is certainly not close to *Artibeus* or its allies (*e.g*. proposed *Dermanura*).

A clade uniting *Platyrrhinus* and *Vampyrodes* was uniformly strongly supported by all partitions and by the total evidence data (figs. 16 to 20). This leaves doubts as to if *Vampyrodes* should be considered to be included in

Platyrrhinus, acknowledging such well supported clade by different sources of data. On the other hand, this clade was diagnosed by only two unambiguous changes while lots of homoplasies were at that node (table 4). I suspect that resolution of relationships between Vampyrodes and Platyrrhinus depend on phylogenetic analyses to test them in the broad context of stenodermatines (as done in this study) but with a denser sampling within Platyrrhinus. Since I restrict the representation of the speciose genus Platyrrhinus (as recently redefined by Velazco, 2005) in my analysis to only one taxon I conservatively suggest the maintenance of Vampyrodes and Platyrrhinus as separate genus pending further reevaluation of these taxa.

Relationships between Stenodermatina, Enchisthenes, Artibeus, and Koopmania

Close relationships between some of the short-faced bats, subtribe Stenodermatina (Ametrida, Ardops, Ariteus, Phyllops, Pygoderma, and Stenoderma) and several Artibeus (Dermanura) species, Enchisthenes, and Artibeus (Koopmania) have been early suggested by many authors based on karyological and morphological data (e.g. Baker, 1967, 1979; Baker and Hsu, 1970; Greenbaum et al., 1975; Smith, 1976; Gardner, 1977a; Baker et al., 1979, 1982; Myers, 1981).

Owen (1991) demonstrated that Enchisthenes is apart from Artibeus (s.l.), and proposed the designation a new genus named A. concolor (Koopmania) (see discussion on Artibeus s.l. below). Also, in Owens' (1991) analysis, Artibeus

(Dermanura) was sucessively sister to Enchisthenes, Artibeus concolor and a to clade formed with “short-faced” bats (s. Wetterer et al., 2000, subtribe Stenodermatina), which lead Owen (1991) to comment that the small Artibeus (Dermanura) should be “primitive” (i.e. basal) in relation to the rest of the clade he recovered. It is noteworthy that one of the novel hypotheses placed by Owen’s (1987 and 1991) studies was related to potential homologies of Artibeus (small forms) and Artibeus concolor and Enchisthenes, and the short-faced bats (s. Wetterer et al., 2000, subtribe Stenodermatina).

The RAG2 data placed Enchisthenes and Ectophylla basal to Artibeus (s.l.), which was successively sister to short-faced bats. In contrast, as given by the analysis of RAG2 and cytb data combined, Enchisthenes and Ectophylla form a clade basal to Artibeus (s.l.). Finally, the total evidence analysis recovered weakly supported (less than 50%) sister relationships of Enchisthenes as basal this clade and of Ectophylla as successive sister of Enchisthenes and therefore basal to a clade formed by Enchisthenes, A. cinereus, A. concolor, and A. jamaicensis (fig. 20). In the fundamental trees, Ectophylla and Enchisthenes are together in a clade but this relationship has gotten no support. Again in the total evidence tree, this clade formed by Enchisthenes, Ectophylla and Artibeus (s.l.) is sister to the short-faced bats. Based on these results, it is probable that Enchisthenes, Ectophylla and Artibeus (s.l.) share close historical relationships; that they could share a more recent common ancestor than with short-faced bats, Sturnira, or the Vampyressina (s. Baker et al., 2003).

The conclusion so far is that the relationships of Enchisthenes and Ectophylla, among them and to other stenodermatines and their position within Stenodermatinae is unclear although it is clear already that Enchisthenes is not part of a monophyletic Artibeus and that Ectophylla is not a synonym of Mesophylla, as discussed in a previous section.

Stenodermatina

Short-faced bats (subtribe Stenodermatina) formed a strongly supported clade in all the analyses. A total of seven unambiguous morphological characters (table 5) attested and strengthened the substantiation for for this clade. Evidence of the monophyly of short-faced bats has been accumulating over the decades (de la Torre, 1961; Greenbaum et al., 1975, Lim, 1993; Wetterer, 2003, Baker et al., 2003, Dávalos, 2007), and now includes chromosomal data (e.g. Baker, 1973; Greenbaum et al., 1975), restriction sites in the 18S ribosomal-DNA gene (Van den Bussche, 1992), morphology and gene sequence data (Owen, 1987; 1991; Tavares and Simmons, 2001; Baker et al., 2003; Dávalos, 2007; and this paper).

Several studies have discussed systematics and evolutionary relationships of "short-faced" genera (e.g. Baker, 1973; Jones and Schwartz, 1967, Koopman, 1968; Owen, 1987, Van den Bussche, 1992, Tavares and Simmons, 2001, Dávalos, 2007) but some interrelationships within the clade are still uncertain.

Greenbaum et al. (1975) suggested, based on chromosomal data, that the Antillean genera were derived from a single invasion from the mainland. Based on restriction site data, Van den Bussche (1992) recovered a clade with the mainland Pygoderma and the island forms Ariteus (Jamaica) and Stenoderma (Puerto Rico), and another with the island form Ardops (Lesser Antilles).

A set of molecular and morphological analyses have consensually supported two nodes within Stenodermatina (besides the monophyly of Stenodermatina itself): the monophyly of continental short-faced forms

(Pygoderma, Centurio, Ametrida, and Sphaeronycteris) and the sister relationship between Ariteus and Ardops (Lim, 1993; Baker et al., 2000, 2003; Tavares & Simmons, 2000; Wetterer et al., 2000; Dávalos, 2007). According to the analysis of Dávalos (2007) the Antillean forms of Stenodermatina bats were not monophyletic. She recovered a sister relationships between Ardops and Ariteus as previous authors, but also between Phyllops and Stenoderma and suggested the hypothesis that Antillean short-faced bats revealed to be split in two independent Caribbean lineages.

The present results acknowledge the hypotheses that continental Stenodermatina are monophyletic as it has been consensual in the more recent literature, and the two Caribbean lineages hypothesis of Dávalos (2007), one formed by Ardops + Ariteus, and the other, by Phyllops and Stenoderma. Both Dávalos (2007) that used a multi-gene matrix analysed with Maximum likelihood and Bayesian analysis, and the present study that analysed combined evidence from genes and morphology through parsimony recovered the same relationships, which may attest for the robustness of this hypothesis of relationships.

The two Caribbean lineages as proposed by Dávalos (2007), were mirrored in supported clades throughout the analyses in the present study (Ardops + Ariteus; and Phyllops falcatus + Stenoderma); those were supported by total evidence, genes combined, RAG2, and cytb. However, of the two lineages only the clade Ardops + Ariteus had unambiguous support from morphology, signifying that molecules may have played a major weight to the definition the second Caribbean lineage. Morphology when analysed alone, offered the alternative placement of Stenoderma as basal to the Ardops and Ariteus clade, leaving position of Phyllops falcatus unresolved (see fig. 16). In fact, while the clade Ardops + Ariteus was sustained by two unambiguous morphological characters (table 5), the clade Phyllops + Stenoderma was not supported unambiguously morphologically.

The mainland species (Pygoderma, Centurio, Ametrida and Sphaeronycteris) formed a moderately supported clade in the MP analysis of morphological data and most partitions and a strongly corroborated clade according to the total evidence data (figs. 16 to 20, table 3). Inside this clade, the more stable relationship across the analyses was that of Ametrida and Sphaeronycteris, recovered in the total evidence analysis, by the morphological data (including the craniodental data analysed in separate, here represented by the unambiguous characters 142 and 170) and by the RAG2 analysis. Sister relationships between Ametrida and Sphaeronycteris have also been detected from some previous studies (e.g. Owen, 1987).

On the other hand, the alternative sister relationship between Ametrida and Pygoderma was recovered by the cytb and the gene data combined in the MP analysis of this study (figs. 17 and 19), as it occurred in Dávalos (2007), who analysed data through other optimality criteria. Thus, the relationships within continental forms of Stenodermatina bats appear to remain unclear.

One interesting source of evidence that have not been explored up to this moment is the inclusion of fossil forms in analyses of the phylogeny of stenodermatines. In addition to the until recently single known fossil form of Stenodermatina, Phyllops vetus, the recent discovery of two previously unknown and well preserved fossil forms of Phyllops from Cuba (Cubanycteris silvai and Phyllops silvai) appears a opportune source of new evidence for further testing interrelationships within stenodermatina bats as to put the morphology from fossil forms in the context of stenodermatina phylogeny. These data have been gathered and will be published elsewhere (V. Tavares and C. Mancina, in prep.).

Relationships between Artibeus, Artibeus (Dermanura), Enchisthenes and Koopmania

Owen (1987) suggested that Artibeus (s.l. Simmons, 2005) was not monophyletic and that small Artibeus (including Artibeus concolor and Artibeus hartii, currently Enchisthenes) should be placed in their own genus, Dermanura. Owen (1991) further demonstrated that Enchisthenes represents a separate genus, apart from Artibeus and Artibeus (Dermanura). In addition, based on the fact that Artibeus concolor fell outside the Dermanura clade in his tree and lie basal to Enchisthenes, Owen (1991) proposed the designation a new genus name for A. concolor (Koopmania).

The present results confirm affinities of Artibeus (A. Artibeus represented by A. jamaicensis and A. Dermanura represented by A. cinereus), and Artibeus (Koopmania concolor) a clade that received high support from the analysis of cytb, RAG2, both genes combined, and total evidence (fig. 20), On the other hand morphology indicate different relationships among Artibeus (s.l.) (fig. 16).

All data indicated that Enchisthenes does not belong to the Artibeus (s.l). clade, as initially proposed by Owen (1991).

In relation to previous hypotheses of relationships within Artibeus (s.l.; including subgenera Artibeus, Koopmania and Dermanura, e.g. Owen 1991, Lim, 1993, Wetterer et al., 2000) my analysis was novel because it recovered a clade uniting Artibeus concolor and Artibeus jamaicensis rather than between either of these two subgenera and Artibeus (Dermanura). That gives no support to Owen's (1991) proposition of a new genus for Artibeus concolor (Koopmania) and place this species more parsimoniously within Artibeus (Artibeus) than Artibeus (Dermanura). Placement of Artibeus concolor within Dermanura was suggested by Owen (1987) together with all other species of small-bodied Artibeus.

Based on the present morphological data a clade formed by the Artibeus (Artibeus) and Artibeus (Koopmania) appeared as basal to Artibeus (Dermanura), and Artibeus (Dermanura) basal to "vampyressines" (s. Hoofer and Baker, 2006). Morphologically, as in the case for Vampyriscus and Metavampyressa, there are few synapomorphies uniting Artibeus (sensu lato) and unique characters defining Artibeus (Dermanura). Following that reasoning, the recognition of Dermanura as a distinct genus could be suggested as firstly proposed by Owen (1987) but to the exclusion of Artibeus concolor. I however refrain to formally propose that division of the genus Artibeus because to accomplish a necessary diagnosis of this taxon it is needed a comprehensive phylogenetic study of Artibeus (s.l.) with a denser sampling of species. Also according to the present results, a monophyletic Artibeus (Artibeus) should include Artibeus concolor, and the name and definition of this taxon should remain the same, as currently recognized by Simmons (2005).

I also documented a relationship in all trees and analyses, which was the non-monophyly of an Artibeus (lato sensu) + Uroderma group. These taxa that have been previously been thought to be allied by particular sets of characters (e.g. lingual characters, Gimenez, 1993) but in my simultaneous analysis of many systems become clearly paraphyletic.

Taxonomic considerations

The most recent suggestions concerning classification of stenodermatines inferred from phylogenetic analyses are those of Wetterer et al. (2000) and Baker et al. (2003). I will focus in discussing both in light of my results. No names are made available in this dissertation, which will not be disseminated until publication of this proposal classification. A definitive manuscript containing it will include a list of characters clearly defining and differentiating higher-level taxa so as to make these names available under article 13 of the International Code of Zoological Nomenclature.

I define Stenodermatinae as the clade arising from the last common ancestor of Sturnirini, Ectophylla, Enchisthenes, and three other proposed tribes (Vampyressini and Artibeini, see below).

Sturnirini is a tribal level taxon that has been recognized by several previous authors (e.g., Koopman 1994, Wetterer et al., 2000; Baker et al., 2003;

Simmons, 2005), and the present analysis was highly supportive of its recognition.

As pointed out by Wetterer *et al.* (2000) ‘‘short-faced’’ and “long-faced” stenodermatines have been recognized as unique assemblages by many authors (*e.g.*, Miller, 1907; de la Torre, 1961; Smith, 1976; Lim, 1993; Wetterer *et al.*, 2000). My analyses provide strong and unambiguous support for the short-faced clade, subtribe Stenodermatina, which I suggest should be elevated to the rank of tribe (see further). On the other hand, a clade encompassing all ‘‘long-faced’’ stenodermatines (*i.e.* the remaining stenodermatines) was not supported by my data, a result compatible with most recent molecular evidences (*e.g.* Baker *et al.*, 2003).

Wetterer *et al.* (2000) named a clade as subtribe Ectophyllina to encompass the genera *Artibeus*, *Chiroderma*, *Ectophylla*, *Mesophylla*, *Vampyressa*, *Uroderma*, *Platyrrhinus,* and *Vampyrodes*. On the other hand, Baker *et al.* (2003) named a somewhat different clade Vampyressina for *Mesophylla*, *Vampyressa*, *Chiroderma*, *Uroderma*, *Platyrrhinus* and *Vampyrodes*, and recognized two other subtribes to accommodate *Artibeus* and *Ectophylla*: Artibeina to encompass all *Artibeus* (including small *Artibeus* from the subgenus *Dermanura*, and large *Artibeus*), and a sharply restricted Ectophyllina for *Ectophylla*.

According to results of my analyses of non-molecular data, the subtribe Ectophyllina (including *Artibeus*) as suggested by Wetterer *et al.* (2000) could be an alternative clade to Vampyressina if *Artibeus* is removed. However, support for this revised Ectophyllina was not unanimously recovered across most analyses and subsets and support values, and when recovered it was generally low. Therefore I do not recognize Ectophyllina.

Three clades were recovered by most of my analyses and received strong support, and I therefore propose recognition as tribes to acknowledge the robust evidence herein compiled for their monophyly. Additionally, I recommend that two well-defined clades nested within a tribe (Stenodermatini) are to be formally recognized as to bear an hierarchical name:

Tribe Vampyressini

I define tribe Vampyressini as the clade of taxa within Stenodermatinae that share a more recent common ancestor with Vampyressa than with Stenoderma, Artibeus, or Sturnira. As so defined, Vampyressini includes Chiroderma, Mesophylla, Metavampyressa, Platyrrhinus, Uroderma, Vampyressa, Vampyriscus, and Vampyrodes. This name was used by Ferrarezi and Gimenez et al. (1996).

Tribe Stenodermatini

I define Stenodermatini as the clade of taxa within Stenodermatinae that share a more recent common ancestor with Centurio than with Sturnira or Vampyressa, or with Artibeus, or with Enchisthenes, or with Ectophylla. As so defined, Stenodermatini includes Ametrida, Ardops, Ariteus, Centurio, Phyllops falcatus, Pygoderma, Stenoderma, and Sphaeronycteris (extant), and Phyllops vetus, P. silvai and Cubanycteris (extinct).

The subtribe Stenodermatina was proposed by Wetterer et al. (2000) in recognition to the monophyly of short-faced bats. Since then, all analyses performed with different systems have reinforced support for this clade including the present (also see Dávalos, 2007). The absolute and unambiguous support for this clade as presently diagnosed by this total-evidence analysis justifies recognition at the tribal level as Stenodermatini.

Within Stenodermatini, there are two clearly well defined clades; the one with all continental forms (Pygoderma, Centurio, Ametrida, Sphaeronycteris), the one with Ariteus and Ardops as sister taxa. To acknowledge these so consistently defined clades I suggest the division of Stenodermatini in subtribes Centurionina and Ariteina (see table 6).

I define Centurionina as the clade of taxa within Stenodermatini that share a more recent common ancestor with Centurio than with Ariteus, Phyllops, or Stenoderma. As so defined, Centurionina includes Ametrida, Centurio, Pygoderma, and Sphaeronycteris.

I define Ariteina as the clade of taxa within Stenodermatini that share a more recent common ancestor with Ariteus than with Centurio, or Phyllops, or Stenoderma. As so defined, Centurionina includes Ariteus and Ardops.

Concerning to Phyllops falcatus and Stenoderma, I believe it is early to assign any separate rank to each of these species, and therefore recognized them as genera incertae sedis within tribe Stenodermatini.

Tribe Artibeini

I define tribe Artibeini as the clade of taxa within Stenodermatinae that share a more recent common ancestor with Artibeus than with Centurio or Sturnira, or Vampyressa, or Enchisthenes, or Ectophylla. As so defined, Artibeini includes Artibeus (Artibeus), Artibeus (Dermanura), Artibeus (Koopmania).

Artibeus (s.l.) is paraphyletic according to morphological data, which in my view convincingly acknowledges the differentiation between Artibeus s.s. and Dermanura, as previously suggested by Baker et al. (2003). However, according to RAG2 data, cyt-b data, and the combined evidence (morphology and molecular) Artibeus is monophyletic, or, in an alternative view, there is a highly supported relationship between two well-defined taxa by the current evidence; those taxa are Artibeus (Artibeus + Koopmania) and Artibeus (Dermanura), (Fig. 16 to 20). I conservatively refrained from a formal proposal of splitting Artibeus (s.l.) pending a comprehensive phylogeny with a denser sample within Artibeus (s.l.) to build a more solid hypothesis. I also found insufficent evidence for a differentiation worthy of generic rearrangements within “non-Dermanura” Artibeus (Artibeus + Koopmania) and therefore recommend keeping Koopmania as a subgenus.

Ferrarezi and Gimenez et al. (1996) first used the name Artibeini.

Ectophylla and Enchisthenes

The positions of *Ectophylla* and *Enchisthenes* remain unclear, although there is more evidence for a close relationship between *Enchisthenes* and Stenodermatini, than for possible relations of *Ectophylla* to other stenodermatines. In any case, I believe it is premature to assign any separate rank to each of these species, and therefore recognized them as genera incertae sedis within Stenodermatinae.

Tables

Table 1. List of taxa selected for the study of Stenodermatinae interrelationships.[1]

Phyllostomidae	**Species**
Phyllostominae Gray, 1825	
Phyllostomus	Phyllostomus hastatus (Pallas, 1767)
Carolliinae Miller, 1924	
Carollia	Carollia perspicillata (Linnaeus, 1758)
Rhinophylla	Rhinophylla pumilio Peters, 1865
Stenodermatinae Gervais, 1856	
Sturnira	Sturnira lilium (E. Geoffroy, 1810)
Ametrida	Ametrida centurio Gray, 1847
Ardops	Ardops nichollsi (Thomas, 1891)
Ariteus	Ariteus flavescens (Gray, 1831)
Artibeus	Artibeus cinereus (Gervais, 1855)
	Artibeus concolor Peters, 1865
	Artibeus jamaicensis Leach, 1821
Centurio	Centurio senex Gray, 1842
Chiroderma	Chiroderma villosum Peters, 1860
Ectophylla	Ectophylla alba H. Allen, 1892

Enchistenes	*Enchisthenes hartii* (Thomas, 1892)
Mesophylla	*Mesophylla macconnelli* Thomas, 1901
Phyllops	*Phyllops falcatus* (Gray, 1839)
Platyrrhinus	*Platyrrhinus helleri* (Peters, 1866)
Pygoderma	*Pygoderma bilabiatum* (Wagner, 1843)
Sphaeronycteris	*Sphaeronycteris toxophyllum* Peters, 1882
Stenoderma	*Stenoderma rufum* Desmarest, 1820
Uroderma	*Uroderma bilobatum* Peters, 1866
Vampyressa	*Vampyressa bidens* (Dobson, 1878)
	Vampyressa brocki Peterson, 1968
	Vampyressa nymphaea Thomas, 1909
	Vampyressa pusilla (Wagner, 1843)
	Vampyressa thyone Thomas, 1909
	Vampyressa melissa Thomas, 1926
Vampyrodes	*Vampyrodes caracciolli* (Thomas, 1889)

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[1] Taxonomy follows Simmons (2005).

Table 2. List of sequences selected for the study of Stenodermatinae interrelationships, including sequences downloaded from genbank and those produced in the present study. Institutional abbreviations are provided in the text.

Cytochrome b

Species	**ACC number / tissue voucher number**
Phyllostomus hastatus	LBEM MOL71
Carollia brevicauda	AF511959
Rhinophylla pumilio	DQ312397
Sturnira lilium	DQ312398
Ametrida centurio	AY604446
Ardops nichollsi	AY572329
Ariteus flavescens	AY604435
Artibeus cinereus	LBEM AD437
Artibeus concolor	LBEM AD850
Artibeus jamaicensis	AF316432
Centurio senex	AY604441
Chiroderma villosum	DQ312414
Ectophylla alba	AY157033
Enchisthenes hartii	FMNH 174703
Mesophylla macconnelli	AY157035
Phyllops falcatus	DQ211651
Platyrrhinus helleri	DQ312409

Pygoderma bilabiatum	AY604438
Sphaeronycteris toxophyllum	AY604452
Stenoderma rufum	DQ312400
Uroderma bilobatum	DQ312406
Vampyressa bidens	AY157045
Vampyressa brocki	DQ312421
Vampyressa melissa	DQ312427
Vampyressa nymphaea	ROM 104236; F38072
Vampyressa pusilla	LBEM Peti016-VP
Vampyressa thyone	AY157049
Vampyrodes caraccioli	DQ312407

RAG2

Species	**ACC number / tissue voucher number**
Phyllostomus hastatus	AF316479
Carollia brevicauda	AF316437
Rhinophylla pumilio	AF316484
Sturnira lilium	AF316488
Ametrida centurio	AF316430
Ardops nichollsi	AF316434
Ariteus flavescens	AF316435
Artibeus cinereus	AF316443
Artibeus concolor	AF316432
Artibeus jamaicensis	AY834663

Centurio senex	AF316438
Chiroderma villosum	AF316439
Ectophylla alba	AF316448
Enchisthenes hartii	AF316449
Mesophylla macconnelli	AF316462
Phyllops falcatus	AY604453
Platyrrhinus helleri	AF316481
Pygoderma bilabiatum	AF316483
Sphaeronycteris toxophyllum	AF316486
Stenoderma rufum	AF316487
Uroderma bilobatum	AF316491
Vampyressa bidens	AF316492
Vampyressa brocki	ROM 107227; F39220
Vampyressa melissa	FMNH 174909
Vampyressa melissa	FMNH 174910
Vampyressa nymphaea	ROM 104236; F38072
Vampyressa pusilla	DQ903843
Vampyressa thyone	AF316493
Vampyrodes caraccioli	AF316494

Table 3. Tree descriptions and bootstrap support[1] values for identified clades from each analysis performed.

Taxa	**Analysis**					
	Skull and tooth	**Morphology**	**Cyt b**	**RAG2**	**Cyt b and RAG2**	**All characters**
INGROUP						
Stenodermatinae	84	93	-	97	66	94
Stenodermatinae without *Sturnira*	80	99	60	71	90	100
Artibeus (s.l.), Chiroderma villosum, *Ectophylla*, *Mesophylla*, *Platyrrhinus*, *Uroderma*, *all Vampyressa (s.l)*, *Vampyrodes*	-	41	-	-	-	-
Chiroderma, *Ectophylla*, *Mesophylla*, *all Vampyressa*	-	79	-	-	-	-

(s.l)						
Ectophylla, Mesophylla, Chiroderma, Vampyressa nymphaea, V. bidens, V. brocki	39	-	-	-	-	-
Vampyressina[2] + Ectophylla	32	79	-	-	-	-
Vampyressina[2]	-	-	19	86	76	78
Platyrrhinus helleri, Vampyrodes, Chiroderma, Uroderma bilobatum, Mesophylla, Vampyressa melissa, V. pusilla, V. thyone	-	-	-	65	42	-
Mesophylla, Chiroderma, Vampyressa nymphaea, V. bidens, V. brocki	37	-	-	-	-	-

Chiroderma, all Vampyressa (s.l.), Mesophylla	-	-	-	-	-	56
Chiroderma, Vampyressa nymphaea, V. bidens, V. brocki	59	53	24	-	-	57
Vampyressa nymphaea, V. bidens, V. brocki	82	93	71	84	87	99
Mesophylla, Vampyressa melissa, V. pusilla, V. thyone	-	-	29	-	-	60
Vampyressa bidens, V. brocki	56	-	-	73	-	-
Vampyressa brocki, V. nymphaea	-	89	100	-	99	100
Ectophylla, Mesophylla	-	89	-	-	-	-
Vampyressa melissa, V.	56	57	66	91	86	99

pusilla, *V. thyone*						
Vampyressa *melissa*, *V*. *pusilla*	-		-	-	42	56
Vampyressa *pusilla*, *V*. *thyone*	30	50	-	-	-	-
Uroderma, *Platyrrhinus*, *Vampyrodes*	28	70	-	-	-	56
Platyrrhinus, *Vampyrodes*	84	99	85	80	98	100
Artibeus, *Enchisthenes*, *Ectophylla*, Stenodermatina[3]	-	-	-	100	94	66
Artibeus, *Enchisthenes*, *Ectophylla*	-	-	-	-	75	-
Enchisthenes, *Ectophylla*	-	-	40	-	74	-
Artibeus, Stenodermatina[3]	18	-	-	87	-	-
Enchistenes,	24	-	-	-	-	-

Stenodermatina[2]						-
Artibeus cinereus, *A. concolor*, *A. jamaicensis*	19	-	91	88	99	99
A. concolor, *A. jamaicensis*	62		59	74	76	89
Stenodermatina[3]	93	100	100	99	100	100
Ardops, *Ariteus*, *Centurio,* *Sphaeronycteris*, *Pygoderma, Ametrida*	-	-	-	-	60	70
Centurio, *Sphaeronycteris*	-	59	57	-	92	99
Ametrida, *Pygoderma*						
Sphaeronycteris, *Ametrida*, *Pygoderma*	-	-	47	-	63	-
Ametrida, *Centurio*, *Sphaeronycteris*	-	77	-	57	-	-
Ametrida, *Sphaeronycteris,*	44	-	-	-	-	-

<u>Stenoderma</u>						
<u>Pygoderma</u>, <u>Ariteus</u>, <u>Ardops</u>	14	-	-	-	-	-
<u>Stenoderma</u>, <u>Ardops</u>, <u>Ariteus</u>	-	55	-	-	-	-
<u>Ametrida</u>, <u>Sphaeronycteris</u>	97	96	-	61	-	69
<u>Ametrida</u>, <u>Centurio</u>	-	-	-	-	-	-
<u>Ametrida</u>, <u>Pygoderma</u>	-	-	100	-	99	-
<u>Ardops</u>, <u>Ariteus</u>	76	84	98	97	100	100
<u>Phyllops</u>, <u>Stenoderma</u>	-	-	98	100	100	99
OUTGROUP						
<u>Rhinophylla</u>, Stenodermatinae	-	-	-	71	-	-
<u>Carollia</u>, <u>Rhinophylla</u>	100	91	36	-	37	66
Number of characters	166 (151)	300(264)	1140(382)	1363(91)	2503(473)	2803(737)
Trees retained	5	4	4	54	1	2
Tree length	770	1238	2166	349	2537	3759

Consistency Index	0.35 (0.34)	0.37(0.35)	0.36(0.35)	0.76(0.57)	0.38(0.31)	0.38 (0.32)
Retention Index	0.6	0.6	0.6	0.76	0.55	0.42

[1] Percentage of 1,000 replicate heuristic searches.

[2] Vampyressina is a name suggested by Baker et al. (2003) based on the molecular phylogenetic analyses of two genes (see text) to encompass Platyrrhinus helleri, Vampyrodes, Chiroderma, Uroderma bilobatum, Mesophylla, Vampyressa melissa, V. pusilla, V. thyone, V. bidens, V. brocki, and V. nymphaea.

[3] Stenodermatina, is a subtribe according to Wetterer et al. (2000), composed of Ametrida, Ardops, Ariteus, Centurio, Phyllops, Pygoderma, Sphaeronycteris, Stenoderma.

Table 4. Morphological characters supporting some of the identified clades and the taxonomic classification proposed in this paper, for Vampyressa (s.l.) and other genera historically considered allied[1]. Unambiguous changes supporting clades and autapomorphies are boldfaced; characters optimized through either ACCTRAN or DELTRAN transformations are indicated. Below each clade (and centered) there is "unnamed" or the name suggested in this paper for each clade or taxon.

Clade **Taxon Name**	**Character listing**
P. helleri + Vampyrodes + U. bilobatum + C. villosum + Vampyressa s.l. + Mesophylla **Vampyressini**	**(230) First lower molar roughly quadrate with a narrowed anterior portion (retangular not narrowed in Mesophylla).** **(246) Right and left upper inner incisors contact each other from roughly the midpoint of the tooth to its tip.**

Chiroderma villosum, Vampyressa bidens, V. brocki and V. nymphaea **Unnamed**	**(137) Posterior border of hard palate somewhat large and straight (as opposed to rounded) shaped, approaches to a “w-shaped” form because it often has a median projection**. (194) Lower canine and second lower premolar of approximate size, and lower canine only slightly higher than second lower premolar - DELTRAN. **(198) Third upper premolar longer than it is high.** (215) Well-developed labial cingulum on the labial face of first upper molar that sometimes develops in a posterolateral stylar projection (state 2); with a well-developed cusp-like projection on posterior labial cingulum (state 3) - DELTRAN.

Vampyressa bidens, V. brocki and V. nymphaea **Unnamed**	(19) Dorsal pelage with white midline stripe - DELTRAN. (67) Most of horseshoe, and two thirds or more of the lateral flap of lancet pale colored, with the column of the central rib brown - DELTRAN. (113) Nasal bowed in the antero-postero direction - ACCTRAN. (220) Metacone on upper first molar approximately two-thirds of the height of the paracone – ACCTRAN. (265) Second phalanx of digit IV is longer than the first phalanx IV – ACCTRAN.

Vampyressa brocki and V. nymphaea **Metavampyressa**	**(6) Dorso-medial facial white stripe consistently wider than the ventro-lateral stripe.** **(8) Paired dorso-medial stripes meet at their anteriormost point.** **(21) Anterior tip of the dorsal stripe largely displaced caudad, located below the base of their neck, often at mid thoracic region.** **(36) One or two genal vibrissae present.** **(48) Colored margins in the ear pinna interrupted in the dorsolateral part**.

		(77) Small papilla just below central large papilla absent – ACCTRAN. (115) Slightly inflated anterodorsal maxilla - DELTRAN. (240) Entoconid lacking from the second lower molar - ACCTRAN.
Vampyressa bidens	**Vampyriscus**	(20) Middorsal stripe has a bright white color that contrasts sharply with the background color of the pelage - ACCTRAN. **(178) Upper outer incisor peg-like and often with a minute posteromedial cusp.**

	(181) A single lower incisor present, and rarely if ever, two. (259) Diastema between the lower canine and the second lower premolar smaller to subequal to that between the second and the fourth lower premolars - DELTRAN**.**
Mesophylla, Vampyressa melissa, V. pusilla, V. thyone **Unnamed**	(19) White midline dorsal stripe lacking – ACCTRAN. (31) Ventral fur predominantly unicolored - ACCTRAN. (215) Poorly developed cingulum on the labial face of first upper molar - ACCTRAN.
Vampyressa melissa + V. pusilla + V. thyone **Vampyressa**	(112) Anterior tip of the nasal ends posterior to the edge of the anterodorsal maxilla ramus, thus creating a recess between those bones – DELTRAN.

(113) Nasal flat or convex – ACCTRAN.

(143) Small medial part of postglenoid process (1/4 to 1/8 of medial articular surface of glenoid fossa) bends over the articular surface of the fossa - ACCTRAN.

(202) - Third upper premolar implanted in a horizontal alveolar surface, roughly in the same plane as the fourth upper premolar – ACCTRAN.

(204) Stylar cusps on the posterior part of the fourth upper premolar sometimes present.

(205) Relatively stout and large postero-lateral cusp arising

	from cingulum of fourth upper premolar, reaching up to 1/3 to a little less than 1/2 the height of its main cusp – DELTRAN. **(237) Metaconid on second lower molar about twice the size of protoconid**. (241) Well-developed crest-like straight directed entoconid onto second lower molar - DELTRAN.
<u>Vampyressa pusilla</u>, <u>V. melissa</u> **Unnamed**	(69) No leaflet observed behind the lancet of the noseleaf – ACCTRAN. (83) Dactylopatagium minus pigmented – ACCTRAN. (200) – Third upper premolar more than 2/3 the size of fourth

	upper premolar - ACCTRAN.
(U. bilobatum, P. helleri, Vampyrodes) **Unnamed**	(19) Dorsal pelage with white midline stripe - DELTRAN. (30) Dorsal fur bicolored - ACCTRAN. (83) Dactylopatagium minus pigmented – ACCTRAN. **(204) Two stylar cusps on fourth upper premolar**. **(214) One stylar cusp on fourth lower premolar.** (215) Well-developed labial cingulum on the labial face of first upper molar present (state 1) that sometimes develops in a posterolateral stylar projection (state 2) - DELTRAN.

	(232) First lower molar situated above fourth lower premolar – DELTRAN. (240) Entoconid lacking from the second lower molar - ACCTRAN.
Platyrrhinus helleri + Vampyrodes **Unnamed**	**(21) Dorsal stripe extends anteriorly to the top head running parallel and medial to the dorso-medial facial stripes along at least one fourth of the length of the latter.** (154) Paraoccipital process poorly developed - DELTRAN. (210) Second lower premolar triangular - ACCTRAN.

(213) Two cusps present on posterior fourth lower premolar.

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[1] Those genera are Artibeus (s.l.), Platyrrhinus, Vampyrodes, Uroderma , Chiroderma, Ectophylla, and Mesophylla.

Table 5. Comparative list of characters differentiating Ectophylla and Mesophylla and supporting their generic status. Numbers in parentheses refer to those in the character descriptions list. Unique characters of each species (among stenodermatines) are boldfaced.

SYSTEM	**GENUS**	
	Ectophylla	**Mesophylla**
External	**Dorsal and ventral fur white and grayish white.**[1]	**Dorsal and ventral fur pale buff.** [1]
	(5) Facial stripes absent.	(5) Facial stripes rudimentary or absent.
	(15) Forearm virtually hairless.	(12) Hair covering the proximal half of the forearm up to two thirds of its length.
	(71) Smooth and rounded lateral horseshoe.	(71) Lateral border of horseshoe rough edged.
Skull	(113) Nasals arched and located above maxilla.	(113) Nasals slightly twisted along the lateromedial axis (with the medial part down)

	(115) Posterior maxilla, at fronto-maxilar junction slightly inflated.	(115) Maxilla non-inflated.
	(143) Large part of the post glenoid process bent over the articular fossa of the mandible to form a curved surface.	(143) Post-glenoid process poorly developed and articular glenoid surface mostly directed ventrally.
Tooth	(166) Upper inner incisor triangular, conic shaped; with a pointed tip.	(166) Upper inner incisor approaches to the form of an elongated cylinder.
	(178) Single-tipped and pointed upper outer incisor that looks like a small version of the conic upper inner incisor of this species.	(178) Simple acuspidate peg-like upper outer incisor.

(184) Lower incisors in the shape of blunt cones.	(184) Lower incisors with shallow longitudinal groove on the anterior tooth face.
(186) Lower outer incisor lies largely or completely anterior to the canine; tooth may be largely hidden when seen from its posterior face.	(186) Only a small part of the lateral portion of the outer lower incisors overlaps the canine in lateral view, the rest of the tooth lying more medial to the canine; tooth may be largely seen from its posterior face.
(192) Secondary cusp on the upper canine positioned posterolingually.	(192) Secondary cusp on the upper canine positioned posterolaterally.
(226) Median ridge present in the second upper	(226) Median ridge absent in the second upper molar.

molar.	(231) Subovoide second lower molar.
(231) Circular second lower molar that is greater in diameter than the breadth of mandibular ramus.	(243) Consistently have a third lower molar.
(243) Consistently lack a third lower molar.	(247) Inner and upper outer incisors are in close contact with each other.
(247) Inner and upper outer incisors separated by a small diastema.	(252) First upper molar not separated from the second upper molar by a diastema.
(252) First upper molar always separated from the second upper molar by a diastema.	(255) Lower canine and second lower premolar not separated by a diastema.
(255) Lower canine and second lower premolar	(258) First lower molar not separated from the

separated by a diastema.	second lower molar by a small diastema.
(258) First lower molar sometimes separated from the second lower molar by a small diastema.	(259) Diastemata according to the gap formula: gap between fourth lower premolar and first lower molar < gap between second and fourth lower premolars.
(259) Diastemata distributed in lower postcanine teeth according to the following gap formula: gap between lower canine and the second lower premolar ≅ gap between first and second lower molar; both < gap between fourth lower premolar and first lower molar < gap between the second and the fourth lower premolars.	(261) Tiny gaps formed between cheek teeth when jaws are closed.
	(268) Medial anterior face of the manubrium

(261) A single large lateral gap located between upper and lower premolars when jaws are in occlusion.	with large, quadrate shaped crest.
(268) Simple crest-like projection rounded in shape lie at medial part of anterior face of the manubrium.	
(274) Fourth rib attached to the mid-point of third rib; only three costal cartilages articulate directly with the mesosternum.	(274) Five or more costal cartilages posterior to second rib articulates with the mesosternum.
(290) Pair of lateral circumvallated papillae on the dorsal surface of the tongue.	(290) Pair of lateral circumvallated papillae on the lateral surfaces of the tongue.

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[1] Although character 16 aimed to reconstruct overall pelage color tonalities (dark, medium, light), these specific color patterns (white, buff) were not included.

Table 6. Morphological characters supporting identified clades within short-faced (Stenodermatina, according to Wetterer et al. 2000, and Stenodermatini as suggested in this paper) bats and the so proposed tribe itself. Unambiguous changes supporting clades are boldfaced; characters optimized through either ACCTRAN or DELTRAN transformations are indicated.

Clade **Taxon Name**	**Character listing**
Stenodermatini	(5) Facial pelage is uniform in color; facial stripes completely absent - ACCTRAN. **(13) Spot formed by completely white fur always present in each shoulder.** (14) White spot sometimes present in the neck (reversed in Ardops + Ariteus) – ACCTRAN. **(46) Dorsal emargination of the ear pinna located in its proximal half.** **(79) Widespread internal oral papillae covering inner cheeks.**

	(81) Very broad dactylopatagium minus. **(133) Hard palate does not extend posteriorly into the interorbital region.** **(194) Lower canine and second lower premolar of approximate size.** **(196) Lower canine virtually straight; not divergent laterally and not recurved anteroposteriorly.** **(209) Second lower premolar is approximately two-thirds of the lower canine and two-thirds or more of the fourth lower premolar.**
Ardops + Ariteus + Pygoderma + Centurio + Ametrida + Sphaeronycteris	**(178) Outer incisor longitudinally deep grooved.** (291) Completely unpapillated pharyngeal tongue – DELTRAN.
Pygoderma + Centurio + Ametrida + Sphaeronycteris **Centurionina**	(14) White spot in the neck present – DELTRAN. (86) Uropatagium broad with a deep medial notch – ACCTRAN.

		(88) Prominent eyelids and/or periorbital glands present. **(107) Narial opening located in a plane that faces primarily anterior.** **(143) Postglenoid processes well developed; oriented roughly perpendicular to the glenoid fossa so that half of its articular surface faces ventrally and and the other half rostrally.** (235) Metaconid lacking on first lower molar – ACCTRAN. **(267) Neural spines in the lumbar vertebrae well developed and increase gradually in height from the first to the third, and sometimes to the fourth lumbar vertebra.**
Ardops + Ariteus	**Ariteina**	(14) White spot in the neck absent – ACCTRAN. **(73) Thickened inferior border of the horseshoe have a v-shaped.** **(136) Vertical palatine laminae run roughly parallel to each other.** (154) Paraoccipital process well developed – DELTRAN.

	(168) Triangular upper inner incisor with a crown that is roughly as high as it is wide. (234) Protoconid on first lower molar is just a little smaller than the height of fourth lower premolar, minimally 2/3 of the height of that tooth – ACCTRAN.
Phyllops falcatus + Stenoderma **Unnamed**	(14) White spot in the neck present – DELTRAN. (130) Strongly arched palate; does not slope continuously: lateral walls roughly vertical, and the medial palate is horizontal, roughly flat – ACCTRAN. (178) Asymmetrically bilobed upper outer incisor; inner lobe is larger than the outer and directed medially - DELTRAN. (244) Relatively well-developed third lower molar; about one-third or more the size of second lower molar in occlusal view – ACCTRAN.
Centurio + Ametrida + Sphaeronycteris **Unnamed**	**(38) Three vibrissae in the column adjacent to noseleaf.** **(101) Anterior maxillary rami widely spread.**

	(132) Posterior maxillary toothrow are roughly parallel sided – ACCTRAN. **(135) Emargination in the posterior palate “v”-shaped.** (154) Paraoccipital process poorly developed – DELTRAN.
Ametrida + Sphaeronycteris **Unnamed**	(91) Submandibular mass of tissue absent – ACCTRAN. **(105) Facial process of the maxilla oriented horizontally, lying roughly parallel to the palatal process.** (109) Anteroventral edge of the narial opening situated dorsal to the distal half of P4 - ACCTRAN. **(113) Nasal bone retracted between orbits and located in a plane above facial maxilla.** **(139) Choana (= internal narial aperture) higher than wider.** **(142) Basisphenoid pits pushed to a region just anterior to the cochlea; basicranium rotated forward.** **(170) Main cusp on the upper inner incisor centered in the**

	middle of the tooth. (221) Lingual cingulum extending from lingual paracone to posterior edge of lingual metacone of upper first molar – ACCTRAN. (228) Third upper molar present – ACCTRAN. (244) Relatively well-developed third lower molar; about one-third or more the size of second lower molar in occlusal view – ACCTRAN. (269) Obtuse angle formed between the body and ventral process of manubrium – DELTRAN.

Table 7. Classification proposed for Stenodermatinae (Chiroptera: Phyllostomidae) in this paper contrasted with Wetterer et al. (2000) and Baker et al. (2003). Tribal names for stenodermatines suggested in the present study are boldfaced. Genus names followed the generic rearrangements discussed in this paper.

Author and type of data		
Wetterer et al. (2000); morphology and restriction sites	Baker et al. (2003); RAG2, mtDNA	This paper; morphology, RAG2, Cytochrome b
Stenodermatinae	Stenodermatinae	Stenodermatinae
Sturnirini	Sturnirini	**Sturnirini**
Sturnira	Sturnira	Sturnira
Stenodermatini	Stenodermatini	**Stenodermatini**
Ectophyllina	Vampyressina	Ametrida
Artibeus	Chiroderma	Ardops
Chiroderma	Vampyriscus	Ariteus
Ectophylla	Uroderma	Centurio

Enchistenes	Vampyressa	Phyllops
Platyrrhinus	Mesophylla	Pygoderma
Uroderma	Vampyrodes	Sphaeronycteris
Vampyressa	Platyrrhinus	Stenoderma
Vampyrodes		
Stenodermatina	Mesostenodermatini	**Vampyressini**
Ametrida	Enchisthenina	Chiroderma
Ardops	Enchisthenes	Mesophylla
Ariteus	Ectophyllina	Metavampyressa
Centurio	Ectophylla	Platyrrhinus
Phyllops	Artibeina	Uroderma
Pygoderma	Artibeus	Vampyressa
Sphaeronycteris	Dermanura	Vampyrodes
Stenoderma	Stenodermatina	Vampyriscus[a]
	Ariteus	
	Ardops	**Artibeini**
	Stenoderma	Artibeus[c]

	Centurio	Dermanura
	Pygoderma	
	Sphaeronycteris	Incertae sedis:
	Ametrida	Ectophylla
	Phyllops	Enchistenes

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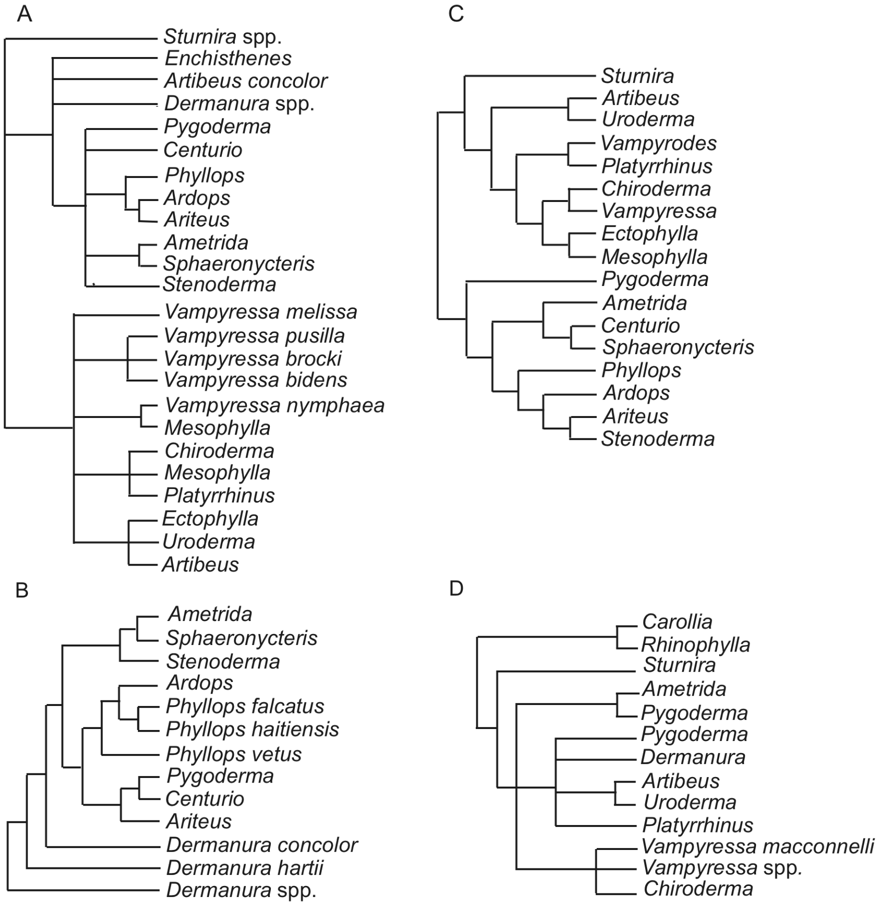
[a] Includes only Vampyriscus bidens.

[b] Includes Metavampyressa brocki and M. nymphaea.

[c] Includes Koopmania.

Figures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Enchisthenes
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Dermanura spp.
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Sphaeronycteris
Stenoderma
Vampyressa melissa
Vampyressa pusilla
Vampyressa brocki
Vampyressa bidens
Vampyressa nymphaea
Mesophylla
Chiroderma
Mesophylla
Platyrrhinus
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Uroderma
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C
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Artibeus
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Platyrrhinus
Chiroderma
Vampyressa
Ectophylla
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Stenoderma
Ardops
Phyllops falcatus
Phyllops haitiensis
Phyllops vetus
Pygoderma
Centurio
Ariteus
Dermanura concolor
Dermanura hartii
Dermanura spp.
D
Carollia
Rhinophylla
Sturnira
Ametrida
Pygoderma
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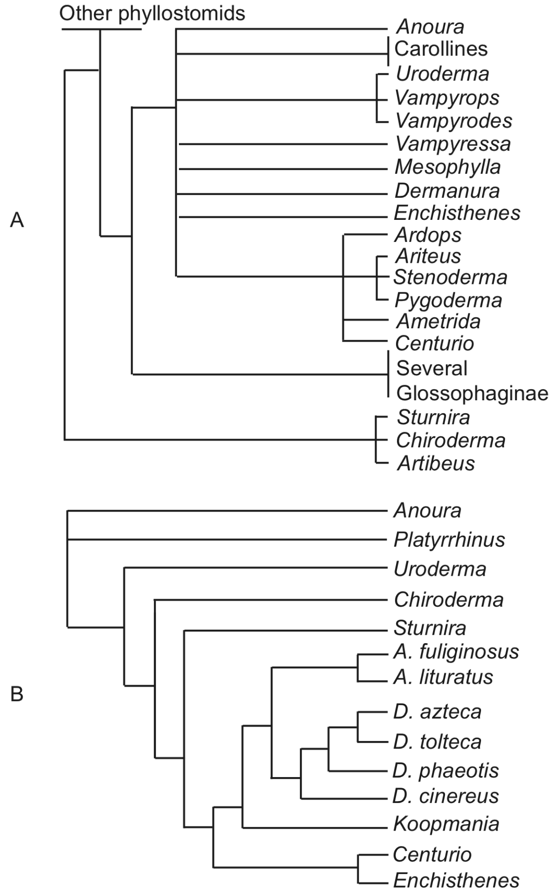
Vampyressa macconnelli
Vampyressa spp.
Chiroderma

Figure 1.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Ardops
Ariteus
Stenoderma
Pygoderma
Ametrida
Centurio
Several
Glossophaginae
Sturnira
Chiroderma
Artibeus
B
Anoura
Platyrrhinus
Uroderma
Chiroderma
Sturnira
A. fuliginosus
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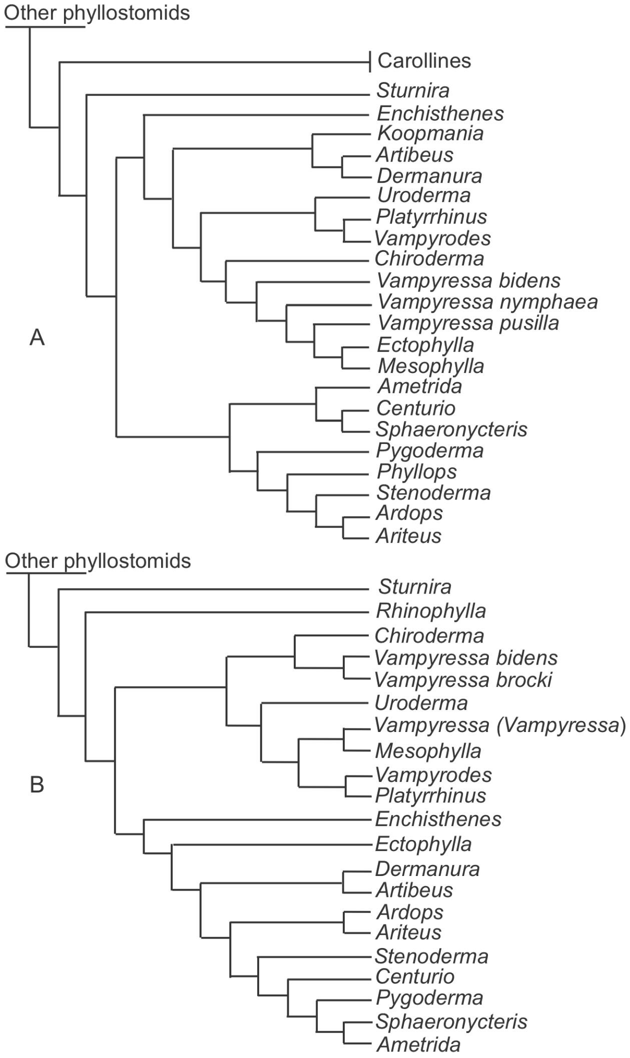
Koopmania
Centurio
Enchisthenes

Figure 2.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Vampyressa nymphaea
Vampyressa pusilla
Ectophylla
Mesophylla
Ametrida
Centurio
Sphaeronycteris
Pygoderma
Phyllops
Stenoderma
Ardops
Ariteus
A
Other phyllostomids
Sturnira
Rhinophylla
Chiroderma
Vampyressa bidens
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Uroderma
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Dermanura
Artibeus
Ardops
Ariteus
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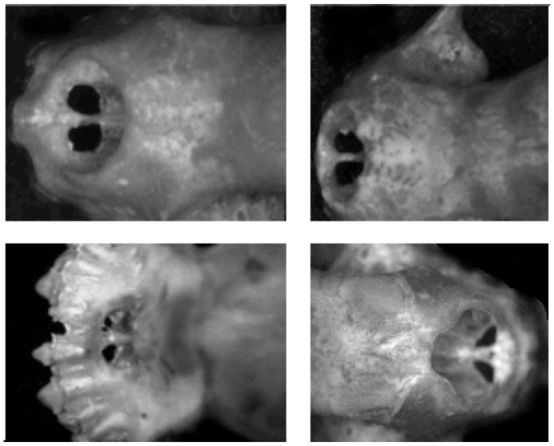
Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.



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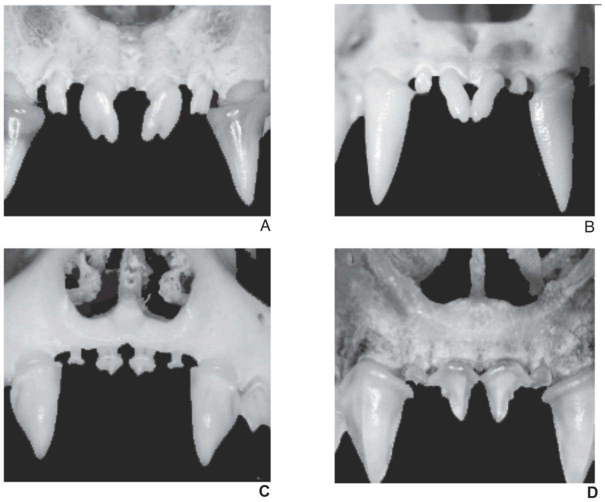

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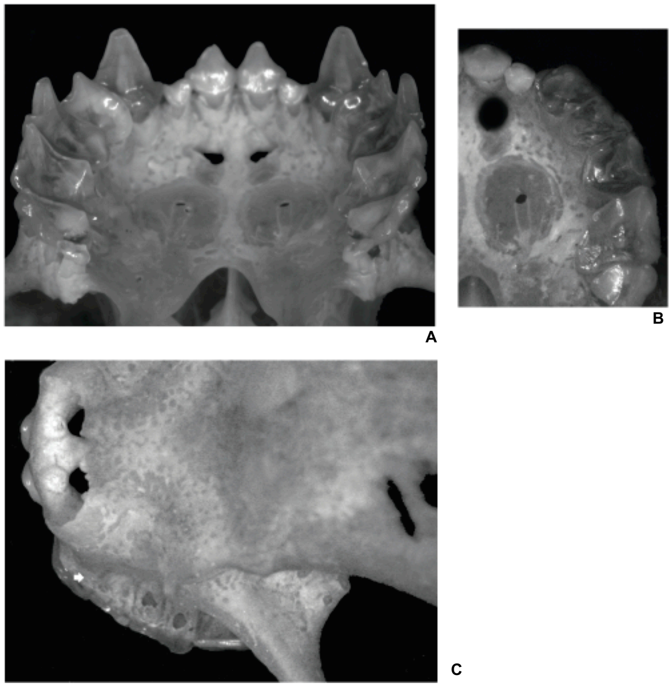
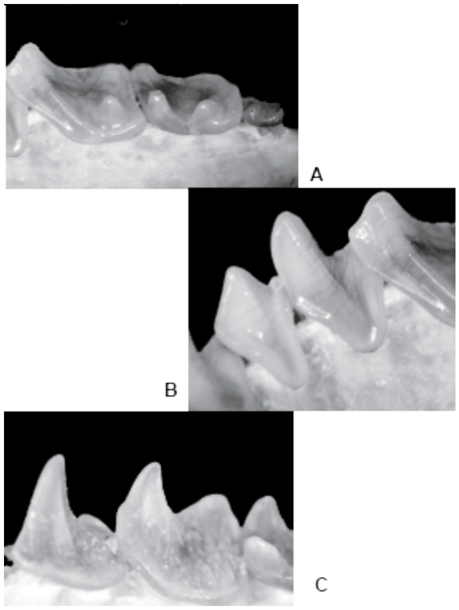


Figure 10.

Figure 11.

Figure 12.



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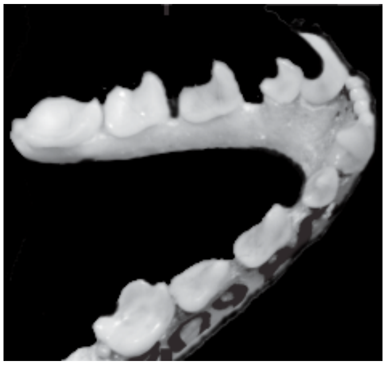

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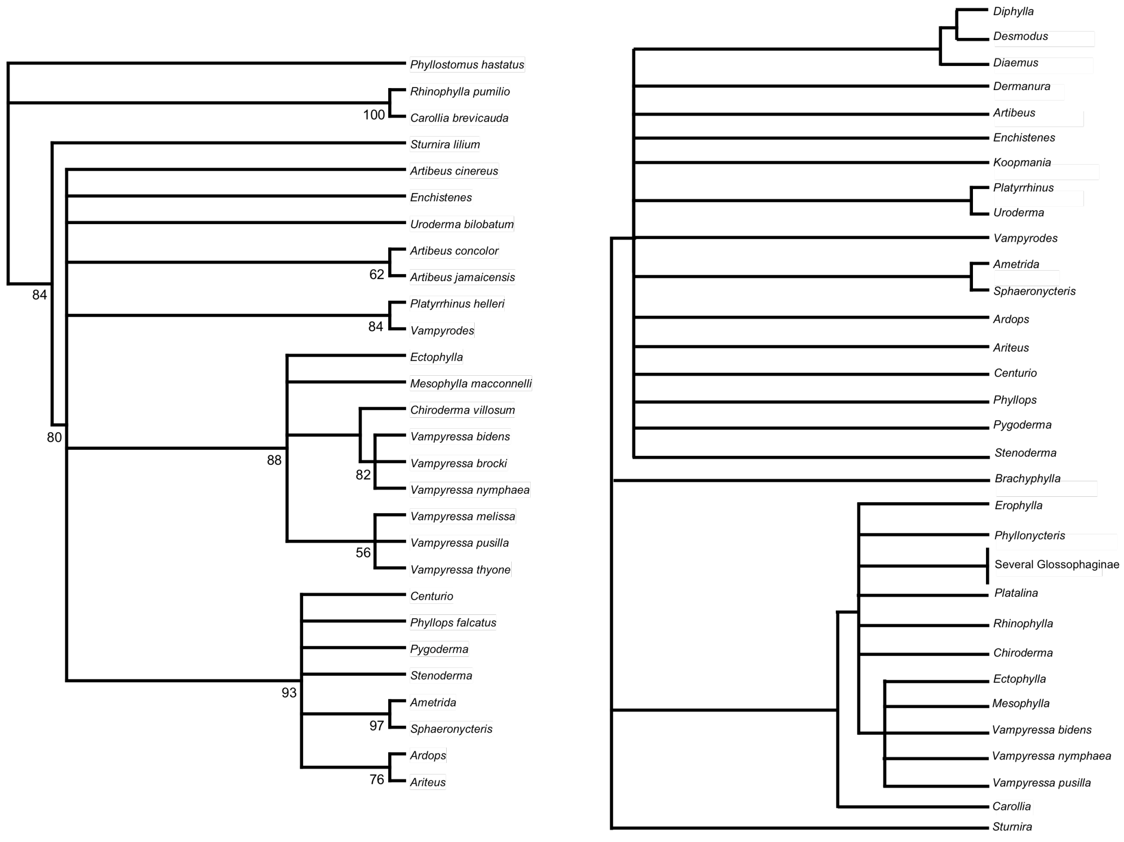
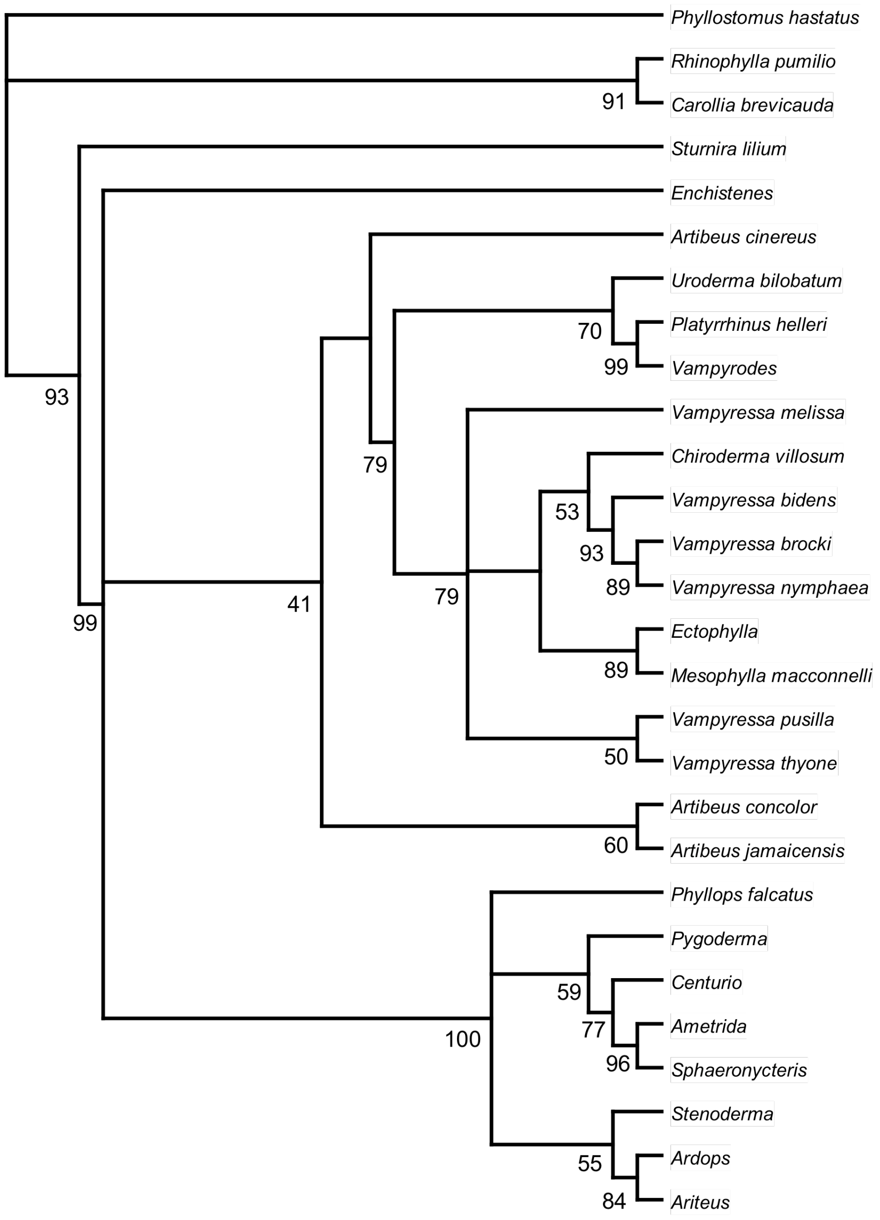


This paper

Wetterer *et al.* (2000)

Figure 15.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Enchistenes
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Uroderma bilobatum
Platyrrhinus helleri
Vampyrodes
70
99
93
Vampyressa melissa
Chiroderma villosum
Vampyressa bidens
Vampyressa brocki
Vampyressa nymphaea
79
53
93
89
41
79
99
Ectophylla
Mesophylla macconnelli
89
Vampyressa pusilla
Vampyressa thyone
50
Artibeus concolor
Artibeus jamaicensis
60
Phyllops falcatus
Pygoderma
Centurio
Ametrida
Sphaeronycteris
59
77
96
100
Stenoderma
Ardops
Ariteus
55
84

Figure 16.

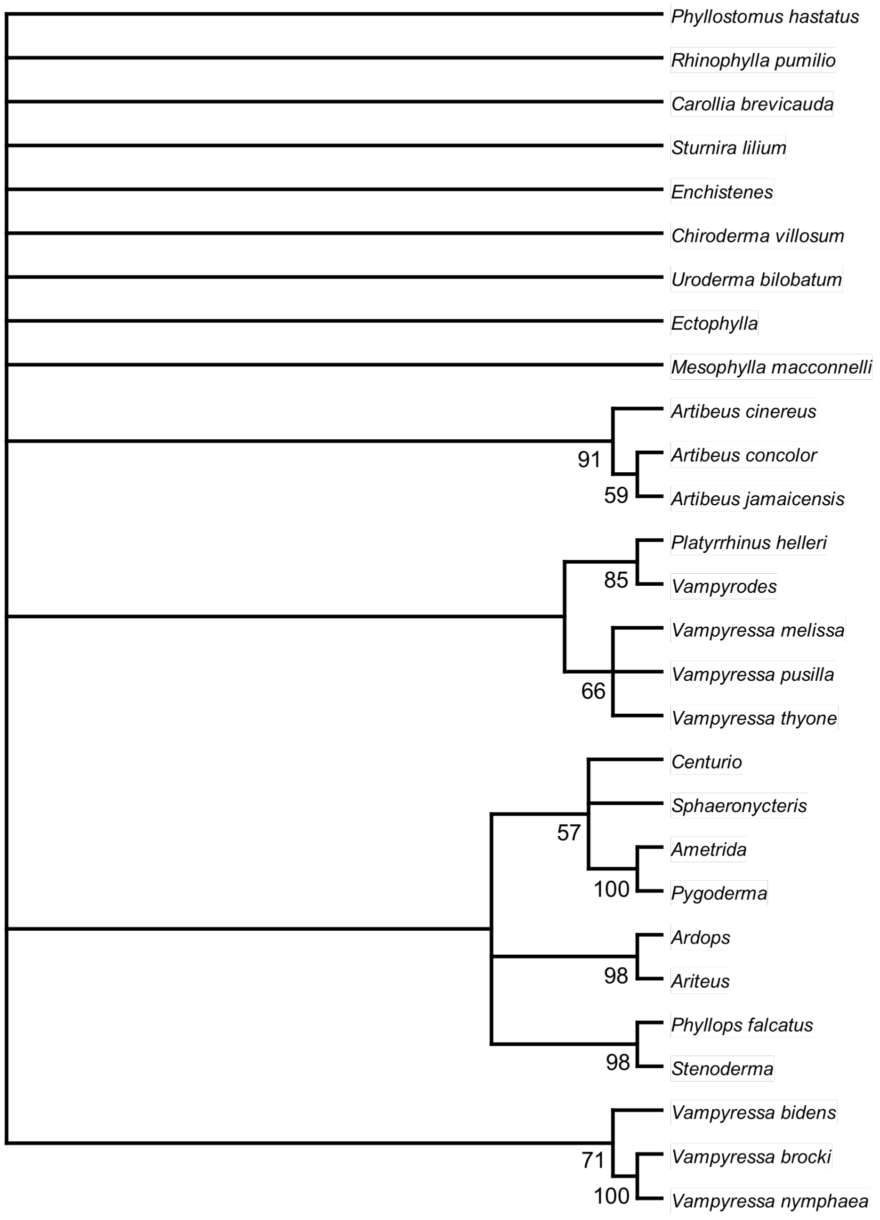
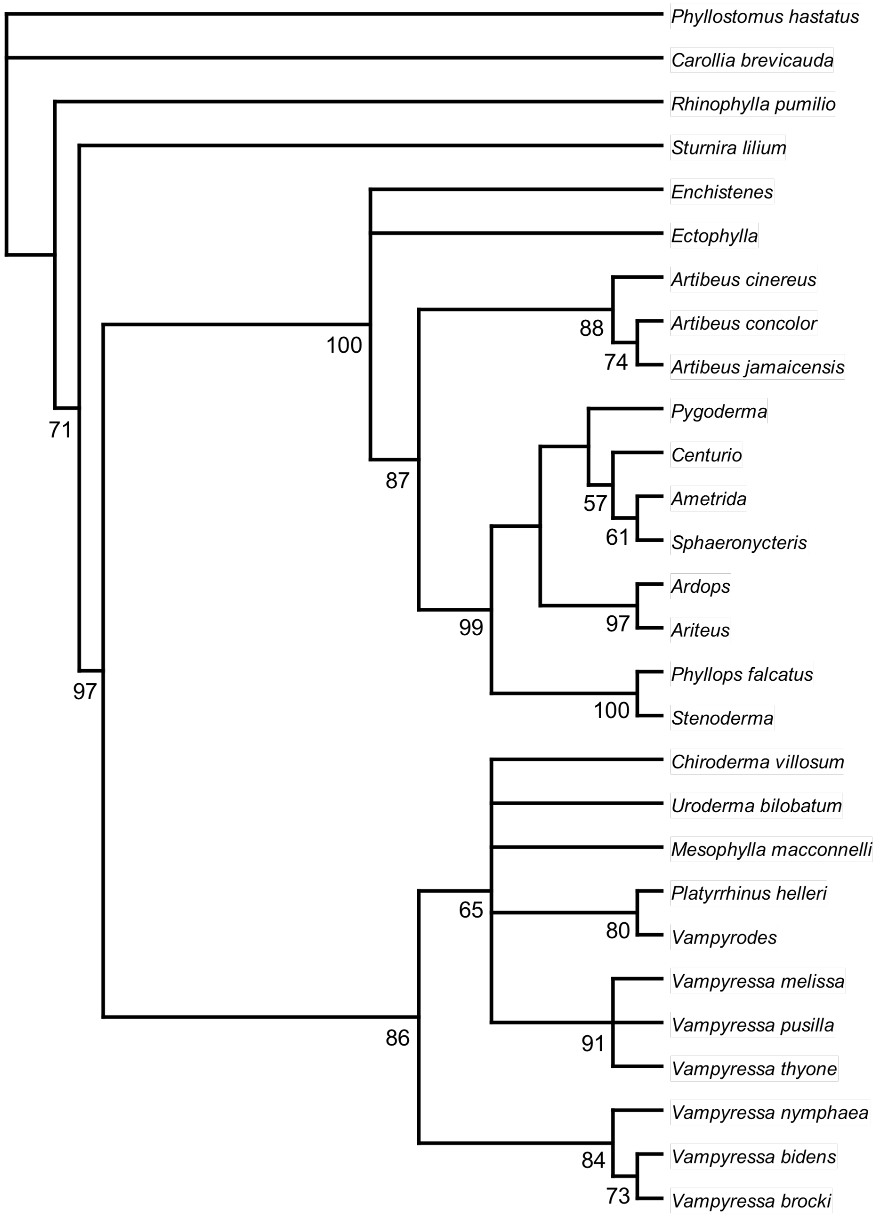

Phyllostomus hastatus
Rhinophylla pumilio
Carollia brevicauda
Sturnira lilium
Enchistenes
Chiroderma villosum
Uroderma bilobatum
Ectophylla
Mesophylla macconnelli
Artibeus cinereus
Artibeus concolor
Artibeus jamaicensis
91
59
Platyrrhinus helleri
Vampyrodes
85
Vampyressa melissa
Vampyressa pusilla
Vampyressa thyone
66
Centurio
Sphaeronycteris
Ametrida
Pygoderma
57
100
Ardops
Ariteus
98
Phyllops falcatus
Stenoderma
98
Vampyressa bidens
Vampyressa brocki
Vampyressa nymphaea
71
100

Figure 17.


Phyllostomus hastatus
Carollia brevicauda
Rhinophylla pumilio
Sturnira lilium
Enchistenes
Ectophylla
Artibeus cinereus
Artibeus concolor
Artibeus jamaicensis
Pygoderma
Centurio
Ametrida
Sphaeronycteris
Ardops
Ariteus
Phyllops falcatus
Stenoderma
Chiroderma villosum
Uroderma bilobatum
Mesophylla macconnelli
Platyrrhinus helleri
Vampyrodes
Vampyressa melissa
Vampyressa pusilla
Vampyressa thyone
Vampyressa nymphaea
Vampyressa bidens
Vampyressa brocki
100
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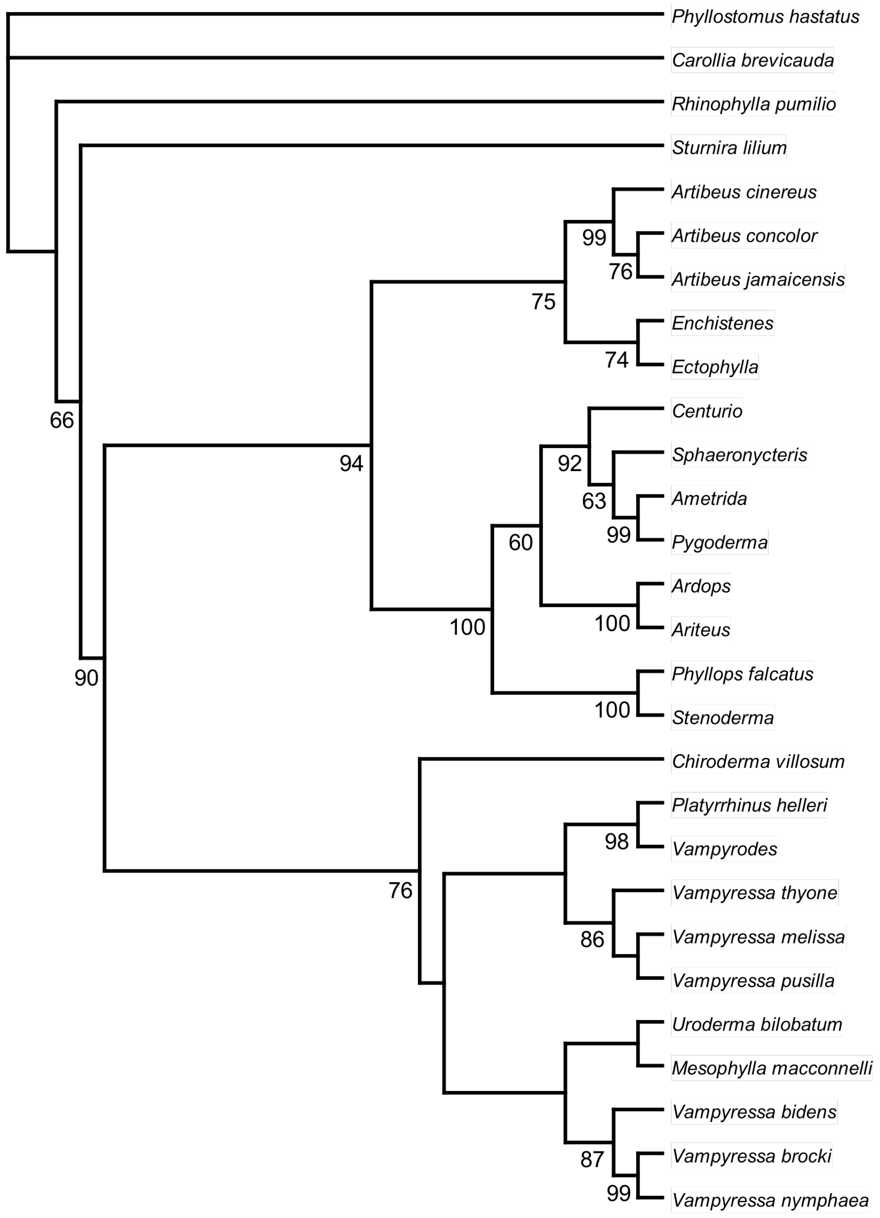
74
71
87
57
61
99
97
97
100
65
80
86
91
84
73

Figure 18.


Phyllostomus hastatus
Carollia brevicauda
Rhinophylla pumilio
Sturnira lilium
Artibeus cinereus
Artibeus concolor
Artibeus jamaicensis
Enchistenes
Ectophylla
Centurio
Sphaeronycteris
Ametrida
Pygoderma
Ardops
Ariteus
Phyllops falcatus
Stenoderma
Chiroderma villosum
Platyrrhinus helleri
Vampyrodes
Vampyressa thyone
Vampyressa melissa
Vampyressa pusilla
Uroderma bilobatum
Mesophylla macconnelli
Vampyressa bidens
Vampyressa brocki
Vampyressa nymphaea
99
76
75
74
66
94
92
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99
60
100
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90
100
98
76
86
87
99

Figure 19.

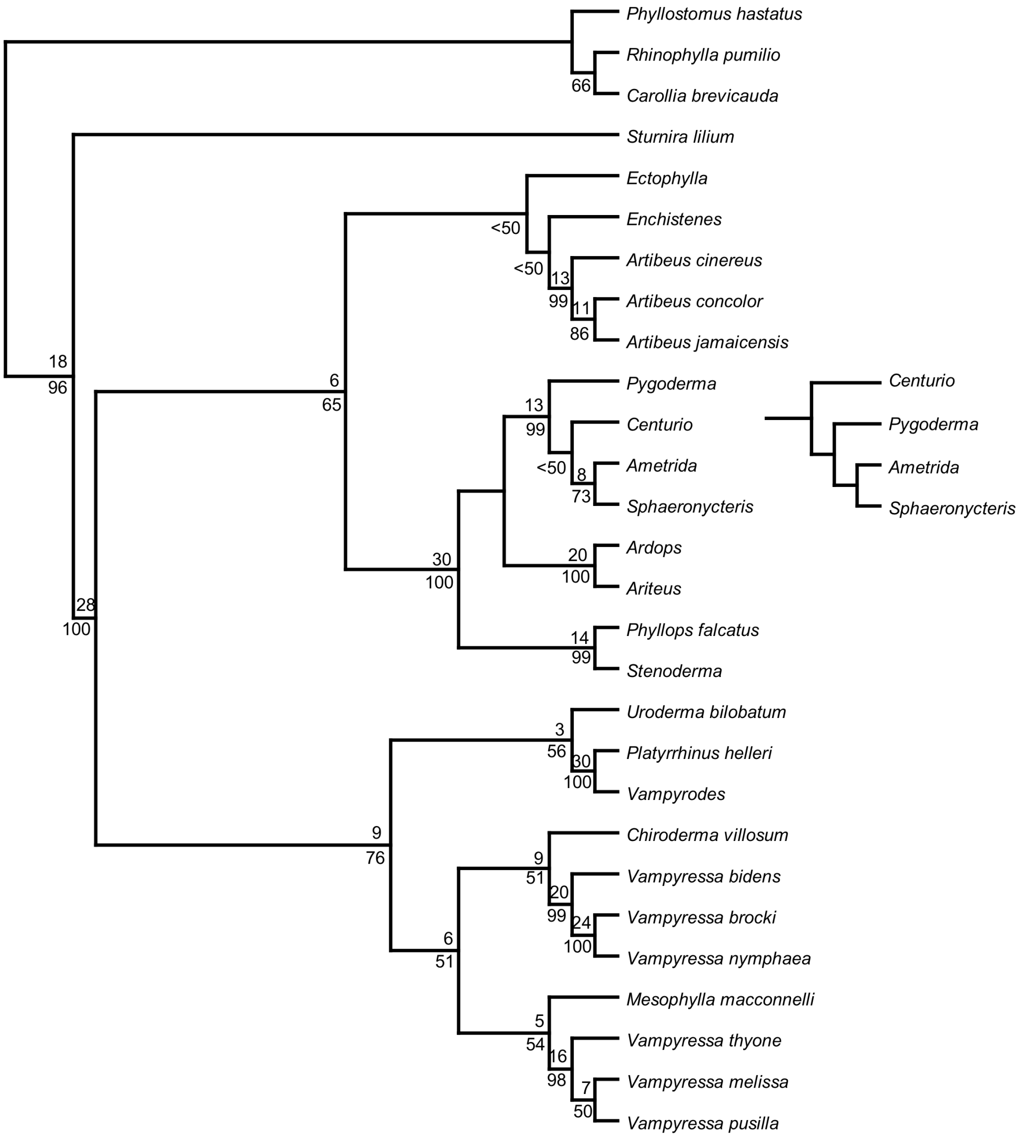
Phyllostomus hastatus
Rhinophylla pumilio
Carollia brevicauda
Sturnira lilium
Ectophylla
Enchistenes
Artibeus cinereus
Artibeus concolor
Artibeus jamaicensis
Pygoderma
Centurio
Ametrida
Sphaeronycteris
Ardops
Ariteus
Phyllops falcatus
Stenoderma
Uroderma bilobatum
Platyrrhinus helleri
Vampyrodes
Chiroderma villosum
Vampyressa bidens
Vampyressa brocki
Vampyressa nymphaea
Mesophylla macconnelli
Vampyressa thyone
Vampyressa melissa
Vampyressa pusilla
66
18
96
<50
<50
13
99
11
86
6
65
13
99
<50
8
73
30
100
20
100
28
100
14
99
3
56
30
100
9
76
9
51
20
99
24
100
6
51
5
54
16
98
7
50
Centurio
Pygoderma
Ametrida
Sphaeronycteris

Figure 20.

Figure 1. Trees resulting from the phylogenetic analysis of Stenodermatinae from the works of Owen (1987) (A); Owen (1991) (B); Lim (1993) (C); and Gimenez (1993) (D). Redrawn from the original and modified to focus on stenodermatine relationships.

Figure 2. Phylogenetic relationships of stenodermatines presented by Van Den Bussche, 1991 (A); and Van Den Bussche et al., 1993 (B); using restriction sites. Redrawn from the original and modified to focus on stenodermatine relationships.

Figure 3. (A) Wetterer et al. (2000) phylogeny of the family Phyllostomidae based on multiple systems, mostly morphology; and (B) Baker et al. (2003) phylogeny of phyllostomids based on the combined analysis of RAG2 and mtDNA gene (12S rRNA, $tRNA^{Val}$, and 16S rRNA). Redrawn from the original and modified to focus on stenodermatine relationships.

Figure 4. (A) Sphaeronycteris toxophyllum, from Venezuela, showing the thin guard hairs in its head, above the regular pelage (character 2), the large bare area in the face (character 5), the two genal papillae (character 35) with wart-like shape (character 40), the dorsal emargination of the ear pinna located in the proximal half of ear pinna (character 44), the central rib restricted to the proximal spear (character 62), the swollen region around eyes (character 86), and the outgrowth behind the noseleaf (character 87). Picture is a courtesy of Jesus Molinari; **(B)** Ametrida centurio, from Rio Madeira, AM, Brazil, showing the fur in the internal ear pinna (character 12), the three vibrissae

surrounding the noseleaf (character 38) and their respective vibrissal papilla forming flesh skin flaps (character 40), the hairless lip region (character 3), the white spots in the neck (character 14), the shallow folds separating the edges of the spear from the central rib of the noseleaf (character 62), the virtually unicolored noseleaf (character 65), and the roughly regularly toothed lateral edge of the tragus (character 55). Picture is a courtesy of Paulo Bobrowieck; **(C)** Mesophylla macconnelli, from Rio Madeira, AM, Brazil, showing the rudimentary white spots in its face (character 5), the pale body coloration overall (character 16), the bright uniformly yellow-colored ear pinna and noseleaf (characters 47, 65 and 66). Picture is a courtesy of Paulo E. D. Bobrowieck; **(D)** Chiroderma villosum, from Porto Trombetas, PA, northern Brazil, showing the broad-ovate shape of the noseleaf lancet (character 61), the deep folds of the lateral edges of the spear separating them from the central rib (character 62), the noseleaf with indistinctive gradations of color (characters 65) but overall dull-colored (character 66). Picture by Valéria C. Tavares; **(E, F)** Vampyressa bidens (=Vampyriscus bidens) from eastern, Pará, Brazil, showing the pair of facial white stripes of similar breadth (character 6), bright white (character 7), dorsal facial white stripes that run all the way in parallel (character 8), the dorsal terminating up to the level of posterior insertion of the cone of ear pinna (character 9), the yellow stripe bordering the ear pinna and the part of the internal pinna shell pale-colored (character 47), the contrasting-colored tip of tragus (character 54), and the bicolored noseleaf (characters 65, 67, 68). Picture by Filipe M. H. Nunes.

Figure 5. Skin of Vampyressa nymphaea (= Metavampyressa nymphaea) (UNIVALLE 3827) from Rio Pato, Chocó, Colombia showing the paired dorso-medial stripes that usually meet at their anteriormost point (character 8).

Figure 6. Pygoderma bilabiatum (Santa Cruz, Bolivia AMNH 246399 – holotype showing the ventral chiropatagium that has pale, conspicuous fur distributed in a large area, extending posteriorly up to the level of a plane passing through half of the length of the abdomen (character 24).

Figure 7. Vampyressa thyone, from Costa Rica, fluid preserved showing the leaflet just behind the noseleaf (character 69).

Figure 8. Dorsal view of the skulls of Vampyressa nymphaea (= Metavampyressa nymphaea), from Costa Rica (up, to the left), Ariteus flavescens, from Jamaica (up, to the right), Sphaeronycteris toxophyllum, from Colombia (below, to the left) and Vampyressa thyone, from Humaitá, AM, Brazil (below, to the right), showing the differences in the angle formed by anterior arched maxilla (character 101), differences in the shape and orientation of premaxilla and maxilla (characters 104, 105, 106), and the variation in the direction of external nares (character 107). Note the recess between anterior nasals and anterodorsal ramus of maxilla in V. thyone (character 112).

Figure 9. (A) Frontal view of the skull of Vampyressa melissa, from Paucartambo, Peru; note the upper inner incisor tending to quadrate proportions (breadth and height subequal), with a rounded occlusal margin (character 166), and always bilobed (character 172), with a deep and open distally notch (character 173). Note also the upper outer incisor that is roughly one-halfthe length of upper inner incisor and resembles it in form, although being much smaller (characters 177 and 178); **(B)** frontal view of the skull of Vampyressa nymphaea (= Metavampyressa nymphaea), from Chocó, Colombia, showing its elongated cylindric form (character 166) that converge medially (character 167), and may touch from their medial part to tip (character 246); **(C)** Frontal view of the skull of Centurio senex, from Guatemala showing the vertical oriented premaxilla (character 102), the smooth and uncompressed premaxilla and lateral maxilla (characters 103, 104, 105, 106), the anteriorly oriented external nare (character 107), and the large straight base of the ventral border of the external nare, its lateral edges terminating at level of I2 (character 110); and **(D)** frontal view of the skull of Pygoderma bilabiatum from Paraguay; note the triangular shaped, conic incisors (character 166) and the small accessory cusps in the inner upper incisors (character 169, 170). Compare also (among all specimens listed above) the patterns of contact/diastema between the upper incisors (characters 245, 246).

Figure 10. Ventral and posterior oblique (A, to the top left) and detail of ventral view (B, to the top right) of the palate of Phyllops falcatus, showing the unique perforated inflation in the ventropalatine bone (character 131). Below (C) a detail of the dorsal skull

of Phyllops falcatus from Haiti, showing the excavated facial maxilla, also unique for the genus (character 105).

Figure 11. Rostral aspect of the skull of Vampyressa bidens (= Vampyriscus bidens) from Guyana (above) illustrating the minute posteromedial tip onto I2 (below in the detail, and see character 178).

Figure 12. Lingual (oblique) view of lower premolars of Vampyressa bidens (= Vampyriscus bidens) from Mazaruni, Guyana. Note the median ridge onto the posterolingual face of p2 and p4 (characters 211 and 212).

Figure 13. Lingual aspect of the cheek teeth (right mandibullar ramus) of Ardops nichollsi annectens from Guadeloupe **(A and B)**, and Vampyressa brocki, from Loreto, Peru **(C)**. See the anterior lower molar (= first) situated above distal lower premolar (= fourth) (character 232).

Figure 14. Oblique view of the mandible of Mesophylla macconnelli from Manaus, Brazil (USNM 530980) showing the distribution of diastemata between lower teeth (characters 253 to 259).

Figure 15: To the left, tree resulting from the maximum parsimony analysis (heuristic search) of 166 craniodental characters for 28 stenodermatine taxa (Chiroptera:

Phyllostomidae, Stenodermatinae). The tree shown here is the consensus (strict) from four (5) most-parsimonious (fundamental) trees (with 770 steps). Numbers above branches indicate bootstrap support values for clades that received support > 50. For a summary of those values, and for other relationships not consensually supported see table 2. To the right, strict consensus tree from the analysis of 35 craniodental characters for phyllostomids, redrawn from Wetterer et al. (2000: 129).

Figure 16: Tree resulting from the maximum parsimony analysis of 300 morphological characters coded for 28 stenodermatine taxa (Chiroptera: Phyllostomidae, Stenodermatinae). The tree shown here is the consensus (strict) from four (4) most-parsimonious (fundamental) trees (with 1238 steps). Numbers above branches indicate bootstrap support values > 50. For a summary of those values, and for other relationships not consensually supported see table 2.

Figure 17. Tree resulting from the maximum parsimony analysis of 1140 bp of cyt-b data for 28 species of stenodermatines (Chiroptera: Phyllostomidae, Stenodermatinae). The tree shown here is the consensus (strict) from four (4) most-parsimonious (fundamental) trees (with 1238 steps). Numbers above branches indicate bootstrap support values for clades that received support > 50. For a summary of those values, and for other relationships not consensually supported see table 2.

Figure 18. Tree resulting from the maximum parsimony analysis (heuristic search) of 1363 bp of RAG-2 data for 28 species of stenodermatines (Chiroptera: Phyllostomidae, Stenodermatinae). The tree shown here is the consensus (strict) from fifth-four (54) most-parsimonious (fundamental) trees (with 349 steps). Numbers above branches indicate bootstrap support values for clades that received support > 50. For a summary of those values, and for other relationships not consensually supported see table 2.

Figure 19: Tree resulting from the maximum parsimony analysis (heuristic search) of 2503 bp of RAG-2 and cytb data combined for 28 species of stenodermatines (Chiroptera: Phyllostomidae, Stenodermatinae). The tree shown here is the single most-parsimonious (fundamental) tree (with 2537 steps). Numbers above branches indicate bootstrap support values for clades that received support > 50. For a summary of those values and lower values not shown see table 2.

Figure 20: Results of maximum parsimony (MP) analysis of combined 2803 morphological and molecular (RAG 2 and Cyt-b) characters for 28 stenodermatine taxa. The tree shown here is one of the two most-parsimonious trees that resulted from the analysis (3760 steps). The detail on the right side shows the single difference in tree topology of the alternative fundamental tree, which is the shift in the positions of Centurio and Pygoderma. Numbers above branches indicate values for Bremer support (= decay index) and numbers below are bootstrap support values. Other relationships contemplated with lower values of support are shown in the table 2.

Appendix 1

Specimens examined

Stenodermatinae

Ametrida centurio (n = 133)

AMNH 142612–142613, 142909, 172127, 187224–187225, 207967, 247645, 267274–267276, 267278–267279, 267375, 267973, 267975.

IAVH 2917.

UFMG VCT 553 (field number).

USNM 370783–370786, 370795, 393758, 460135–460136, 494488, 494510, 494520, 531106–531108, 535108, 542285, 554827.

Ardops nichollsi (n = 45)

AMNH 212557, 212896, 213925, 213952–213955, 217104, 238150–238151.

USNM 110918, 113186, 113498–113499, 113501, 361905, 544871–544872, 580675–580676).

KU 104804-11; 104813-14; 152362.

Ariteus flavescens (n = 37)

AMNH 4121, 214944, 239109.

FMNH 91291.

KU 151327.

USNM 53097, 96179–96181, 113926, 114042, 122658–122659, 252771, 534909–534911, 545167-545175, 545177–545184, 545203–545204, 546358.

<u>Artibeus(Artibeus) jamaicensis</u> (n = 29)

AMNH 39101, 72247, 74305, 131819, 140462, 202321, 207877, 217432–217433, 236678, 239933, 239937, 245331, 248326, 248510–248513, 263604–263605, 263610, 266321–266322, 266327–266328, 266331, 266334–266335, 266337, 267202.

<u>Artibeus (Dermanura) cinereus</u> (n = 30)

AMNH 97075–97076, 212279, 212880–212881, 233782, 233784, 233777, 237964, 244084, 246627–246628, 246632, 248177, 256374, 266258–266261, 266265–266266, 266270, 266290–266291, 266302, 266305, 266307, 267197–267198, 267499.

USNM 540678, 549429, 549330, 549437–549438.

<u>Artibeus (Koopmania) concolor</u> (n = 26)

AMNH 80340, 89945, 260014, 266267-266269, 267192–267195, 267477–267478, 267480–267485, 267488, 267502, 267981.

USNM 405206, 549439–549441.

<u>Centurio senex</u> (n = 35)

AMNH 99645, 175650–175651, 177419, 179989–179991, 180401, 183862, 208879, 214422, 243786–
243788, 256330, 256846, 265125.

USNM 6322, 310237–310239, 310242, 310245, 335392, 346821–346822, 346827, 346832, 346840, 503837, 511740–511741, 511855–511856, 511859.

<u>Chiroderma villosum</u> (n = 30)

AMNH 209542–209544, 209547, 209552, 209554, 209560–209564, 209576, 243926, 243929, 245326–245327, 262526–262532, 262534, 262539, 267190–267191, 267474–267476, 268533–268534, 268536.

<u>Ectophylla alba</u> (n = 16)

FMNH 137219–137221.

USNM 315563, 319426, 324926, 335310, 335321–335325, 336259–336262, 563298, 579079.

<u>Mesophylla macconelli</u> (n = 174)

AMNH 186433, 207067-8, 187223, 172125-6, 246226, 214368, 208073, 233740-49, 75255, 76254, 74100, 76095, 76565, 76567-71, 78856, 209578, 209581, 215025, 261078, 209577, 209579-209580, 26178-261679, 246626, 48273-74, 48269-72, 267560-267561, 267563-64, 267281, 267556-59, 267562, 268537, 268538-39, 268539, 248886-87, 262540-41, 262541, 67990, 71495, 71679, 71665, 71668, 71674, 71686.

FMNH 174721, 125813, 98030-33, 170247.

IAVH 5277, 5125, 3539.

ICN 17916, 11929.

INPA 1562, 1570, 2377, 4121, PEB 308, PEB 348, PEB 278-9, PEB 301, PEB 334, PEB 277, PEB 284, PEB 330, PEB 282, PEB 262, PEB 286, PEB 302, PEB 267, PEB 333 (field numbers).

UNIVALLE 11898-900, 12114, 11361, 11370, 11385, 11394, 4298, 4585, 4704, 7002, 10117.

USNM 269397, 309978, 315564, 331687-89, 361726, 362921-22, 364419, 387224, 393715, 405184, 405185-86, 405188-89, 408816, 408818-19, 408823-25, 408830, 408844, 408846-47, 408850, 408852-53, 440772, 460131-33, 483778-79, 499483-84, 530918, 530980-81, 548243-44, 549426-28, 560608-11, 560773, 566546-48, 574540, 575553, 579602, 582327, 582869.

Enchisthenes hartii (n = 30)

AMNH 126239, 206872, 214367, 233598–233599, 233791–233800.

USNM 310213–310217, 323538–323539, 370726–370727, 370729–370731, 483909–483910, 483919–483920, 562916–562917.

Phyllops falcatus (n = 80)

AMNH 41008, 143662, 176190, 213890–213891, 219701, 236690–236696, 238146–238147; USNM 113250, 143844, 181300, 300504, 300590–300595, 520534, 535313, 538317–538318, 538337–538345, 538374, 538376, 542273.

KU 151286, 151303-04, 151290-1, 151298-99, 151287-151288.

USNM 143844, 300504, 538318, 113250, 542273, 520534, 538337-45.

Platyrrhinus helleri (n = 34)

AMNH 207863, 207871–207872, 209511,209517, 230635, 246222–246223, 261070–261072, 261074–261075, 263616, 265119–265120, 266254, 267179–267182, 267552, 267554–267555, 267562.

USNM 315538–315540, 315542, 315544–315545, 544894–544895, 562896.

Pygoderma bilabiatum (n = 71)

AMNH 234286, 234289–234301, 246401, 246405, 246408, 248334, 248336–248339, 261758, 261761–261762, 261764.

CML2158, 2162, 4792, 4799, 1889.

FMNH 3191BDP, 3183BDP, 3261BDPunc, 3208-9BDP, 3258BDP, 3285BDP, 3257BDP, GTE 73, 3210BDP (field numbers).

MACNL 17997-98, 17039, 17999, 17040-2, 17038, 18000-1, 18481, 18883.

MVZ 144465-6, 185695. USNMH 542744, 542745-49, 105685.

UMMZ 125824, 125804-5, 124374, 125806, 125814, 125809, 37502, 148161, 460507, 542744, 542745–542748.

Sphaeronycteris toxophyllum (n = 153)

AMNH 21344–21345, 24379–24380, 76251, 92248, 194213, 209741, 235561, 261765, 262637, 265354.

USNM 35405, 35410, 122785, 143657, 168230, 241107, 370797–370801, 370805, 370839–370840, 370843–370847, 372391, 372393, 405663, 455936, 494533, 494538–494539, 494544–494550, 496843, 522053.

IAVH 701, 116, 2918, 5149.

ICN 499, 9521, 12750, 14616, 14617.

Stenoderma rufum (n = 13)

AMNH 208982–83.

USNM 239110, 522706-8, 580647.

KU 151321, 114009-10, 151320, 74029-31.

Sturnira lilium (n = 21)

AMNH 185320–21, 189893–94, 189946, 233541–42, 249096-97, 266203–7, 266228–266234, 267169.

USNM 502257–502259.

Uroderma bilobatum (n = 23)

AMNH 179994–5, 233184–5, 260196–7, 267172–8, 267465–70, 268564–5.

USNM 522357–8, 549406-7.

Vampyressa bidens (n =176)

AMNH 67997–67998, 71656, 76090, 208072, 214351, 233734–233737, 233785, 261625–261627, 261633, 261640.

(uncatal.): MAP 215.

FMNH 113643; 104755; 124982; 124996; 31074; 93581; 93558; 93564; 139531; 139532;139534-139536; 139538; 139540; 125897; 125898; 125899; 125934; 125962; 29176; 29177; 29178; 122139; 122881; 122882; 87071; 87072; 87075; 87076; 87081.

INPA 2708; 1031; 1095; 1381; 1524; 1525.

INPA (uncatal.): PEB 264; PEB 303; PEB 287; PEB 289; PEB 261.

MZUSP 28237; 12285; 20246; 20347; 20247-20249; 22830; 4373; 4399; 4406; 4414; 4416; 4419; 4436; 4475.

ROM 45277; 103425; 109260; 106592; 107053; 107153; 107163; 107174; 107204; 107306; 107453; 107333; 107451; 107384; 107447; 108792; 108518; 108686; 108715; 108822; 108639; 104742; 104759; 106616; 106718; 100339; 100964; 103506; 103425; 59895; 108143; 108174; 37296; 103043; 104551; 103994; 103995; 104065; 105134; 105162; 105169; 77376.

UNIVALLE 11902-11905.

USNM 361713–361714, 408573, 408578, 496590, 530997, 554778, 562584–562585, 579598).

Metavampyressa brocki (n = 18)

MZUSP 22683; 5942; 6979.

ROM 108850; 107227.

AMNH 268566; 268562; 266311; 267184; 267471.

ICN 14912;14913.

FMNH 87100; 89069.

USNM 549425

(uncatal.): MAP 037; VCT 830; 1396.

Metavampyressa nymphaea (n = 129)

AMNH 233189–233190, 235789–235790.

FMNH 114010-12;114012; 114013; 114014; 104844; 113329; 114028; 113577; 113589; 113592.

ICN 6207; 9399; 9400; 9401-9405; 9457; 12266; 16165.

USNM 304903, 305382, 305384, 309062, 309883–309889, 315555–315556, 318130, 379076, 483686–483687, 483693–483696, 520005–520006, 520009–520011, 579076.

ROM 94246; 108288; 104236.

UNIVALLE 2169; 2295; 2814; 5781-5784; 3656-3658; 3824 ; 3826-3828; 10166; 11271; 11296; 11300; 11301; 11304; 11305; 11311; 11312; 11338; 11346; 3715.

Vampyressa melissa (n = 17)

BMNH 26.5.3.4.

FMNH 114028, 114017; 174909.

MUSM 8914-8916.

AMNH 233769; 233761

USNM 548310; 319282-319285; 520851

IaVH 132.

<u>Vampyressa thyone</u> (n = 267)

AMNH 31501, 67986–67987, 71675, 71680, 141996–141997, 233191–233193, 238219, 256827, 262559, 266311, 267471–267472, 267185.

DZSJRP 14133.

FMNH 89137; 89138-89145; 133990; 89053-89067; 87097-87099; 87101-87107; 68458; 78689; 78690; 139560-139562; 139564; 125897; 125887; 113324; 113340; 113343; 113994-113996; 113603; 113576; 113579; 113593; 113633; 113649; 113635; 123151; 124098; 104758; 58259-58262; 120968; 120969; 127108-127111.

IAVH 864; 939; 941; 960; 983-984; 7541; 3583; 5123; 6708; 6731; 6752; 6729; 6759; 4351-4358; 6765; 7535; 4208; 4350; 246; 2078; 3470; 2043; 3300.

INPA 2364; 3887; 5013; 5006; 5012.

MUSM 3166; 3167; 354; 361; 10613; 323-325; 14059-14067; 12622; 12623.

MZUSP

ROM 104535; 104536; 108145; 62500; 63209; 84983; 104237-104239; 104322; 77380; 104453;

104544-104547; 104550; 104414; 104391.

UNIVALLE 11906; 3059; 11323; 11331; 10119; 10120; 10841; 7201; 11283; 11291; 4589; 4597; 5580-5583.

USNM 370525, 372143, 408571, 440660–440661, 440668, 483729–483730, 483734–483736, 496566, 496584, 496586–496587, 503630, 503633–503635, 534302–534303, 535095, 574639.

Vampyrodes caraccioli (n = 20)

AMNH 29431, 175642, 186381, 209518, 230649–230651, 230653–230655, 239254, 256828.

USNM 447012–447017, 519716–7, 519721, 579658.

Carolliinae:

Carollia brevicauda (n = 20)

AMNH 76801, 239901, 261421-27.

Rhinophylla pumilio (n =20)

AMNH 233523–5, 262421–3, 262468–9, 266171–2, 266186–7, 266189–94, 267158–60, 267162–64.

Appendix 2

Morphological matrix

Phyllostomus hastatus

```
00000-----00000000--0000-000000000000100001000--0-000000100010000--0100-
000000000000100000000000???0-000-003220001000000000000000000000---
00000000000000-0000000000000---------0000000000000000-000000100000-
000000000000000-?0000?0000000000000-0000-000000000000-
000000??????????0000000000000000000000000000000-00------------------------------
0?00
```

Rhinophylla_pumilio

```
11000-----01001200--1111101111002002100020000--0-1001001000010100--0002--
01000000001000000001000?-?0-000-001310001020010001000000000---
000001110010----10010011000000---------0000001100100010-200101001010-
0000001000111-0002100100000???0?000-00?0-000000000000-
000021??????????0110??????0??00010001-
?01101130310000000000?0000000000-00000000001?00
```

Carollia_brevicauda

```
10000-----01000000--0000-00022002002130010000--0-0001001000010100--0002--
0100000000000000001000?-?0-000-001310001020010001000000000---
000001110010----10010011000000---------0000001100100010-200101001010-
0000001000111-00021001002000001000-0000-000000000000-
```

```
000011000?0000000010?01100000000100000?0111113101-------------------------------
0?00
Sturnira_lilium
00000-----01101300--000111212010200210001100O--0-000100100011100--0122-
0010110000004-0000100000-10010010330-00122101000120011000010---
10110001011011-000000001000101---------1000000100100010-
20010030101100000001100111-0002000101020110010110000100000000000000-
{01}00120011???0??0?11?11111-00?0011000000121011310 1--------------------------------
0?00
Artibeus_cinereus
10002000201100120 0--0110-010100010001000230021 00-01201110000101-200120-
00101100010110000010000???10011000232100002101011110001000 10---
100140111100000-10?0?00100?011-----3000013010000100 0100-200100301011-
1010000000110111010000?1-0111100101100011-000000000000-
20011011??1????0?11???????0??0021111000???0101031010111000 0?1100100010
-100100001?2?00
Artibeus_concolor
11001-----01002100--01110000200??002110112000--0-011211100100000--0120-
1010110000011000001000???1001100023210010000100011200100020---
10114111120001-110?0?00100?011-----3000014010010000 0100-200100301010-
00100001001001120100 0?0100111001011000 11-000000000000-
```

201010????1??100?11???????0??002111100???11102?1?----------?---------------------

0?00

Artibeus_jamaicensis

100020002001001000--0110-01012001002110012000--0-011011100000000--0100-

1010110000011000001000???1001100013210000000100012000010020---

10114000120001-11000000101?011-----300001401000010001010210000311011-

101000110{01}10011201000?0101112001010-0011-000000000000-

2010101?1???0????11?00110101?002111100012111032020001010210?1010010001

0100001110?2?00

Enchistenes

100020102001002000--0121022111001002100033000--0-000200100100000--0122--

010110000013100001000???1001100013110312200100111100001010---

{01}1121011110011-10000110101?111-----0---0101100000001100-100000301010-

101001010110011201000?01001110101100001-000000000000-

200130???????????110??????0??002111100?12111?????----------?---------------------

2?20

Platyrrhinus_helleri

110020100001002201000121020111001001120122002101101221100000101-

010100-1010110000012100001000???1000101013210010110100111001110010---

101041101200000-10011001000020-----0---0000100100101100-000000200103-

0010010211111-1212000?0112111101010-001{12}1110100110000-

201100????1???10?11??0?0010??001010110112101012{13}?0----00211?-------000-
111000000?2?00

Vampyrodes

1000201000010021010000020-20011011002110102002001001211100000101-010100-
10101100000121000010000???1001000033210010210100111000010010---
10104010120011-11001100100?110-----0---0000100100100100-000000200003-
0010010212101-1012010?1-10111101010-001{01}1000000000000-
000110?????????0?111??1???0??00101111011210121211----------?---------------------
0?10

Chiroderma_villosum

11001-----00003110--0121100022001000100113000--0-010010010101000--0110-
10111100000110000010001101001120013214100000100110201110020---
20114011114011-11000000000?121-----0---1040100001100000-010102201100-000-
301002121-200201011-11010111001011-0-111110100100-
020211??0?1??0?21110??????0??0021111001???012421?--------------------------------
0?00

Uroderma_bilobatum

100020100111002101011110-01011001000110122002101000201100000001-010100-
10101100000110000010000111001001011210013210101011000101010---
100041101130000-00000001000011-----30000130100101000100-000010201003-
100211001210011201000?0121110101010-0002-100100000000-

20011000??1?00?0?1100011010??001111111112101212310001011000?1110111110

-101110111?2{12}00

Ametrida

11210-----00213200--0121012120012000001133011--0-110000010111001--

012100011120112012010001012???112-1501552045003120112111111101102---

232300132111-21011012002?1320011-----0020100010011200-221200301010-

1011001000100112120000010111000101120000-110000000000-

20000012???????1?111??????0??002210111?1211111???--------------------------------

0?10

Ardops

01200-----20203200--?121012121000000110013011--0-110010110111000--

012110010120112013000001001???101-100031110310000100110011003031300--

0032001100000-1100?10010013110000----1021100011011200-020200301011-

1011010100100121120000010111010001100000-000000000000-

2001100130211100?11???????0??002210111???11?1?1?--------------------------------

0?20

Ariteus

01100-----10203200--?121012120011000110023011--0-010010110111001--

012110010120112013000001001???101-000031100310000000210000003031300--

0032001200000-1000010010013110000----0021100011011200-220200301011-

10110100001001211201001-01110101010-0010-000000000000-

20001001301111??11???????0??00221011?12111?1???------------------------------
0?20

Centurio

11300-----30213200--0121012120-12100002112111--2-010300011-------------1-0-
2011211201012100 3???111-001130204010210010201000101011 12---013311125111-
1100101000001312010-----00211000100111 00-221200301010-
1011000000100111010 0001-0111100101120012-110000000000-
20000212?01121??1111?0????10111-210111112101?1???------------------------------
0?10

Phyllops_falcatus

11100-----10213200--01210121220110001110 13011--0-010010110111001--
012100010120112013000001001???101-0300212003101001012110110 0211121---
0042001130000-0110012100013200 10-----0040100011011100-020200301011-
1011001000100112010000010111 1000010-0000-000000000000-
2001221100?121??11?0?11010??002{12}10111???11?1???------------------------------
-0?20

Pygoderma

11210-----20213200--01210121220020101101 13011--0-010300010111001--
012100010120112012010111102???101-000111200009210201012000003031001--
020310141001-0000001000001 3101001----0021100011011200-020200301011-
1011010000100130021100 1-02011001010-0210-000000000000-

20022012??1????2?11???????0??002210111????11?1???--------------------------------

0?10

<u>Sphaeronycteris</u>

11300-----30212200--0121011021002000002113011--0-010300010110101--0121001-

0-20112012011021003???112-140145204507302011211011111011112---

222300130101-210110120000132001 1-----0020100011011200-021200301010-

1011010000100132110000010111200101120000-000000000000-

20011012??2??1?1?11???????0??102210111???01?1???--------------------------------

0?20

<u>Stenoderma</u>

11200-----20212200--0121012120001000111113011--0-010011010111000--0120-

0010120112013000001001???10011002442144003020000100110020313 01--

003210010001-201000100100132000 01----0040100011011200-221200301010-

1011010100100132110000010111010101 0-0000-000000000000-

200110???????????111??????0??002{12}10111????11?1???-------------------------------

-0?20

<u>Ectophylla</u>

10000-----11--4210--1000-00010002000120032003--11110000100010002--0120-001-

112002012000001000???10011100132103162100011110001010 00---

001002100?0011-10010000100113100 10-----015010012010111110101002011 10-

0110201100111-40?211101-04010111010-01-

1?1111110011110120211?13??01000?11???????0??002010100?12101?1?311----

00111?-------000-1011000001 1?20

Mesophylla_macconnelli

10001-----01002210--0000-0002000100011003200З--1111001110001000 2--1110-

0010111002012000001000???100012022321011021011201110010102 0---

11101111030011-010?10000000020-----11110000100100001001000000 1211110-

0000101000121-4002110?1-0301{01}111010-

001210{01}11100001102011211011100201?0111??????0??000011100????0111?31

0101100211?1001000000-10000100101?00

Vampyriscus_bidens

10002010010100{12}111011110-000210010001000220 02{01}11101101210000101-

110100-10111100010121000010 00???10001010232122122101120111001100 20---

20124111114001-010011001000020-----2111001011--11-00000-

0100022111010000211000 2111-120211001-111101111111021111101121-

010010202000?210?201?111???????0??001111100?????1?1???????????????????

????????????????2?00

Metavampyressa_brocki

100021111101001101121110-010210??0201001320020111011211100001 01-110100-

1010110001012000001000???10001202332122112101120111011100 20---

201141111230000-10011001000020-----2111004010{01}101000000-

01000{12}2{01}110101102110002101-120211001-11{01}10111110-01-

11110100100100-

0202000?2101200?111???????0??001111100?????1?1????????????????????????
???????????2?00

Vampyressa_melissa

11002101112000310 0--01011221201??000100?13002001101001110000101-110120-
1010110000013000001000???101-1000130-10142101000120011 01000---
0011101111300 1-000110001000110-----
300001301001010001010000 00{01}10100210010200000101-220001001-
1101011201120012-
10011000111021212210111 01?1??111???????0??000111100?????1?1???????????
????????????????????????2?1

Metavampyressa_nymphaea

1000211111010021111201 10-010210??02010002200201110110111 0000101-110100-
10101100010120000010 00???1000120223213 2111{01}10{01}2111100110020---
20111010110001-010111000000020-----211100{04}0100100{01}00000-
110002211101011021100031 21-120211001-11011111010-01-1?1{01}0112000101-
02121001110120 12?110??????0??0011111001????1?12?11111010211?-------
0010100000100?2010

Vampyressa_pusilla

100020002120002200--0111102120011000100033002{01}01101001110000101-
010100-10101100000120000010 00???101-1010121{01}1015210112?12100101000---
111110101230101-1001000100012{01}-----
21110040100101100 00{01}02000001{01}10021001020 0000101-220211001-

11000112011201-

2111111000111020212110?2?0020???11???????0??000111100????01?1?310----

00011?-------0011100000000?2?10

Vampyressa_thyone

10002000210100{12}210--0010-0102001100010003300 2{01}11111001110000101-

011120-10101100010120000 01000???101-

12001{23}{01}{01}101{34}2101{01}2{01}11100101000---10101010113001-

01011000100012{01}-----

3{01}1{012}004010010100000{01}020000{01}{12}1100210{01}10200000101-

210211001-?1000112011201-

{12}1{01}011121011{01}020212210121002 01??1110010010??000111100112101 0123

11010000211?-------0010100000000?2?10

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