

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION OF THE HIGHER CATEGORIES OF THE NEW WORLD BAT FAMILY PHYLLOSTOMIDAE

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Abstract.—A new classification of the higher taxonomic levels within the New World bat family Phyllostomidae is presented which designates evolutionary relationships, provides a phylogenetic framework upon which modifications can be made as new comparative data are produced, and resolves certain obvious unnatural taxa that exist in the traditional classification. This new classification is a synthesis of classical morphological, chromosomal, and biochemical data. Within the family three subfamilies, the Desmodontinae, Phyllostominae, and Vampyrinae are recognized. The Desmodontinae includes the three genera of vampires, the Vampyrinae includes *Vampyrum*, *Trachops*, and *Chrotopterus*, and the Phyllostominae contains three tribes, the Phyllostomini (including *Phyllostomus*, *Tonatia*, *Mimon*, *Lonchorhina*, and *Macrophyllum*), the Glossophagini (including genera of the previously recognized Glossophaginae and Brachyphyllinae), and Stenodermatini (including genera of the previously recognized Stenodermatinae and Carollinae). Two genera (*Macrotus* and *Micronycteris*), do not share synapomorphies with any of these subfamilies, but have retained a large number of plesiomorphic features and are placed as *incertae sedis*. [Classification; phylogenetic reconstruction; Phyllostomidae.]

"A classification, in contradistinction to an identification scheme, functions as a biological theory (with all the explanatory, predictive, and heuristic properties of a theory)" Mayr (1974:94). Such a theory should reflect evolutionary relationships, and be of use for comparative biological studies. Therefore, the first step toward developing a biological classification is the derivation of a phylogenetic hypothesis which reflects the evolutionary relationships among the organisms to be classified. The object, then, of any classification is to maximize congruence among independent character sets to the degree to which they parallel phylogenetic patterns (Farris, 1971; Mickevich and Johnson, 1976; Mickevich, 1978; Arnold et al., 1982; Hillis, 1987).

The New World leaf-nosed bat family Phyllostomidae represents an ideal group upon which to apply the above concepts. This family of mammals is taxonomically diverse and the current classification is un-

natural in that it does not reflect phylogenetic relationships as defined by synapomorphies (Hood and Smith, 1982; Honeycutt and Sarich, 1987a). In addition, four independent character sets including chromosomes, protein electrophoresis, immunology, and morphology exist for this family. These data and the resultant proposed phylogenies produced from each character set provide an opportunity to both propose a new classification for the Phyllostomidae and evaluate taxonomic congruence among multiple data sets. Conflicts and compromises presented by multiple data sets are becoming important as more systematic studies incorporate characters as diverse as molecules and morphology (Hillis, 1987; Patterson, 1987). Our study on phyllostomid bats provides a practical example of problems and compromises encountered in developing an estimate of phylogenetic relatedness when using multiple character sets.

HISTORICAL PERSPECTIVE

The New World leaf-nosed bats (family Phyllostomidae) includes about 46 genera

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TABLE 1. Higher taxonomic classifications of phyllostomid bats.¹

Miller (1907)	Smith (1972, 1976)
Fam. Phyllostomidae	Fam. Mormoopidae
Chilonycterinae ²	Fam. Phyllostomatidae
Phyllostomidae	Phyllostomatinae
Glossophaginae	Glossophaginae
Hemiderminae ³	Carolliinae
Sturnirinae	Stenodermatinae ⁵
Stenoderminae ⁴	Phyllonycterinae ⁴
Phyllonycterinae	Desmodontinae
Fam. Desmodontidae	
Koopman and Cockrum (1967); and Hall (1981)	Griffiths (1982)
Fam. Phyllostomidae	Fam. Mormoopidae
Chilonycterinae ²	Fam. Phyllostomatidae
Phyllostomatinae	Phyllostominae
Glossophaginae	Glossophaginae (in part)
Carolliinae	Lonchophyllinae (new)
Sturnirinae	Brachyphyllinae ⁴
Stenodermatinae ⁴	Phyllonycterinae
Phyllonycterinae	Carolliinae
Fam. Desmodontidae	Stenodermatinae ⁵
	Desmodontinae

¹ Handley (1980) has discussed the proper formation of family-group names in the Chiroptera.

² Now known as the family Mormoopidae (see Smith, 1972).

³ Later known as the subfamily Carolliinae.

⁴ Includes *Brachyphylla*. See Silva Taboada and Pine (1969) and Baker (1979) for discussion.

⁵ Includes Sturnirinae (see Baker, 1967).

and 140 species (Koopman, 1984). The family has a long history of nomenclatural problems, particularly with respect to taxonomic groupings below the familial level (Smith and Hood, 1984). Within the order Chiroptera, phyllostomids have been aligned with various families, but recent workers have associated the Phyllostomidae with the Neotropical families Noctilionidae and Mormoopidae and the New Zealand bat family Mystacinidae (Walton and Walton, 1968; Smith, 1972; Patton and Baker, 1978; Arnold et al., 1982; Hood and Smith, 1982; Pierson et al., 1986). Reviews of the higher systematic relationships of bats exist in Smith (1976, 1980), Hill (1974), Hill and Smith (1984:33–39) and Koopman (1984).

The classification of the Phyllostomidae historically has followed that presented by Miller (1907) (Table 1). This classification provided a detailed review of all earlier classifications (Peters, 1865; Gray, 1866; Dobson, 1875; Winge, 1892), and with little modification (Simpson, 1945), remained unchanged for more than 60 years (Baker, 1967; Forman et al., 1968; Smith, 1972; for a review see Smith and Hood 1984). The

primary changes are placing the Sturnirinae in the taxonomically diverse subfamily Stenodermatinae (Baker, 1967), including the vampires as a subfamily within the Phyllostomidae (Forman et al., 1968), and moving the mormoopids (=Miller's Chilonycterinae) to familial status (Smith, 1972).

The genealogy of the New World nectar-feeding bats (subfamily Glossophaginae) has proved controversial. Baker (1967) suggested that the group was polyphyletic, a suggestion tested by several workers. Study of glossophagine monophyly has been further complicated by the consideration of the close phylogenetic relationship of some glossophagine genera to the Brachyphyllinae (including the genera *Brachyphylla*, *Erophylla*, and *Phyllonycteris*: Silva Taboada and Pine, 1969; Baker, 1979; Baker et al., 1981; Honeycutt, 1981). Griffiths (1982) proposed a new subfamily, the Lonchophyllinae, which includes three genera from the traditionally recognized Glossophaginae. He also restricted the Brachyphyllinae as monogeneric and included only two genera in the Phyllonycterinae. Study of brachyphylline/glossophagine

phylogenetic relationships has stimulated considerable debate (Haiduk and Baker, 1982, 1984; Griffiths, 1983; Warner, 1983; Smith and Hood, 1984).

Several workers have suggested that the subfamily Phyllostominae is paraphyletic (Walton and Walton, 1968; Slaughter, 1970; Smith, 1972, 1976; Hood and Smith, 1982; Honeycutt and Sarich, 1987a). Paraphyly is apparent for the Phyllostominae, because two lineages (*Macrotus* group and *Phyllostomus* group) are sister to different phyllostomid subfamilies rather than to each other (see the traditional classification in Table 1).

PHYLOGENETIC RELATIONSHIPS

The monophyly of phyllostomid bats has been supported by a large body of evidence including morphology (Walton and Walton, 1968; Smith, 1972; Hood and Smith, 1982), G-banded chromosomes (Patton and Baker, 1978; Baker, 1979), and biochemical data (Honeycutt et al., 1981; Arnold et al., 1982, 1983; Honeycutt and Sarich, 1987a). However, the phylogenetic relationships of taxa within the family have not been clearly established.

Hood and Smith (1982) presented an hypothesis of phylogenetic relationships within the Phyllostomidae based on a cladistic analysis of female reproductive histomorphology using outgroup comparison (Fig. 1A). Prior to this study, several authors had suggested relationships for various phyllostomid groups, but few of these were presented in a phylogenetic framework. Nonetheless, these earlier studies did provide comparative data from a variety of anatomical systems, including sperm morphology (Forman, 1968; Forman et al., 1968; Forman and Genoways, 1979), anatomy and histology of the alimentary tract (Forman, 1972, 1973; Phillips et al., 1977; Forman et al., 1979), brain morphology (McDaniel, 1976), dentition (Slaughter, 1970; Phillips, 1971), and postcranial osteology (Walton and Walton, 1968; Smith, 1972).

Recent studies on phyllostomid relationships have utilized other approaches including immunological distance data (Ba-

ker et al., 1981; Honeycutt, 1981; Honeycutt et al., 1981; Arnold et al., 1982; Honeycutt and Sarich, 1987a, b), protein electrophoretic data (Straney et al., 1979; Straney, 1981; Baker et al., 1981, 1988a; Honeycutt et al., 1981; Arnold et al., 1983; Koop and Baker, 1983), and data based on G-banded chromosomes (Patton and Baker, 1978; Baker and Bass, 1979; Baker et al., 1979, 1982; Haiduk and Baker, 1982). Figures 1B and 1C present the results of these studies, which are discussed in greater detail below.

Desmodontine (vampire bats) adaptations to blood feeding have led some taxonomists to advocate familial status for them. Although phylogenetic analyses of structures and functions involved in this specialized feeding habit indicate that vampires possess many autapomorphies, data from such unrelated areas as ectoparasite/host relationships (Machado-Allison, 1967), sperm morphology, serology and karyology (Forman et al., 1968) and female reproductive histomorphology (Hood and Smith, 1982) document that vampire bats share derived character states with other phyllostomids and are members of that larger monophyletic group.

The basal phylogenetic position of desmodontines predicted by morphological data (Hood and Smith, 1982) is supported by the immunological distance data (Honeycutt and Sarich, 1987a). However, the immunological association of *Macrotus* with the desmodontines is not supported by either chromosomes or morphology. This association is probably the result of equally divergent albumins in *Macrotus* and vampire bats relative to other phyllostomid albumins (Honeycutt, 1981; Honeycutt et al., 1981; Honeycutt and Sarich, 1987a). Data from G-banded chromosomes are incongruent with the immunological and morphological data in that desmodontines also share synapomorphic rearrangements (Baker et al., 1988b) with other phyllostomid subfamilies (exclusive of the genera *Macrotus* and *Micronycteris*, Fig. 1). The incongruence in the phylogenetic position of desmodontines as illustrated in the morphological and chromosomal cladograms suggests homoplastic events or misiden-

tification of the primitive or derived character states.

The morphological, chromosomal and immunological data demonstrate that the Phyllostominae is paraphyletic and consists of at least two phylogenetically distinct groups (Fig. 1A-C). The *Macrotus*-group includes taxa (*Macrotus*, *Micronycteris*, *Trachops*, *Chrotopterus*, *Vampyrum*) that have retained primitive character states or exhibit autapomorphic character states (postcranial osteology, Walton and Walton, 1968; dentition, Slaughter, 1970; female reproductive histomorphology, Hood and Smith, 1982; G-band chromosomes, Patton and Baker, 1978; protein electrophoresis, Straney et al., 1979; Arnold et al., 1983; immunology, Honeycutt and Sarich, 1987a). Although these taxa are distinguished from other members of the Phyllostominae (see below), we note that no known morphological or chromosomal synapomorphies support the monophyly of *Macrotus*, *Micronycteris*, *Trachops*, *Chrotopterus* and *Vampyrum*. The immunological data (Honeycutt and Sarich, 1987a) provide strong evidence that some taxa within the group are monophyletic (e.g., *Trachops-Chrotopterus-Vampyrum*). The relationships of *Macrotus* and *Micronycteris* to each other and to other members of the family cannot be determined with available data (Honeycutt and Sarich, 1987a).

The *Phyllostomus*-group includes the genera *Phyllostomus* (including *Phylloderma*, Baker et al., 1988a), *Lonchorhina*, *Tonatia*, and *Mimon* (post-cranial osteology, Walton and Walton, 1968; female reproductive histomorphology, Hood and Smith, 1982; G-band chromosomes, Patton and Baker, 1978; protein electrophoresis, Straney et al., 1979; Arnold et al., 1983; Baker et al., 1988b; immunology, Honeycutt and Sarich, 1987a). The monophyly of this group is supported by chromosomal and immunological data. *Macrophyllum* shares relatively primitive uterine character states with members of the *Macrotus*-group, whereas this taxon is immunologically nearest to members of the *Phyllostomus*-group. This suggests that *Macrophyllum* is the sister-group of the *Phyllostomus*-group with the

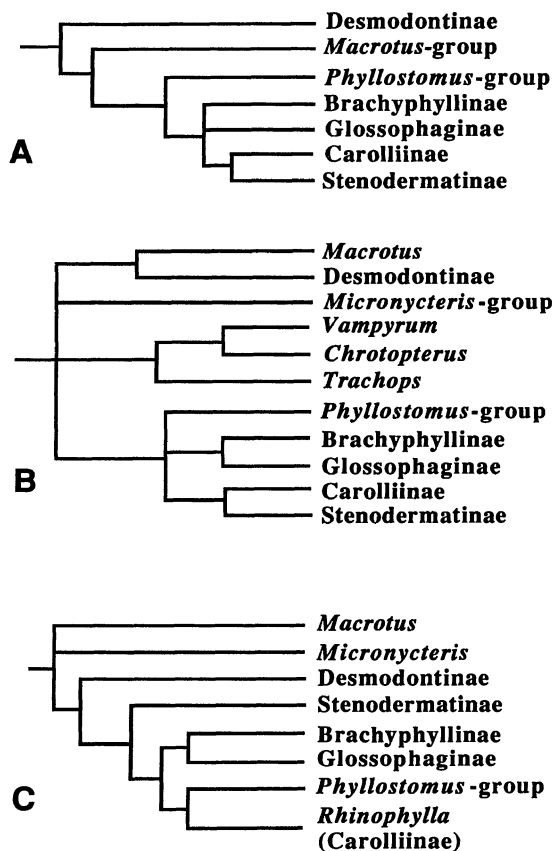


FIG. 1. Phylogenetic relationships among phyllostomid bats. A, female reproductive morphology; B, immunological distance data; C, G-band chromosomal data. See Table 3 for references on which branching order is based.

Macrotus-group sister to the other two lineages.

The *Phyllostomus*-group is part of a clade consisting of the brachyphyllines, glossophagines, carollines, and stenodermatines (Fig. 1A-C). Although the branching patterns within this clade are not entirely concordant, certain patterns are corroborated.

The relationships of brachyphyllines and glossophagines have been extensively studied. Immunological data support a sister-group relationship for these taxa (Baker et al., 1981; Honeycutt, 1981; Honeycutt and Sarich, 1987a). Other data, including protein electrophoretic studies (Baker et al., 1981); chromosomal banding studies (Haiduk and Baker, 1982); studies of the female

TABLE 2. Revised classification of the New World bat family Phyllostomidae.

Family Phyllostomidae
Genera of uncertain position
<i>Macrotus, incertae sedis</i>
<i>Micronycteris, incertae sedis</i>
(All genera <i>Sedis mutabilis</i>)
Subfamily Desmodontinae
(All genera <i>Sedis mutabilis</i>)
<i>Desmodus</i>
<i>Diaemus</i>
<i>Diphylla</i>
Subfamily Vampyrinae
(All genera <i>Sedis mutabilis</i>)
<i>Vampyrum</i>
<i>Trachops</i>
<i>Chrotopterus</i>
Subfamily Phyllostominae
(All tribes <i>Sedis mutabilis</i>)
Tribe Phyllostomini
(All genera <i>Sedis mutabilis</i>)
<i>Phyllostomus</i> ¹
<i>Tonatia</i>
<i>Mimon</i>
<i>Lonchorhina</i>
<i>Macrophyllum</i>
Tribe Glossophagini
(All genera <i>Sedis mutabilis</i>)
<i>Glossophaga</i>
<i>Monophyllus</i>
<i>Leptonycteris</i>
<i>Lonchophylla</i>
<i>Lionycteris</i>
<i>Scleronycteris</i>
<i>Lichonycteris</i>
<i>Hylonycteris</i>
<i>Choeromiscus</i>
<i>Choeronycteris</i>
<i>Musonycteris</i>
<i>Platalina</i>
<i>Brachyphylla</i>
<i>Erophylla</i>
<i>Phyllonycteris</i>
Tribe Stenodermatini
(All genera <i>Sedis mutabilis</i>)
<i>Carollia</i>
<i>Rhinophylla</i>
<i>Sturnira</i>
<i>Uroderma</i>
<i>Vampyrops</i>
<i>Vampyrodes</i>
<i>Vampyressa</i> ²
<i>Chiroderma</i>
<i>Ectophylla</i>
<i>Artibeus</i>
<i>Dermanura</i> ³
<i>Ardops</i>
<i>Phyllops</i>
<i>Ariteus</i>
<i>Stenoderma</i>
<i>Pygoderma</i>
<i>Ametrida</i>

TABLE 2. Continued.

Sphaeronycteris
Centurio

¹ Includes *Phylloderma* (Baker et al., 1988a).² Includes *Mesophylla* (Owen, 1987).³ Includes *Enchisthenes* (Owen, 1987).

reproductive tract (Hood and Smith, 1982) and anatomical studies of the lingual and hyoid regions (Griffiths, 1982) are either consistent with or do not contradict the relationships inferred from immunological data. The one area where the data are problematical involves the genera *Lonchophylla*, *Lionycteris*, and *Platalina*, that Griffiths (1982), considering the anatomy of the tongue and hyoid region, proposed as a separate subfamily. Although the immunological distance data indicate that *Lonchophylla* is more distant from the remainder of the Glossophaginae than are the other genera (Baker et al., 1981), this genus is more closely aligned with glossophagine and brachyphylline genera than to other phyllostomid genera. Reciprocal immunological comparisons of *Lonchophylla* to the glossophagines and brachyphyllines would clarify the placement of this taxon. Nevertheless it is clear that the nominate Glossophaginae, Phyllonycterinae and Brachyphyllinae share a unique common ancestor. The placement of *Lonchophylla*, *Lionycteris*, and *Platalina* outside of this clade would require homoplastic events in both uterine and lingual morphology.

Early studies of phyllostomids did not resolve the relationship of carolliines and stenodermatines to other phyllostomid subfamilies. However, phylogenetic analysis of female reproductive histomorphology (Hood and Smith, 1982) and immunology (Honeycutt and Sarich, 1987a) provided strong evidence for a sister-group relationship of these two taxa. Phylogenetic studies of qualitative and functional variation in external morphology, cranial, and postcranial osteology also suggest a sister-group relationship between the stenodermatines and carolliines (Owen, 1987).

Chromosomal data are inconclusive be-

TABLE 3. List of synapomorphies and distance data used as evidence for the proposed new classification of the phyllostomid bats. Morph. = female reproductive morphology; Chrom. = chromosomal banding data; Immun. = albumin immunological data (AID).

Family Phyllostomidae

- Morph.: restriction of oviductal folds to the extramural oviduct.¹
 Chrom.: *Macrotus* has the primitive karyotype for the family.^{2,3}
 Immun.: phyllostomids are each others' closest relatives and are 48 AID units from outgroups (mormoopids and noctilionids).^{4,5}

Subfamily Desmondontinae

- Morph.: desmodontines share the family oviductal synapomorphy.¹
 Chrom.: at least seven unique chromosomal rearrangements unite the three genera of vampire bats.^{6,7}
 Immun.: desmodontines are each others' closest relatives and are 45 AID units from *Macrotus* and an additional 16 AID units from other phyllostomids.^{5,8}

Subfamily Vampyrinae

- Morph.: female reproductive features are plesiomorphic at this level.
 Chrom.: G-banded chromosomes are either plesiomorphic, or are highly autapomorphic in *Vampyrum* and *Chrotopterus*.^{3,9} G-bands for *Trachops* are inconclusive because of poor quality.⁹
 Immun.: members of this clade are each others' closest relative; *Trachops* is associated with the *Vampyrum*-lineage by an internode distance of 3 AID units. The next closest taxon, *Micronycteris*, 11.5 units distant.⁵

Subfamily Phyllostominae

- Morph.: external uterine anatomy fused and internal uterine anatomy fused.¹
 Chrom.: three chromosomal rearrangements tentatively identified as the 17/3, 21/12 and 22/13 are found in some members of each tribe.⁹ In other species the karyotypes are highly autapomorphic.
 Immun.: members of this clade are each others' closest relatives and are 6.5 AID units from a common ancestor with other members of the family. The Vampyrinae are 1 AID unit from this ancestor, whereas desmodontines and *Macrotus* have an internode distance of 16 units from the ancestor.⁵

Tribe Phyllostomini

- Morph.: female reproductive features are plesiomorphic for the subfamily at this level.¹
 Chrom.: the G-band chromosomes are uninformative for this clade.
 Immun.: members of this clade are each others' closest relatives and are 8.5 AID units from a common ancestor to other members of the subfamily. Within the tribe, *Phyllostomus*, *Tonatia*, and *Mimon* are closely associated, whereas *Lonchorhina* and *Macrophyllum* are more distant.^{5,10}

Tribe Glossophagini

- Morph.: relationship of the oviduct to the uterus is derived in the Glossophagini and Stenodermatini.
 Chrom.: at least seven rearrangements with the exception of *Lonchophylla* and *Lionycteris*.^{11,12}
 Immun.: glossophagines and brachyphyllines are each others' closest relatives, with the possible exception of *Lonchophylla* and *Lionycteris*.¹³ Comparisons by Honeycutt and Sarich (1987a) reveal that the tribe is 1.2 AID units from a common ancestor with other members of the subfamily.

Tribe Stenodermatini

- Morph.: modified placement of the ovarian ligament.¹ See also Glossophagini above.
 Chrom.: no chromosomal synapomorphies unite *Carollia* with the other members of the Stenodermatini and *Rhinophylla* appears best placed within the Phyllostomini,¹⁴ the remainder of the Stenodermatini are united by six rearrangements,^{15,16} or are highly autapomorphic.¹⁶
 Immun.: stenodermatines and carolliines are each others' closest relatives and are 7 AID units from a common ancestor with other members of the subfamily.⁵

¹ Hood and Smith (1982).

² Patton and Baker (1978).

³ Baker (1979).

⁴ Arnold et al. (1982).

⁵ Honeycutt and Sarich (1987a).

⁶ Bass (1977).

⁷ Baker et al. (1988b).

⁸ Honeycutt et al. (1981).

⁹ Baker (unpublished data).

¹⁰ Honeycutt and Sarich (1987b).

¹¹ Haiduk and Baker (1982).

¹² Baker and Bass (1979).

¹³ Baker et al. (1981).

¹⁴ Baker et al. (1987).

¹⁵ Baker et al. (1979).

¹⁶ Johnson (1979).

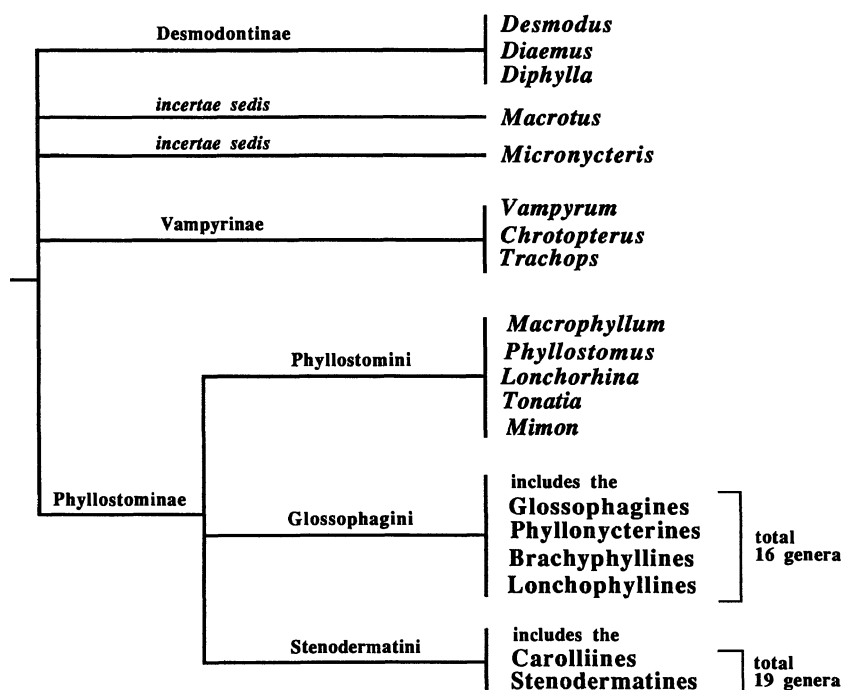


FIG. 2. Consensus cladogram depicting proposed phylogenetic relationships. Name above branch length is the taxonomic designation accorded in this study to the taxa composing that branch. Names to the right of each branch are either the genera or the previous higher taxonomic categories composing the new taxon. Table 3 contains the references and summary of data on which this figure is based.

cause at the current level of resolution of G-bands, the chromosomes of *Carollia* cannot be related to those of any other phyllostomid. The other carolliine genus, *Rhinophylla*, has undergone considerable chromosomal evolution but shares at least one and in some cases as many as four chromosomal synapomorphies with members of a clade containing the *Phyllostomus*-group, the Glossophaginae, the Stenodermatinae and the Desmodontinae (Baker et al., 1987) (Fig. 1C).

A REVISED CLASSIFICATION

We propose a revised classification that reflects the combined evidence from the morphological, immunological and chromosomal studies. Our new classification is shown in Table 2 (see also Fig. 2), and a list of synapomorphies diagnosing branching patterns is presented in Table 3.

The cladogram (Fig. 2) from which our classification is derived is not based on strict

or Adam's consensus. As noted by Miyamoto (1985), a consensus approach minimizes the resolving power associated with multiple data sets. Therefore, our classification maximizes resolution in the following manner: 1) In cases where all three data sets disagree, the taxon involved is placed in the phylogeny as *incertae sedis* (Wiley, 1981) or in a position within the phylogeny that is consistent with all three data sets; 2) *sedis mutabilis* is used to define taxa of unclear phylogenetic position (Wiley, 1981); 3) If data sets provide no resolution of a particular branching pattern, they are not considered as contradictory to a data set that provides resolution; 4) When two data sets support a particular branching pattern contrary to the third data set, the relationships depicted by the majority of data sets are included in the classification.

Within the New World leaf-nosed bats there are three major clades that are identified by synapomorphies (either morphological or chromosomal) or immunological

distance data. These are 1) the vampire bats (*Desmodus*, *Diphylla*, and *Diaemus*), 2) a clade that includes part of the old Phyllostominae (*Phyllostomus*, *Tonatia*, *Mimon*, *Lonchorhina*, and *Macrophyllum*), the Stenodermatinae, the Carollinae, and the Glossophaginae (including the Brachyphyllinae), and 3) a clade consisting of *Vampyrum*, *Trachops*, and *Chrotopterus*. We recognize these three clades as subfamilies.

A classic example of the adherence to magnitude of change as the primary prerequisite for taxonomic rank can be seen in Miller's (1907) revision of the families and genera of bats. Miller states (1907:177) "The Desmodontidae are somewhat closely related to the Phyllostomidae, as shown by the structure of the palate, wings and shoulder girdle, but their modification for strictly sanguivorous habits is so extreme that it seems quite unnatural to retain them in the same family." As suggested in this paper, the continued inclusion of vampire bats in a separate family Desmodontidae as proposed by two recent texts (Hall, 1981; Vaughan, 1986) is inconsistent with the morphological, immunological, and chromosomal data. All three data sets provide evidence for monophyly of the Phyllostomidae including the vampire bats. These three data sets, however, do differ in the placement of vampire bats within the family. Both immunology and morphology are congruent in that they suggest a more basal phylogenetic position of vampire bats relative to the other phyllostomid lineages. Chromosomal data indicate that the vampires shared a common ancestry with the Phyllostominae after diverging from the two genera (*Micronycteris* and *Macrotus*) that are *incertae sedis*. No chromosomal data are available from the Vampirinae. Nevertheless, in our classification, the vampires are recognized as a subfamily, Desmodontinae, which is the appropriate phylogenetic position based on the three character sets.

Our revised classification departs from the traditional view by the elimination of the paraphyletic arrangement of the subfamily Phyllostominae. The phyllostomines have been a "wastebasket" taxon with all forms united primarily by ple-

siomorphies even though at least two groups have been informally recognized for some time. As described in the previous section, several phyllostomine genera have synapomorphies that link them with the subfamilies Glossophaginae, Stenodermatinae, and Carollinae. Therefore, we recognize three tribes, the Phyllostomini, Glossophagini, and Stenodermatini within the revised subfamily Phyllostominae. The tribe Phyllostomini, which includes six genera of the *Phyllostomus* group, is recognized on the basis of immunological distance data, whereas morphology and chromosomes are uninformative. The tribe Glossophagini contains genera of the previously recognized Glossophaginae and Brachyphyllinae. The monophyly of this tribe is supported by lingual morphology, chromosomes, and immunology. The tribe Stenodermatini includes genera from the previously recognized subfamilies Carollinae and Stenodermatinae. The monophyly of all members of this tribe is supported by morphology and immunology, but is contradicted by the chromosomal data, which would place one of the two genera (*Rhinophylla*, Baker et al., 1987) of the Carollinae outside this tribe. Chromosomal data reinforce the monophyly of the remainder of this tribe.

The immunological data support a monophyletic group consisting of *Vampyrum*, *Trachops*, and *Chrotopterus*. Chromosomes and morphology do not contradict this alignment, and therefore, this clade is recognized as the subfamily Vampirinae.

Although two genera, *Macrotus* and *Micronycteris*, have synapomorphies identifying them as members of the Phyllostomidae, no synapomorphies document that they share a specific sister-group relationship with either the Desmodontinae, Phyllostominae, or Vampirinae. We choose to designate these genera as *incertae sedis* within our revised classification. Assigning the two genera to a single subfamily not defined by synapomorphies, or to separate subfamilies serves little purpose, and contradicts the goals of this revision. Our classification thusly brings into focus the

need to resolve the evolutionary affinities of these two genera.

Our study reveals the value of multiple data sets in phylogeny reconstruction. In several cases, phylogenetic resolution was maximized because some data sets provided phylogenetic information not contained or contradicted by other data sets. Overall, the level of congruence among the chromosomal, immunological, and morphological data sets was high. There were conflicts, however, among these data sets, and a compromise had to be reached with respect to deriving a classification. Thus, the resultant phylogenetic tree in Figure 2 is not a strict consensus tree, but rather one which depicts phylogenetic relationships in a manner most consistent with all characters used in this study. This tree provides the necessary framework upon which to base a biological classification that should allow for more accurate comparative studies.

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