# PHYLOGENY OF PHYLLOSTOMID BATS (MAMMALIA: CHIROPTERA): DATA FROM DIVERSE MORPHOLOGICAL SYSTEMS, SEX CHROMOSOMES, AND RESTRICTION SITES

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## ABSTRACT

Phyllostomidae is a large (> 140 species), diverse clade of Neotropical bats. Different species in this family feed on blood, insects, vertebrates, nectar, pollen, and fruits. We investigated phylogenetic relationships among all genera of phyllostomid bats and tested monophyly of several genera (e.g., *Micronycteris*, *Mimon*, *Artibeus*, *Vampyressa*) using 150 morphological, karyological, and molecular characters. Results of parsimony analyses of these combined data indicate that all traditionally recognized phyllostomid subfamilies are monophyletic and that most taxa that share feeding specializations form clades. These results largely agree with studies that have used a taxonomic congruence approach to evaluate karyological, immunological, and limited sets of morphological characters, although our finding that Phyllostominae is monophyletic is novel. Our results indicate that several genera (*Micronycteris*, *Artibeus*, and *Vampyressa*) are not monophyletic. We propose a new classification for Phyllostomidae that better reflects hypothesized evolutionary relationships. Important features of this new classification include: (1) formal recognition of two clades that group nectarivorous and frugivorous subfamilies, respectively, (2) redefinition of Glossophaginae and recognition of two tribal-level taxa within that subfamily, (3) recognition of several tribal-level taxa in Phyllostominae, (4) formal recognition of two clades that have been colloquially referred to as ''short-faced'' and ''long-faced'' stenodermatines, (5) elevation of the subgenera of *Micronycteris* to generic rank, (6) recognition of *Mesophylla* as a junior synonym of *Ectophylla*, (7) recognition of *Enchisthenes* as a distinct genus, and (8) retention of *Dermanura* and *Koopmania* as subgenera of *Artibeus*. Although *Vampyressa* is not monophyletic in our tree, we recommend no nomenclatural change because we did not include all *Vampyressa* species in our study.

Comparisons of character and taxonomic congruence approaches indicate that character congruence provides improved resolution of relationships among phyllostomids. Many data sets are informative only at limited hierarchical levels or in certain portions of the phyllostomid tree. Although both chromosomal and immunological data provide additional support for several clades that we identified, these data sets are incongruent with many aspects of our phylogenetic results. These conflicts may be due to methodological constraints associated with the use of karyological and immunological data (e.g., problems with assessing homologies and distinguishing primitive from derived traits). Among other observations, we find that *Macrotus waterhousii*, which has been thought to have the primitive karyotype for the family, nests well within the phyllostomine clade. This suggests that results of previous analyses of chromosomal data may need to be reevaluated.

Mapping characters and behaviors on our phylogenetic tree provides a context for evaluating hypotheses of evolution in Phyllostomidae. Although previous studies of uterine evolution in phyllostomids and other mammals have generally supported the unidirectional progressive fusion hypothesis, our results indicate that intermediate stages of external uterine fusion are often derived relative to the fully simplex condition, and that reversals also occur with respect to internal uterine fusion. Uterine fusion therefore appears to be neither completely unidirectional nor progressive in Phyllostomidae.

Evolution of the vibrissae and noseleaf is similarly complex and homoplasy is common in these structures; however, many transformations in these systems diagnose clades of phyllostomids. Within Phyllostomidae, there is considerable derived reduction in numbers of vibrissae present in various vibrissal clusters. The phyllostomid noseleaf seems to have become a much more elaborate and complex structure over evolutionary time. Primitively within the family, the spear was short, the internarial region was flat, and the horseshoe was undifferentiated from the upper lip. Subsequently, within the various subfamilies, the spear became more elongate, the central rib and other internarial structures evolved, and the labial horseshoe became flaplike or cupped in some taxa.

Dietary evolution in phyllostomids appears somewhat more complex than previously thought. We find that most of the major dietary guilds (e.g., frugivory, sanguivory) are represented by a single large clade within Phyllostomidae, indicating that each feeding specialization evolved once. However, reversals do occur (e.g., loss of nectar- and pollen-feeding in many phyllostomines and stenodermatines), and some specializations may have evolved more than once (e.g., carnivory).

# INTRODUCTION

Of the 17 families of extant microchiropteran bats, Phyllostomidae is the largest family endemic to the New World, with 49 genera and more than 140 species (Koopman, 1993, Simmons, 1998). Feeding habits are unusually diverse in this family; dietary specializations include sanguivory (blood-feeding), insectivory, carnivory, omnivory, nectarivory, palynivory (pollen-feeding), and frugivory. Interest in the evolutionary origins of these feeding habits has motivated numerous studies of phyllostomid relationships. Data sets that have been applied to this problem include allozymes, chromosomal morphology, host-parasite associations, immunological distances, morphology, rDNA restriction sites, and mitochondrial DNA sequences (see table 1). Analyses of these data sets have produced a large number of competing hypotheses of phyllostomid relationships. Few attempts have been made to investigate congruence and explore conflicts among data sets; consequently, there are many disagreements concerning phyllostomid relationships at all taxonomic levels.

Historically, Phyllostomidae has been divided into as few as two and as many as eight subfamilies (see table 2). Koopman's (1993) classification, which recognized the largest number of subfamilial groupings proposed to date, included one subfamily of sanguivores (Desmodontinae), one of insectivores, carnivores, and omnivores (Phyllostominae), four of nectarivores and palynivores (Brachyphyllinae, Phyllonycterinae, Glossophaginae, and Lonchophyllinae), and two of frugivores (Carolliinae and Stenodermatinae). Monophyly of some of these subfamilies has been questioned. For example, many authors agree that Phyllostominae (sensu Koopman, 1993) is not monophyletic (e.g., Walton and Walton, 1968; Slaughter, 1970; Smith, 1972, 1976; Hood and Smith, 1982; Honeycutt and Sarich, 1987a; Baker et al., 1989). However, this consensus view has not been reflected in classifications because there is little agreement about how Phyllostominae should be subdivided. Considerable attention has been focused on the monophyly and relationships of the nectar-feeding subfamilies (e.g., Baker and Lopez, 1970; Forman, 1971; Phillips, 1971; Smith, 1976; Wilder, 1976; Gardner, 1977a; Baker and Bass, 1979; Baker et al., 1981a; Griffiths, 1982; Haiduk and Baker, 1982; Warner, 1983; Smith and Hood, 1984; Honeycutt and Sarich, 1987a; and Baker et al., 1989). Monophyly of several phyllostomid genera, including *Micronycteris*, *Mimon*, *Phyllostomus* (sensu Baker et al., 1988a) *Artibeus*, and *Vampyressa*, has also been questioned (Anderson, 1906; Miller, 1907; Straney et al., 1979; Honeycutt, 1981; Straney 1980; Koop and Baker, 1983; Owen, 1987, 1991; Baker et al., 1988a; Van Den Bussche, 1992; Van Den Bussche and Baker, 1993; Van Den Bussche et al., 1993, 1998; Simmons, 1996; Jassal and Simmons, 1996).

This study principally addresses phyllostomid relationships at and above the generic level. We examine phyllostomid relationships using characters of the integument, pelage, skull, dentition, postcranium, hyoid apparatus, tongue, digestive tract, urogenital tract, brain, sex chromosomes, and rDNA restriction sites. Previous studies that examined multiple data sets relied soley on taxonomic congruence, an approach that may have serious limitations when used as the only method of phylogenetic reconstruction (see Materials and Methods below). Here, we use taxonomic congruence to explore conflicts among data sets, but do not rely on this method to reconstruct phylogeny; instead, we employ character congruence ("total evidence") to resolve the branching pattern within the family and to test the monophyly of previously recognized clades. Our goal is to develop a robust, well-resolved phylogeny of phyllostomid genera that will serve as a framework for future studies of the biology and evolution of this unusually diverse group of bats.

TABLE 1
**Data Used in Previous Higher-Level Phylogenetic Studies of Phyllostomid Relationships**

| Study | Type of data | | | | |
|---|---|---|---|---|---|
| | Karyology[a] | Immunology[b] | Other molecular data | Host–parasite associations | Morphology[c] |
| Baker (1967, 1970, 1973, 1979) | X | | | | |
| Baker and Bass (1979) | X | | | | |
| Baker and Bleier (1971) | X | | | | |
| Baker and Hsu (1970) | X | | | | |
| Baker and Lopez (1970) | X | | | | |
| Baker et al. (1979) | X | | | | |
| Baker et al. (1981a) | | X | X[d] | | |
| Baker et al. (1982) | X | | | | |
| Baker et al. (1989) | X | X | | | X |
| Bass (1978) | X | | | | |
| Cadena and Baker (1976) | X | | | | |
| de la Torre (1961) | | | | | X |
| Forman et al. (1968) | X | X | | | X |
| Forman (1971, 1973) | | | | | X |
| Gardner (1977a) | X | | | | |
| Gerber (1968) | | X | | | |
| Gerber and Leone (1971) | | X | | | |
| Gimenez (1993) | | | | | X |
| Gimenez et al. (1996) | | | | | X |
| Greenbaum et al. (1975) | X | | | | |
| Griffiths (1982, 1983b, 1985) | | | | | X |
| Haiduk and Baker (1982) | X | | X[d] | | |
| Honeycutt (1981) | | X | | | |
| Honeycutt and Sarich (1987a) | X | X | X[d] | | X |
| Honeycutt et al. (1981) | | X | | | |
| Hood and Smith (1982, 1983) | | | | | X |
| Hsu et al. (1968) | X | | | | |
| Johnson (1979) | X | | | | |
| Lim (1993) | | | | | X |
| Machado-Allison (1967) | | | | X | |
| McDaniel (1976) | | | | | X |
| Owen (1987, 1991) | | | | | X |
| Patton and Baker (1978) | X | | | | |
| Phillips (1971) | | | | | X |
| Pierson (1986) | | X | | | |
| Savage (1951) | | | | | X |
| Silva-Taboada and Pine (1969) | | | | X | X[e] |
| Slaughter (1970) | | | | | X |
| Smith (1972) | | | | | X |
| Smith (1976) | X | X | X[d] | X | X |
| Solmsen (1994) | | | | | X |
| Stock (1975) | X | | | | |
| Straney et al. (1979) | | | X[d] | | |
| Straney (1980) | X | X | X[d] | | X |
| Uchikawa (1987) | | | | X | |
| Van Den Bussche (1991, 1992) | | | X[f] | | |
| Van Den Bussche et al. (1993) | | | X[g] | | |
| Van Den Bussche et al. (1998) | | | X[h] | | |
| Walton and Walton (1968) | | | | | X |
| Wenzel et al. (1966) | | | | X | |
| Wilder (1976) | | | | | X |

*(Notes appear at bottom of facing page.)*

# HISTORICAL BACKGROUND

We present a summary of more than 200 years of higher-level phyllostomid classification (and see table 2). Although we concentrate on relationships among subfamilies and genera, we occasionally note information relevant to the monophyly of certain genera. When discussing historical classifications we use the original names with the spellings used by the author(s) of each study, including the incorrect Chilonycterinae, Lobostominae, Phyllostomatinae, Hemiderminae, Stenoderminae, Desmodidae, and *Anthorhina*, *Lonchoglossa*, *Vampyriscus*, *Vampyrops* (see Miller, 1924; Cabrera, 1958; Handley, 1960; Smith, 1972; Jones and Carter, 1976; Handley, 1980; Gardner and Ferrell, 1990; for information on other synonymys see Miller, 1924 and Koopman, 1993). We have, however, corrected obvious spelling errors. We use the subfamilial names proposed by Koopman (1993, 1994) in some discussions; our use of these names is for convenience only and does not imply that these taxa are monophyletic.

## PHYLLOSTOMID CLASSIFICATION FROM 1758 TO PRESENT

Linnaeus (1758) recognized seven bat species, all placed in the genus *Vespertilio*. Two of these species, *Vespertilio spectrum* (= *Vampyrum spectrum*) and *V. perspicillata* (= *Carollia perspicillata*), are today placed in the family Phyllostomidae. Subsequent early classifications of bats usually recognized only one or two genera of bats (*Vespertilio* and *Noctilio* or *Pteropus*). These genera were placed in groups with other mammals, including carnivorans, insectivorans, lagomorphs, primates, rodents, and xenarthrans. By the early 19th century, bats were generally recognized as a separate higher-level group, although this group often included dermopterans.

Lacépède (1799) recognized the first phyllostomid genus, *Phyllostomus*. Although only four species and one genus of phyllostomids were named prior to 1800, the pace of discovery quickened remarkably after this date. More than 20 genera and 34 species were described between the years of 1800 and 1850 (see fig. 1). Most authors classified these newly discovered phyllostomids in families or tribes with taxa that are today recognized as members of other families (e.g., Pteropodidae, Emballonuridae, Megadermatidae, Molossidae, Mormoopidae, Noctilionidae, Rhinolophidae, Rhinopomatidae, and Vespertilionidae).

Dumeril (1806), in his "natural classification of animals," was one of the first authors to recognize multiple genera within his single family of bats, Chiroptères. Dumeril (1806) recognized *Phyllostomes* as one of these six genera.

Fischer von Waldheim (1813) recognized bats as the order Dactyloptera, which he split into two divisions ("naso simpli" or "naso cristato"). The single phyllostomid genus *Phyllostoma* with *Megaderma* and *Rhinolophus* formed the "naso cristato" group.

Oken (1816) recognized four "Gattung" (genera) of bats in his natural history text. In one genus, Oken (1816) placed most phyllostomids and *Pteropus minimus*. Oken

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*Notes for Table 1*

[a] Standard karyotype information (e.g., morphology of chromosomes, diploid number [2n], and fundamental number) reported by all authors indicated. G- and C-banding was used in some studies; see Historical Background for details.

[b] Immunologic studies used albumins, transferrins, and whole serum in reactions with antisera.

[c] Morphological work includes gross observations of external features, dentition, cranium, brain, stomach, sperm, tongue, postcranial musculature and skeleton, reproductive tract, and hair. Histological techniques have been used to study some of these systems; see Historical Background for details.

[d] Electrophoresis of various proteins.

[e] Behavioral traits were also considered.

[f] Restriction sites in the transcribed parts of the ribosomal DNA genes.

[g] *Eco*RI-defined nuclear satellite DNA repeat and 402 base pairs of cytochrome *b* sequence.

[h] 1140 base pairs of the cytochrome *b* gene.

TABLE 2
**Selected Higher-Level Classifications of Phyllostomidae**

**Gervais (1854, 1856)**
Phyllostomidés
  Vampyrina
  Glossophagina
  Stenodermina
  Desmodina

**Dobson (1875, 1878)[a]**
Phyllostomidae
  Lobostominae (= Mormoopidae Smith, 1972)
  Phyllostominae
    Group A
      Vampyri (= Phyllostominae + Carolliinae)
      Glossophagae
      Stenodermata (includes *Brachyphylla*)
    Group B
      Desmodontes

**Miller (1907)[b]**
Phyllostomidae
  Chilonycterinae (= Mormoopidae)
  Phyllostominae
  Glossophaginae
  Hemiderminae (= Carolliinae)
  Sturnirinae
  Stenoderminae (includes *Brachyphylla*)
  Phyllonycterinae
Desmodontidae

**de la Torre (1961)[c]**
Phyllostomidae
  Phyllostominae
  Glossophaginae
  Carollinae (sic)
  Stenoderminae (includes *Brachyphylla*)
  Phyllonycterinae

**Koopman and Jones (1970)**
Phyllostomatidae
  Chilonycterinae (= Mormoopidae)
  Phyllostomatinae
  Glossophaginae
  Carolliinae
  Stenoderminae
    Sturnirini
    Brachyphyllini
    Stenodermini
  Phyllonycterinae
  Desmodontinae

**Smith (1976)[d]**
Phyllostomatidae
  Phyllostomatinae
  Glossophaginae
  Carolliinae
  Stenoderminae
  Phyllonycterinae (includes *Brachyphylla*)
  Desmodontinae

**Corbet and Hill (1980)**
Phyllostomatidae
  Phyllostomatinae
  Glossophaginae
  Carolliinae
  Sturnirinae
  Stenoderminae
  Phyllonycterinae (includes *Brachyphylla*)
Desmodontidae

**Griffiths (1982)[e]**
Phyllostomidae
  Phyllostominae
  Glossophaginae
  Lonchophyllinae
  Brachyphyllinae
  Phyllonycterinae
  Carolliinae
  Stenodermatinae
  Desmodontinae

**Baker et al. (1989)[f]**
Phyllostomidae
  *Macrotus* incertae sedis
  *Micronycteris* incertae sedis
  Vampyrinae
    *Chrotopterus, Trachops, Vampyrum*
  Phyllostominae (all tribes sedis mutabilis)
    Phyllostomini (includes *Phyllostomus* [includes
      *Phylloderma*], *Tonatia, Mimon, Lonchorhina,*
      *Macrophyllum*)
    Glossophagini (includes lonchophyllines,
      phyllonycterines, and *Brachyphylla*)
    Stenodermatini (includes *Carollia* and
      *Rhinophylla*)
  Desmodontinae

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[a] Trouessart (1897) used a similar system, but recognized Natalinae, Mormopinae, and Phyllostominae as subfamilies of Phyllostomidae. Within Phyllostominae, Trouessart (1897) recognized sections identical in all but name to those of Dobson (1875, 1878). Flower and Lydekker (1891) also used this classification, but used Chilonycterinae for Dobson's Lobostominae.

[b] Simpson (1945), Hall and Kelson (1959), and Koopman and Cockrum (1967) followed Miller (1907), although spellings (e.g., Phyllostomatidae for Phyllostomidae) and some group names (e.g., Carolliinae for Hemiderminae) were different in their classifications. Hall (1981) followed Miller (1907), but classified *Brachyphylla, Erophylla,* and *Phyllonycteris* in Brachyphyllinae.

[c] de la Torre (1961) did not include desmodontines in his classifications, apparently considering them a separate family.

[d] Classifications by Jones and Carter (1976) and Koopman (1984) are similar to Smith (1976), but Koopman (1984) used the name Brachyphyllinae instead of Phyllonycterinae.

[e] Koopman (1993) employed the same classification.

[f] Baker et al. (1989) classified all genera, except *Macrotus* and *Micronycteris*, as sedis mutabilis.
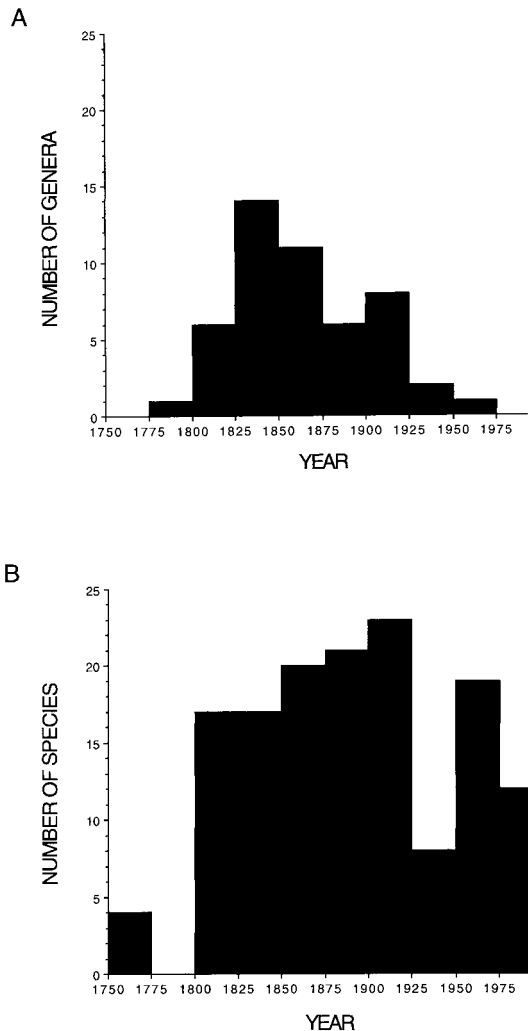
A



B



Fig. 1. The pace of discovery of currently recognized phyllostomid taxa described from 1750 to 1993. **A.** Genera. **B.** Species. There has been a steady decrease in the rate of description of new genera since the early 1800s, but the pace of description of new species has not declined at the same rate. We used dates of publication from Koopman (1993).

(1816) classified *Stenoderma* in another genus with emballonurids, molossids, and vespertilionids.

Although Cuvier (1817) followed Linnaeus (1758) in recognizing only a single genus of bats (*Vespertilio*) in his classification of the animal kingdom, he nevertheless divided this genus into more than 12 groups. Among these groups, two, Phyllostomes and Sténodermes, included phyllostomids.

In his treatise on mammalogy, Desmarest (1820) recognized three phyllostomid genera, *Phyllostome*, *Glossophage*, and *Stenodérme*, among the 16 genera of bats in his famille Cheiroptères, tribu Chauve-souris. While *Glossophage* and *Stenodérme* contained only glossophagines and stenodermatines respectively, the genus *Phyllostome* included a variety of species now recognized as desmodontines, phyllostomines, carolliines, and stenodermatines.

Goldfuss (1820) was the first taxonomist to group bats into families, recognizing four in his classification. Goldfuss (1820) included most phyllostomids in the family Phyllostomata within the genus *Phyllostoma*. Other members of this family were *Megaderma*, *Nycteris*, *Rhinolophus*, and *Rhinopoma*. Goldfuss (1820) placed *Stenodermata* within the family Noctiliones with molossids, noctilionids, and vespertilionids.

Gray (1821) was the first to divide the class Cheiroptera into two groups, the orders Fructivorae and Insectivorae. Gray (1821) placed the three phyllostomid genera, *Phyllostoma*, *Vampyre*, and *Stenodermes*, in the family Noctilionidae, a member of Insectivorae. Other genera in this family were *Mollosses*, *Noctilio*, and *Nyctimones*.

In his monograph on Brazilian bats and primates, Spix (1823) recognized two families of bats, Anistiophori, for genera without noseleaves, and Istiophori, for those with noseleaves. Only the four phyllostomid genera (*Diphylla*, *Phyllostoma*, *Vampyrus*, and *Glossophaga*) were members of Istiophori.

Lesson (1827) followed Spix (1823) by splitting his tribe Chauve-souris into the divisions Anistiophori and Istiophori. Lesson (1827) recognized seven genera of Phyllostomes in his family Istiophori: *Phyllostoma*, *Vampirus*, *Glossophaga*, *Monophyllus*, *Artibeus*, *Madateus* (= *Artibeus*), and *Rhinopoma*. Lesson (1827) did not consider *Stenoderma* a member of this group, but placed it in Noctilonina in the family Anistiophori. Noctilionina included molossids, a mormoopid, noctilionids, and a vespertilionid.

Gray (1826) recognized a single family of bats (Vespertilionidae), which he divided into two sections, Istiophori and Anistiophori.

Gray (1826) divided five subfamilies among these two groups. The subfamily Phyllostomina, placed in Istiophori, included *Rhinopoma* and all phyllostomid genera except "perhaps" *Stenoderma*. Gray (1826: 243) suggested that this genus might belong in the subfamily Noctilionina, a group in Anistiophori.

In a classification of vertebrates, Bonaparte (1831) recognized Phyllostomina as one of five "subfamilies" within his order Chiroptera and its single family Vespertiliones. Phyllostomina included *Phyllostoma* (and as recognized subgroups of this genus *Desmodus*, *Phyllostoma*, and *Vampyrus*), *Glossophaga*, *Megaderma*, *Mormops*, *Nycteris* (not *Nyctinomus* as reported by Miller [1907]), *Nyctophilus*, and *Rhinopoma*. Later, Bonaparte (1838) recognized three families of Chiroptera. The family Vampyridae contained the sole subfamily Vampyrina, but Bonaparte (1838) did not name the genera he included in this subfamily.

Gray's (1838) classification remained similar to his classification of 1826. However, at lower levels, Gray's (1838) tribe Phyllostomina was composed of *Lavia*, *Megaderma*, *Mormoops*, *Rhinopoma*, and all phyllostomid genera save *Ariteus*, which he placed in the tribe Rhinolophina.

Wagner's (1840) classification recognized Chiroptera as a suborder with three families (Frugivora, Istiophora, Gymnorhina). In the family Istiophora, Wagner (1840) included only two tribes ("Sippe"): Desmodina and Phyllostomata. Phyllostomata included four phyllostomid genera (*Phyllostoma*, *Brachyphylla*, *Glossophaga*, and *Stenoderma*), as well as *Megaderma*, *Nycteris*, *Nyctophilus*, *Rhinolophus*, and *Rhinopoma*.

Lesson (1842) abandoned Spix's (1823) divisions Anistiophori and Istiophori; however, he still recognized the same five groups (now families) in the tribe Chiroptera. The family Phyllostomineae included phyllostomid genera, *Megaderma*, *Mormoops*, *Nyctophyllus*, *Nycteris*, and *Rhinopoma*.

Gervais (1854) recognized four families in his order Cheiroptères. In both his natural history of mammals and his work on South American bats, Gervais (1854, 1856) restricted Phyllostomidés to New World leaf-nosed bats and laid the basis for the classification

still in use today (see table 2). Gervais (1856) recognized four tribes of phyllostomids: Desmodina, Vampyrina, Glossophagina (including *Hemiderma* [= *Carollia*]), and Stenodermina (including *Brachyphylla*). These tribes were equivalent to the kinds ("genre") he had previously proposed (Gervais, 1854).

Koch's (1862–63) classification included two suborders, Carpophagen and Entomophagen. Within Entomophagen, Koch (1862–63) recognized two families, Gymnorrhina and Istiophora. Istiophora contained three groups of phyllostomids: Diphyllata included *Choeronycteris*, *Glossophaga*, *Phyllostoma* (this genus included as "Untergattung" *Nyctiplanus* [= *Sturnira*] and *Sturnira*), *Nycteris*, and *Nyctophilus*; Monophyllata included *Desmodus*, *Diphylla*, *Brachyphylla*, and *Rhinopoma*; and Pseudophyllata was composed of a single genus, *Stenodermata*.

Peters (1865) recognized seven families of bats in his classification. Five subfamilies comprised the family Phyllostomata: Vampyri included both carolliine and phyllostomine genera; Glossophagae included glossophagines and *Phyllonycteris*; Stenodermata included *Brachyphylla* and stenodermatines. The remaining two subfamilies Peters (1865) recognized were Desmodi and Mormopes.

Gray's (1866a–d) last classification of bats was presented as a series of papers in which he recognized five families. In the family Phyllostomidae he included Desmodina, Phyllostomina, Vampyrina, Glossophagina, and Stenodermina as tribes. Gray (1866d) also introduced five monotypic tribes: Lonchorhinina, Macrophyllina, Trachyopina, Brachyphyllina, and Centurionina (Rehn [1901] later supported recognition of the latter group as Centurioninae). Gray's (1866d) Phyllostomina included *Alectops* (= *Phyllostomus*), *Guandira* (= *Phylloderma*), *Phyllostoma*, *Schistozoma* (= *Micronycteris*), *Tylostoma* (= *Mimon crenulatum*), *Carollia*, *Rhinophylla*, and *Rhinops* (= *Carollia*). Vampyrina included *Chrotopterus*, *Lophostoma* (= *Tonatia*), *Macrotus*, *Micronycteris*, *Mimon*, and *Vampyrus*.

Gill's (1872) classification divided the order Chiroptera into two suborders, Animalivora and Frugivora. All phyllostomids appeared in families in the suborder Animali-

vora. Although Gill (1872) recognized Phyllostomidae as a distinct family, he placed Vampyrinae, Glossophaginae, and Stenoderminae as subfamilies of another family, Megadermidae. Desmodidae and Mormopidae appear as separate families in Gill's (1872) arrangement.

In an attempt to arrange genera and families of bats according to their "natural affinities," Dobson (1875, 1878; see table 2) split Chiroptera into two currently recognized suborders (Megachiroptera and Microchiroptera) and six families. Dobson (1875, 1878) recognized two subfamilies, Lobostominae (= Mormoopidae) and Phyllostominae, in his family Phyllostomidae. Following Peters (1865), Dobson (1875, 1878) divided Phyllostominae into Desmodontes, Vampyri (= Phyllostominae and Carolliinae), Glossophagae, and Stenodermata (including *Brachyphylla*). Dobson (1875: 353–354) concluded that "*Rhinophylla* leads from the Vampyri to the Glossophagae; and the close connexion of the Vampyri with the Stenodermata is seen in the similarity of the warts of the lower lip." Dobson (1875) also noted the close morphological similarity of *Desmodus* and *Brachyphylla*.

In a natural history text, Gill (1884) divided bats into two suborders, Animalivora and Frugivora, and placed 10 families in these two suborders. Gill (1884) recognized Desmodontidae, Mormopidae, and Phyllostomidae as separate families, and divided phyllostomids into three subfamilies, Phyllostomines, Glossophagines, and Stenodermines.

Flower and Lydekker (1891) recognized groups similar to those named by Dobson (1875, 1878) in their classification (they relied primarily on ordinal accounts of bats written by Dobson). However, these authors used the subfamily name Chilonycterinae rather than Lobostominae.

Allen (1892a) named an additional phyllostomid subfamily for *Natalus*, concluding that presence of a rudimentary noseleaf in late embryonic stages indicated a closer affinity to Phyllostomidae than to Vespertilionidae. However, no subsequent authors followed this suggestion.

Within Chiroptera, Winge (1892, 1941)

recognized five families[1]. Winge (1941) followed Dobson (1875, 1878) in recognizing a division between Mormopini (including *Noctilio*) and Phyllostomatini within Phyllostomatidae. Winge (1941) subdivided Phyllostomatini into four groups: Desmodontes, Phyllostomata, Glossophagae, and Stenodermata. Within Phyllostomata, Winge (1941) placed *Lonchorhina*, *Macrophyllum*, and *Macrotus* in a basal group because of their primitive external and dental morphology. Winge (1941) considered two other lineages relatives of the *Lonchorhina* group: (1) *Lophostoma* (= *Tonatia*), *Phylloderma*, *Schistozoma* (= *Micronycteris*), *Trachyops*, and *Vampyrus*, and (2) *Mimon* (= *Mimon bennettii*), *Phyllostoma*, and *Tylostoma* (= *Mimon crenulatum*). Although Winge (1941) viewed these two lineages as successively more advanced than the *Lonchorhina* group, he recognized *Hemiderma* (= *Carollia*) and *Rhinophylla* as the most derived members of Phyllostomata.

Winge (1941) viewed Phyllostomata as less specialized than Glossophagae and Stenodermata. Within Stenodermata, Winge (1941) recognized *Vampyrops* (= *Platyrrhinus*) and *Sturnira* as the most dentally primitive genera. Another group was composed of *Artibeus*, *Stenoderma*, *Centurio*, and *Pygoderma*; *Chiroderma* represented a separate lineage. Winge (1892) considered *Brachyphylla* to be a member of Desmodontes; however, he (1941) later reclassified *Brachyphylla* as a special, primitive offshoot of Stenodermata.

Allen (1898) recognized three "alliances" within Glossophaginae in his study of this subfamily. *Phyllonycteris* was the sole member of the phyllonycterine alliance. A second group included *Glossophaga*, *Leptonycteris*, and ("probably") *Monophyllus*. *Anoura*, *Choeronycteris*, and *Lonchoglossa* (= *An-*

[1] Winge wrote in Danish, which made his publications largely inaccessible to non-Danish scientists. However, an English translation of Winge's work on interrelationships of mammalian genera was published in 1941. This volume (which we cite simply as "Winge, 1941") was based both on Winge's published works and his unpublished notes. The core of the section on bats was taken from Winge (1892); however, the notes that followed included Winge's comments on papers published between 1892 and 1922.

*oura*) composed the choeronycterine alliance. Allen (1898: 238) derived the latter two groups from Vampyri (= Phyllostominae and Carolliinae), but noted that *Phyllonycteris* "is so near *Brachyphylla* that it would be easy to effect the transition and remove the genus to the alliance expressed by the term brachyphylline. It is akin, therefore, if not annectant to the subfamily Stenoderminae."

In his classification, Weber (1904) recognized two chiropteran suborders and five families, one of which was Phyllostomatidae. This family included three subfamilies: Lobostominae (including *Noctilio*), Desmodontinae, and Phyllostominae. Within Phyllostominae, Weber (1904) identified three groupings that corresponded to Dobson's (1875, 1878) Vampyri (= Phyllostominae and Carolliinae), Glossophagae (which included *Phyllonycteris*), and Stenodermata (including *Brachyphylla*).

Miller's (1907) revision of Chiroptera formed the basis of many subsequent classifications. Miller (1907) recognized two suborders and 17 families within Chiroptera. Miller (1907) relied on his descriptions of craniodental, facial, and postcranial morphology to define seven phyllostomid subfamilies: Chilonycterinae (= Mormoopidae), Phyllostominae, Phyllonycterinae, Glossophaginae, Hemiderminae (= Carolliinae), Sturnirinae, and Stenoderminae (including *Brachyphylla*; see table 2). Miller (1907) recognized Desmodontidae as a separate family. Differences between Miller's (1907) classification and those published previously included recognition of Phyllonycterinae (previously included within Glossophaginae), Hemiderminae (previously included within Phyllostominae), and Sturnirinae (previously included within stenodermatines) as distinct subfamilies. Miller (1907) suggested that hemidermines (carolliines) might be most closely allied to Desmodontidae and Phyllonycterinae.

Miller (1907) also discussed some relationships within subfamilies, suggesting, for example, that *Diphylla* was the least specialized member of Desmodontinae. Within Stenoderminae, Miller (1907: 159) viewed *Mesophylla* as an intermediate between *Ectophylla* and *Vampyrops* (= *Platyrrhinus*),

but suggested that *Ectophylla* and *Mesophylla* formed a "distinct group." Miller (1907: 170) also found that *Ametrida*, *Centurio*, and *Sphaeronycteris* formed a closely related group within "short-snouted" stenodermatines[2], and that *Centurio* could be linked to "typical" stenodermatines through *Phyllops* and *Pygoderma*.

In 1945, Simpson published his influential classification of mammals. The section on Phyllostomidae closely followed Miller's (1907) classification. Simpson (1945) recognized seven phyllostomid subfamilies: Chilonycterinae, Phyllostomatinae, Phyllonycterinae, Glossophaginae, Carolliinae, Sturnirinae, and Stenoderminae. Simpson (1945) placed desmodontines in their own family. Simpson's (1945) main alteration of Miller's (1907) work was to synonymize many genera. For example, Simpson (1945) synonomized *Hylonycteris* with *Choeronycteris*, *Mesophylla* with *Ectophylla*, and *Ariteus*, *Ardops*, and *Phyllops* with *Stenoderma*. These represent only some of Simpson's (1945) generic revisions.

Savage (1951) described a new genus and species of extinct phyllostomid, *Notonycteris magdalenensis*, from late Miocene beds in Colombia. Savage (1951) compared *Notonycteris* with *Phyllostomus*, *Chrotopterus*, and *Vampyrum*, concluding that *Notonycteris* was more similar to the last two genera than to *Phyllostomus*. Savage (1951: 362) even suggested that, "The fossil makes an acceptable structural predecessor for *Vampyrum*. . . ."

In their study of facial histology in bats, Dalquest and Werner (1954: 159) offered a higher-level classification that they considered "more nearly the true phylogenetic order than that adopted by Miller" (1907). Although the authors noted no appreciable differences between mormoopids and phyllostomids, Dalquest and Werner (1954) accorded familial status to Chilonycterinae (Chilonycteridae = Mormoopidae). Later studies of echolocation calls (Griffin and

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[2] The "short-snouted" or "short-faced" stenodermatines are *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Phyllops*, *Pygoderma*, *Stenoderma*, *Sphaeronycteris*. However, some authors (e.g., Smith, 1976) included *Artibeus* species in this group.

Novick, 1955, Novick, 1963) and host-parasite associations (Machado-Allison, 1967; Wenzel et al., 1966) supported recognition of mormoopids as a distinct family.

In their classification, Hall and Kelson (1959) recognized seven phyllostomid subfamilies: Chilonycterinae, Phyllostominae, Phyllonycterinae, Glossophaginae, Carolliinae, Sturnirinae, and Stenoderminae. Hall and Kelson (1959) placed *Brachyphylla* within Stenoderminae and recognized desmodontines as a separate family (Hall's 1981 revised edition differed only in recognizing Brachyphyllinae for *Brachyphylla* and the phyllonycterines).

In his work on the systematics of *Sturnira*, de la Torre (1961) wrote extensively on relationships within Phyllostomidae. Based on his analysis of unspecified "cranial and general morphology," de la Torre (1961: 140) proposed that mormoopids deserved familial status. Using dental morphology to evaluate relationships, de la Torre (1961) recognized five subfamilies: Phyllostominae, Phyllonycterinae, Glossophaginae, Carolliinae, and Stenoderminae (see table 2). Phyllostomines represented the most basal branch of the family (de la Torre, 1961). In addition, de la Torre (1961) recognized a close relationship between phyllonycterines and glossophagines, and suggested that carolliines evolved from a lineage "close to" glossophagines (de la Torre, 1961: 42). However, in a tree of "estimated evolutionary relationships" (fig. 2), the carolliines appeared to be more closely related to stenodermatines than glossophagines.

Within Phyllostominae, de la Torre (1961) identified three groups: (1) *Chrotopterus* and *Vampyrum*; (2) *Trachops*; and (3), *Macrotus*, *Micronycteris*, *Mimon*, *Phyllostomus*, and *Tonatia*. Within Glossophaginae, de la Torre (1961) recognized two evolutionary lines. In one clade, *Glossophaga* and *Lionycteris* were successive sister taxa to *Platalina* and *Lonchophylla*. *Anoura*, *Choeronycteris Leptonycteris*, and *Monophyllus* formed a second clade. Phyllonycterines appeared as the sister group of the glossophagines.

As defined by de la Torre (1961), Stenoderminae consisted of four lineages. The first lineage, *Brachyphylla*, branched off before the carolliines split from the stenoder-matine lineage. Despite this placement, de la Torre (1961) still classified *Brachyphylla* as a member of Stenoderminae. In the second stenodermatine line, *Chiroderma* was the sister taxon of *Vampyriscus* (= *Vampyressa*) and *Mesophylla*. *Vampyressa* was also included in this group, although de la Torre's (1961) tree lacked a branch for this taxon. In the third group, two pairs of sister taxa, *Vampyrops* (= *Platyrrhinus*) and *Enchisthenes* and *Uroderma* and *Artibeus*, formed a clade. *Sturnira* and *Vampyrodes* appeared as successively more basal branches of this group. All "short-faced" taxa formed a clade in de la Torre's (1961) tree. *Phyllops* and *Ariteus* were successive sister taxa to *Pygoderma* and *Ardops*. *Sphaeronycteris* and *Ametrida* appeared as sister taxa, and formed a clade with *Centurio*. *Stenoderma* occupied the basal branch within the *Ametrida* group.

Subsequently, de la Torre made significant changes in this tree (the revised version was published in Wenzel et al., 1966: fig. 144; our fig. 3), dramatically rearranging relationships within Phyllostominae. *Vampyrum*, which de la Torre (1961) had placed in a clade with *Chrotopterus*, was now grouped with *Barticonycteris* (= *Micronycteris*; see Koopman, 1978), *Macrotus*, and *Micronycteris*, formerly members of de la Torre's (1961) *Phyllostomus* line. *Chrotopterus* became the sister taxon of *Tonatia*, and together with *Trachops*, was united with the *Vampyrum* group. Also in the Wenzel et al. (1966) tree, de la Torre recognized *Macrophyllum* and *Lonchorhina* as sister taxa and placed them as the first branch of the *Phyllostomus* group. *Anthorina* (= *Mimon crenulatum*), *Mimon* (*M. bennettii*), *Phylloderma*, and *Phyllostomus* formed the other branches of the *Phyllostomus* group. In the Wenzel et al. (1966) tree, de la Torre aligned *Choeroniscus*, *Hylonycteris*, *Lichonycteris*, *Lonchoglossa* (= *Anoura*), and *Musonycteris* (taxa which had not been included in his previous tree) with the *Monophyllus* lineage of glossophagines (s.l.). Finally, *Brachyphylla*, which de la Torre still classified as a stenodermatine, clearly split from the carolliine branch (Wenzel et al., 1966).

Machado-Allison (1967) described host-parasite associations and interpreted data on echolocation calls (Novick, 1963) as sug-
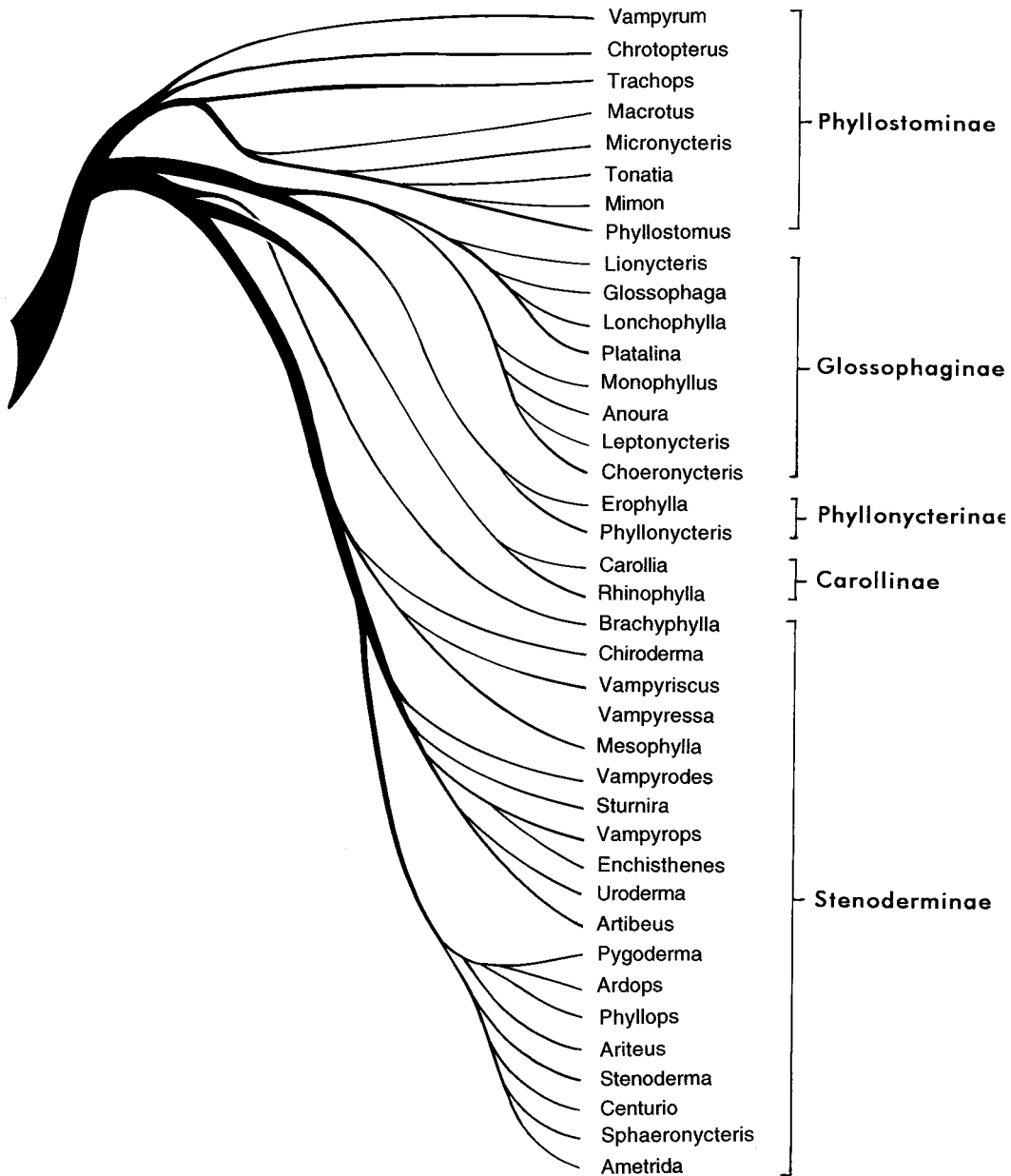
Fig. 2. Intergeneric relationships of phyllostomid bats proposed by de la Torre (1961; redrawn from fig. 4). This tree is based on dental morphology. *Vampyressa* is not connected to the tree in the original figure.

gesting that Desmodidae should be considered a subfamily of Phyllostomidae. Forman et al. (1968) reached the same conclusion based on immunological, karyological, and morphological comparisons of phyllostomids and desmodontines. Uchikawa (1987) later affirmed this placement of desmodontines using host-parasite associations of mites of the genus *Eudusbabekia*.

Baker (1967) used karyological data to identify seven groups of phyllostomids: (1) *Pteronotus*; (2) *Carollia*, *Choeronycteris*,
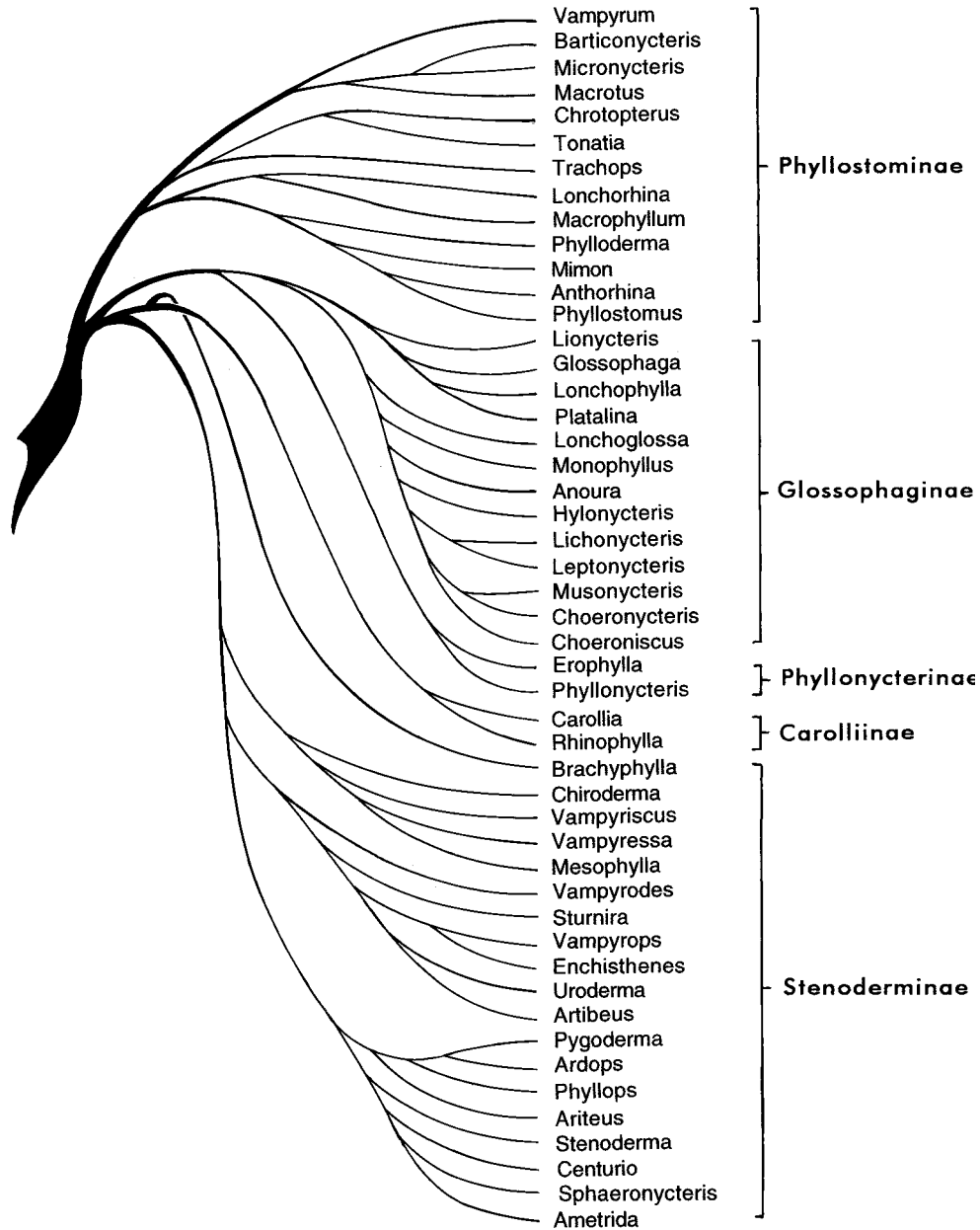
Fig. 3.    Tree from Wenzel et al. (1966; redrawn from fig. 144) by de la Torre.

and *Choeroniscus*; (3) *Leptonycteris, Glossophaga, Phyllostomus, Trachops,* and *Macrotus*; (4) *Micronycteris*; (5) *Anoura*; (6) *Sturnira, Artibeus, Vampyrops* (= *Platyrrhinus*), *Chiroderma, Enchisthenes,* and *Centurio*; and (7) *Uroderma*. Because *Artibeus, Vampyrops,* and *Sturnira* have autosomes

that are superficially identical, Baker (1967) suggested that *Sturnira* should be included in Stenodermatinae. Although *Pteronotus* has a karyotype unique among phyllostomids, Baker (1967: 421) noted only that ''*Pteronotus* and related genera are sufficiently distinct to merit at least subfamily status.'' Baker

(1967, 1970) did not discuss the relationships among these seven groups, but noted that the similarity of fundamental number, diploid number, certain autosomes, and the XX/XY$_1$Y$_2$ sex system in *Carollia* and *Choeroniscus* indicated that Glossophaginae (s.l.) might not be monophyletic (this point was also made by Hsu et al., 1968). However, problems relating the karyotype of *Carollia* to *Choeroniscus* arose when it was discovered that not all *Choeroniscus* species have a translocated X chromosome (Baker, 1970; see discussion below). Further study demonstrated that the karyotype of *Rhinophylla* (unknown in 1967) is more similar to the karyotypes of other glossophagines, phyllostomines, and stenodermatines than to the karyotypes of *Carollia*, *Choeroniscus*, and *Choeronycteris* (Baker and Bleier, 1971). Baker and Bleier (1971) concluded that either a great deal of evolution occurred within Carolliinae, or that this subfamily was not monophyletic.

Koopman and Cockrum (1967) presented a classification of phyllostomids, recognizing Chilonycterinae, Phyllostomatinae, Phyllonycterinae, Glossophaginae, Carolliinae, Sturnirinae, and Stenoderminae (including *Brachyphylla*). These authors placed desmodontines into their own family.

Gerber (1968) and Gerber and Leone (1971) used immunological comparisons to investigate relationships between some glossophagines and *Carollia*. Both studies reported that *Choeronycteris* has a greater affinity for desmodontines and phyllostomines than for glossophagines, and that *Carollia* has the greatest affinity for *Glossophaga* species. Immunological results suggested that a group including *Desmodus*, *Chrotopterus*, *Phyllostomus*, and *Choeronycteris* was more closely related to the *Glossophaga-Carollia* group than to the stenodermatines. Results of these studies supported earlier conclusions that mormoopids should be recognized as a distinct family of bats, that desmodontines should be considered a phyllostomid subfamily, and that *Sturnira* should be placed within Stenodermatinae.

In a study of postcranial osteology, Walton and Walton (1968: 29) suggested that mormoopids, then recognized as Chilonycterinae, were the "most primitive of the subfamilies of the Phyllostomatidae." They concluded that mormoopids were most closely associated with the "*Macrotus*-type" of phyllostomine, a group that included *Chrotopterus* and *Vampyrum*, genera that Savage (1951) allied with an extinct Miocene phyllostomid, *Notonycteris*. Walton and Walton (1968) accepted Savage's (1951) conclusion that there is a division between the genus *Phyllostomus* and his *Vampyrum-Chrotopterus* group (their "*Macrotus*-type").

Walton and Walton (1968) hypothesized that Phyllonycterinae and Carolliinae evolved from the "*Macrotus*-type" of phyllostomine. From the "*Phyllostomus*-type," Walton and Walton (1968) derived Sturnirinae; however, they suggested that this subfamily might be best recognized as a member of Carolliinae. Also associated with the *Phyllostomus*-type was a second lineage that split into Glossophaginae (s.l.) and Stenoderminae. Walton and Walton (1968) further divided Stenoderminae into a primitive "*Vampyrops*-type" (*Vampyrops = Platyrrhinus*) and a derived "*Artibeus*-type." Although Walton and Walton (1968: 31) treated desmodontines as a separate family, they noted that, "Myologically and osteologically they are very close to the phyllostomatids."

In addition to studies that indicated that the taxonomic positions of desmodontines and mormoopids should be evaluated, evidence introduced in the late 1960s suggested that the position of *Brachyphylla* also needed review. Although Allen (1898) had noted that *Brachyphylla* is morphologically similar to *Phyllonycteris* and suggested a name for a subfamily including the two genera (Brachyphyllinae), the most persuasive evidence for an affiliation between *Brachyphylla* and Phyllonycterinae was presented by Silva-Taboada and Pine (1969). Data from behavior, parasites, and craniodental, external, and postcranial morphology indicated to Silva-Taboada and Pine (1969) that *Brachyphylla*, *Erophylla*, and *Phyllonycteris* should be placed in a single subfamily. Later karyological and immunological studies also supported this conclusion (Baker and Lopez, 1970; Baker and Bass, 1979; Baker et al., 1981a).

Baker (1967, 1973), Hsu et al. (1968), Baker and Hsu (1970), Baker and Lopez

(1970), Greenbaum et al. (1975), and Baker et al. (1982) discussed the phylogenetic implications of the sex chromosomes of phyllostomids. Several genera of stenodermatine bats (*Ametrida*, *Ardops*, *Ariteus*, *Artibeus*, most *Dermanura* species, *Enchisthenes*, *Koopmania*, *Phyllops*, *Pygoderma*, and *Stenoderma*) have an $XX/XY_1Y_2$ sex chromosome system (see character 137 for description; Baker, 1967, 1979; Hsu et al., 1968; Baker and Lopez, 1970; Greenbaum et al., 1975; Gardner, 1977a; Baker et al., 1979, 1982; Johnson, 1979; Myers, 1981). Baker and Lopez (1970) suggested that the $XX/XY_1Y_2$ sex system delineates a group consisting of *Ametrida*, *Artibeus*, *Enchisthenes*, and *Stenoderma* (sex chromosomes of other genera mentioned above were not known at this time). Baker and Lopez, (1970) considered *Centurio* a relative of this group, and interpreted its XX/XY sex system as a reversal. Greenbaum et al. (1975) suggested that two ''short-faced'' groups could be identified: (1) *Centurio* and *Sphaeronycteris*, both of which have an XX/XY system, and (2) the remaining ''short-faced'' taxa, all of which have an $XX/XY_1Y_2$ system.

*Carollia brevicauda*, *C. perspicillata*, *C. subrufa* and some individuals of *C. castanea* also have an $XX/XY_1Y_2$ system (Baker, 1967; Hsu et al., 1968; Baker and Bleier, 1971; Patton and Gardner, 1971; Stock, 1975; Baker, 1979; Baker et al., 1982). *Choeroniscus godmani* has a translocated X chromosome, while *C. minor* (= *C. intermedius*) does not (Baker, 1967, 1970; Patton and Gardner, 1971; Stock, 1975; Baker, 1979; Baker et al., 1982). Both Baker (1967, 1970) and Hsu et al. (1968) had previously suggested that the presence of a similar sex chromosome system in *Carollia* and *Choeroniscus* might indicate that Glossophaginae (s.l.) is not monophyletic. Stock (1975) used C- and G-banding techniques to test these assertions, and found that banding patterns of *Choeroniscus* show no recognizable similarity to those in *Carollia*, suggesting that the two genera are not closely related. Baker et al. (1981a) also found that immunological and electrophoretic comparisons provided no evidence for glossophagine (s.l.) diphyly.

Koopman and Jones' (1970; see table 2) classification included seven subfamilies: Chilonycterinae, Desmodontinae, Phyllostomatinae, Phyllonycterinae, Glossophaginae, Carolliinae, and Stenoderminae. Within Stenodermatinae, Koopman and Jones (1970) identified three tribes, placing *Brachyphylla* in Brachyphyllini, *Sturnira* in Sturnirini, and the remaining stenodermatines in Stenodermini.

Slaughter (1970) identified two major groups of phyllostomines in an analysis of chiropteran dental evolution (fig. 4). These two groups were different from those previously proposed by Walton and Walton (1968) and Savage (1951). According to Slaughter (1970), the dentally similar forms *Lonchorhina*, *Mimon*, *Phyllostomus*, *Trachops*, and *Vampyrum* composed one group, while *Macrotus* represented another lineage. Slaughter (1970) suggested that *Lonchorhina*, *Mimon*, and *Phyllostomus* share more dental similarities with each other than with the distinct *Trachops* and *Vampyrum* lines. Slaughter (1970) also noted that the dentitions of phyllostomines, glossophagines (s.l.), and stenodermatines could each be derived independently from the prototypic phyllostomid dentition. Slaughter (1970) echoed de la Torre's (1961) conclusion that Phyllonycterinae and Carolliinae could have easily arisen from within Glossophaginae (s.l.). *Brachyphylla* and *Sturnira* were identified as the most dentally primitive stenodermatines and formed separate branches of Slaughter's (1970) stenodermatine tree. Slaughter (1970) also identified a lineage consisting of *Vampyrops* (= *Platyrrhinus*), *Chiroderma*, and *Ectophylla* (from least to most derived), and a lineage composed of *Uroderma*, *Stenoderma*, *Artibeus*, and *Centurio* (from least to most specialized). Slaughter (1970) proposed that desmodontids arose from a form intermediate between *Carollia* (primitive) and *Rhinophylla* (derived), and recognized two distinct desmodontid dental lineages: *Diphylla* (primitive) and *Desmodus* (derived). Slaughter (1970) identified Chilonycterinae (= Mormoopidae) as the most dentally primitive phyllostomid subfamily.

Phillips (1971) investigated craniodental characters in glossophagine bats and produced a fully dichotomous tree which divided glossophagines (s.l.) into two groups. One group was composed of *Choeroniscus*, *Cho-*
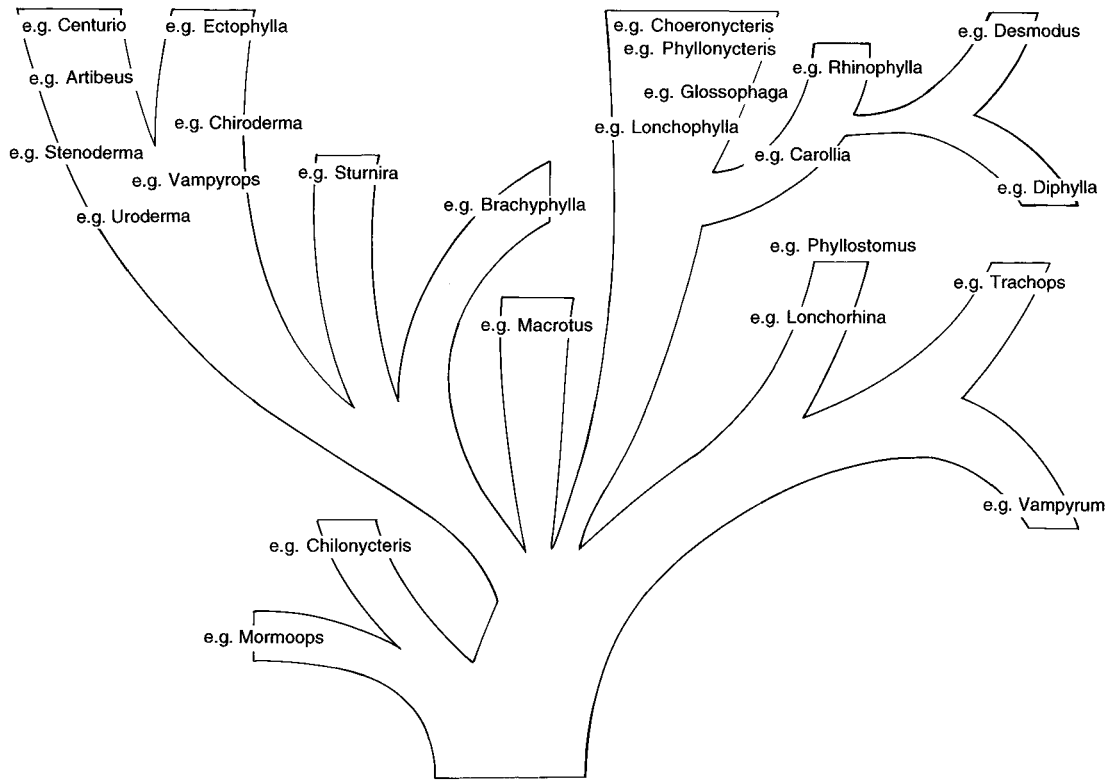
Fig. 4. Slaughter (1970; redrawn after fig. 5) proposed this tree of phyllostomids relationships based on dental character evolution. The original caption read ''Dental morphology tree suggesting types of dentition possessed by ancestral forms of chiropteran groups. Generic names are used merely to denote certain types and/or grades of dental forms.''

*eronycteris*, and *Musonycteris*. The second group consisted of all other glossophagines. Phillips (1971) found that this division also agreed with immunological associations (Gerber, 1968) and karyological data (Baker, 1967). Within the *Glossophaga* group, Phillips (1971) identified three clades: (1) *Glossophaga*, *Leptonycteris*, and *Monophyllus*; (2) *Anoura*, *Lionycteris*, and *Lonchophylla*; and (3) *Hylonycteris*, *Lichonycteris*, *Platalina*, and *Scleronycteris*. In the first clade, *Glossophaga* and *Monophyllus* were sister taxa; *Lonchophylla* and *Lionycteris* appeared as sister taxa in the second clade. Within the third group, *Scleronycteris* and *Platalina* were successive sister taxa to *Lichonycteris* and *Hylonycteris*. Phillips (1971) found that craniodental, karyological, and immunological data provided conflicting information about relationships between glossophagines and other phyllostomids, making an assess-

ment of glossophagine monophyly impossible given the data available.

Forman (1971) used stomach morphology to identify two groups of glossophagines (s.l.): (1) *Anoura*, *Glossophaga*, and *Leptonycteris*; and (2) *Choeroniscus* and *Lichonycteris*. Forman (1971: 282) suggested that these two groups formed an ''unnatural assemblage,'' and noted that *Anoura* was intermediate in certain respects between his two groups.

Smith (1972) raised Chilonycterinae to familial status as Mormoopidae, the older family name having priority over Chilonycteridae. Smith (1972) cited numerous characters from many different systems which together indicated that Mormoopidae is both monophyletic and distinct from Phyllostomidae. Smith (1972: 21) used the morphology of the medial process of the distal humerus to divide phyllostomids into a ''*Micronycteris-*

line" (*Lonchorhina*, *Macrotus*, *Micronycteris*, glossophagines [s.l.], and carolliines) and a "*Phyllostomus*-line" (Phyllonycterinae, *Phylloderma*, *Phyllostomus*, *Trachops*, Sturnirinae, Stenoderminae [= Stenodermatinae], and "probably" Desmodontinae). Smith (1972) allied *Chrotopterus*, *Mimon*, *Tonatia*, and *Vampyrum* with the "*Phyllostomus*-line" despite lacking postcranial skeletons of these genera.

Baker (1973) used chromosomal morphology to resolve relationships among stenodermatine bats, and proposed that the primitive karyotype for stenodermatines is similar to that of *Artibeus*, *Sturnira*, *Vampyrodes*, and *Vampyrops* (= *Platyrrhinus*). He divided these "basal" stenodermatines into three groups based on morphology of the Y chromosome. Baker (1973) divided species of *Sturnira* and *Vampyrops* between groups one and two, and species of *Artibeus* between groups two and three. Species of *Vampyrodes* appeared only in group two. From this basal stock (i.e., groups one, two, and three), Baker (1973) derived four lineages. The first lineage consisted of *Chiroderma*, *Vampyressa*, and *Mesophylla* (from least to most specialized), and was derived from groups one and two. Although no chromosomal data were available for *Ectophylla*, this genus was associated with the end of this lineage because it is morphologically similar to *Mesophylla*, as had been previously noted by Starett and Casebeer (1968). A second lineage consisted only of *Uroderma* species and was derived from groups two and three, whereas the third consisted of *Ametrida*, *Centurio*, *Stenoderma*, and *Sphaeronycteris* and presumably evolved from group three. Baker (1973) associated the karyologically unknown genera *Ardops*, *Ariteus*, *Phyllops*, and *Pygoderma* with the end of this lineage because they are morphologically similar to the other four taxa. *Enchisthenes* appeared as a separate offshoot of group three.

Greenbaum et al. (1975) described the karyotypes of *Ardops*, *Ariteus*, and *Phyllops*, and concluded that Baker (1973) had correctly identified their affinities. Greenbaum et al. (1975) suggested that *Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma* were more closely related to each other than to *Centurio* and *Sphaeronycteris*. However, these authors found that all "short-faced" stenodermatines formed a clade. Karyological data did not support previous associations of *Ectophylla* with *Mesophylla*, which were based on morphologic similarity (Laurie, 1955; Goodwin and Greenhall, 1961; Baker, 1973). Instead, Greenbaum et al. (1975) proposed that *Chiroderma* may be more closely related to *Mesophylla* and *Vampyressa* than is *Ectophylla*, or that *Ectophylla* diverged from the *Mesophylla-Vampyressa* line before a reduction in diploid number occurred. Greenbaum et al.'s (1975) conclusion also contrasted with Starett and Casebeer's (1968) opinion that *Ectophylla* is more derived than *Mesophylla* and *Vampyressa*.

Smith (1976) integrated previously published dental, host-parasite, immunological, karyological, and postcranial data in a "tentative" cladogram of phyllostomid relationships (fig. 5; see table 2). Noting that "much of the evidence up to this time is contradictory and confusing," Smith's (1976: 62) summary interpretation was proposed as a "point of departure for future investigations." Among the traditionally recognized subfamilies, only Phyllostominae and Glossophaginae were not monophyletic in Smith's (1976) tree.

Smith (1976) recognized two primary lineages of phyllostomids. The "*Macrotus*-lineage" consisted of Desmodontinae, a clade of phyllostomines (*Lonchorhina*, *Macrophyllum*, *Macrotus*, and *Micronycteris*), Phyllonycterinae (s.l.), a clade of glossophagines (except *Choeroniscus*, *Choeronycteris*, and *Musonycteris*), and Carolliinae (s.l.). *Brachyphylla* appeared as the sister taxon of *Phyllonycteris* and *Erophylla*, and Desmodontinae, Phyllonycterinae, and Carolliinae formed a clade. Smith's (1976) other group, the "*Phyllostomus*-lineage," included a monophyletic group composed of the remaining phyllostomines (*Chrotopterus*, *Mimon*, the extinct *Notonycteris*, *Phylloderma*, *Phyllostomus*, *Tonatia*, *Trachops*, and *Vampyrum*), a glossophagine clade consisting of *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, and Stenoderminae. Smith (1976) left relationships among the "*Phyllostomus*-lineage" clades unresolved.

At lower taxonomic levels, Smith's (1976) summary tree (fig. 5) indicated that *Diaemus*
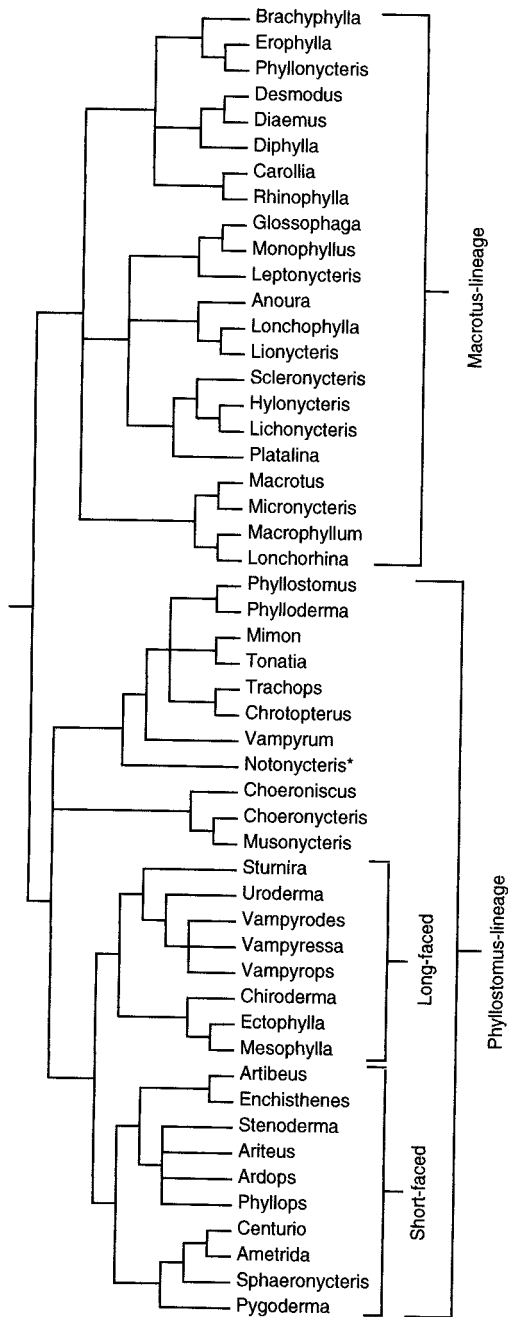
Fig. 5. "Tentative" phylogeny proposed by Smith (1976; redrawn from fig. 2) after an evaluation of previously published data including dental, immunological, karyological, parasitological, and postcranial data. Asterisk indicates an extinct taxon.

and *Desmodus* were sister taxa, forming a clade with *Diphylla*. Among phyllostomines of the "*Macrotus*-lineage," Smith (1976) suggested that *Macrotus* and *Micronycteris* were sister taxa, as were *Lonchorhina* and *Macrophyllum*. Among phyllostomines of the "*Phyllostomus*-lineage," Smith (1976) recognized three pairs of sister taxa: *Phylloderma* and *Phyllostomus*, *Mimon* and *Tonatia*, and *Chrotopterus* and *Trachops*. These three clades formed a polytomy; *Vampyrum* and the extinct *Notonycteris* appeared as successive sister taxa to this group. In Smith's (1976) tree, relationships among genera within the two glossophagine (s.l.) clades were identical to those proposed by Phillips (1971; see above).

Among stenodermines, Smith (1976) recognized a monophyletic group of "long-faced" genera consisting of *Chiroderma*, *Ectophylla*, *Mesophylla*, *Sturnira*, *Uroderma*, *Vampyressa*, *Vampyrodes*, and *Vampyrops* (= *Platyrrhinus*). Within this group, the sister taxa *Ectophylla* and *Mesophylla* formed a clade with *Chiroderma*. *Uroderma* and *Sturnira* were successive sister taxa to a trichotomy of *Vampyressa*, *Vampyrodes*, and *Vampyrops*. The second stenodermatine group recognized by Smith (1976) was composed of "short-faced" genera. Within this lineage, Smith (1976) identified a monophyletic group composed of *Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma*. These genera and the sister taxa *Artibeus* and *Enchisthenes* formed a clade. Finally, *Sphaeronycteris* and *Pygoderma* were successive sister taxa to *Ametrida* and *Centurio*.

McDaniel (1976) described aspects of brain anatomy in phyllostomids and presented two trees of potential phylogenetic relationships. McDaniel (1976) recognized Phyllostomatinae as the basal phyllostomid subfamily. *Brachyphylla* appeared as the sister taxon of Desmodontinae, and together with stenodermatines these taxa formed a clade derived from within Phyllostomatinae. The "*Macrotus*-type" phyllostomine (*Macrophyllum*, *Macrotus*, *Tonatia*, and *Trachops*) was derived from more basal phyllostomines (see below), and gave rise independently to phyllonycterines (s.s.), glossophagines, and carolliines. McDaniel (1976) noted that the brains of *Anoura*, *Choeronycteris*, and *Mon-*

*ophyllus* are very different from those of other glossophagines included in his study, suggesting that Glossophaginae might be diphyletic. McDaniel's (1976) second tree depicted relationships among phyllostomines. The sister taxa *Lonchorhina* and *Mimon* formed the basal branch within Phyllostomatinae. McDaniel (1976) depicted an uncertain relationship between *Vampyrum* and the sister taxa *Phylloderma* and *Phyllostomus* by using a dashed line; however, he provided no comments about this tentative relationship. The "*Macrotus*-type" phyllostomine appeared as the sister taxon of *Micronycteris*.

Wilder (1976) examined histology of the parotid gland in *Anoura*, *Glossophaga*, *Leptonycteris*, and *Monophyllus*. Based on parotid characters, *Anoura* appeared to be the most divergent glossophagine included in this study. Wilder (1976) suggested that an *Anoura*-like ancestor led to both *Anoura* and a group including the other three genera. In this latter group, *Glossophaga* and *Leptonycteris* were sister taxa.

Cadena and Baker (1976) found chromosomal similarities between desmodontines and some members of the subfamilies Phyllostominae, Phyllonycterinae, and Glossophaginae. In addition, these authors suggested that *Diaemus* and *Diphylla* were less derived than *Desmodus* because they had karyotypes more similar to the proposed primitive karyotype for phyllostomids.

Gardner (1977a; fig. 6) presented an "arbitrarily derived" tree of phyllostomid relationships mainly based on chromosomal data. Gardner (1977a) hypothesized that Desmodontinae, Phyllostominae, Carolliinae, and Stenoderminae were each monophyletic. Although Gardner (1977a) discussed the possible independent origin of several glossophagine (s.l.) groups, his tree depicted a single clade of nectar feeders. Relationships among these clades were unresolved.

Gardner's (1977a) Phyllostominae included three clades united in a polytomy: (1) *Lonchorhina* and *Macrophyllum*, (2) *Chrotopterus* and *Tonatia*, and (3) the remaining phyllostomine genera. Within the third clade, *Macrotus* and *Micronycteris* appeared as sister taxa. *Phylloderma* and *Phyllostomus* were also sister taxa, and formed a clade with *Mimon*. These two clades, *Trachops*, and *Vam-*
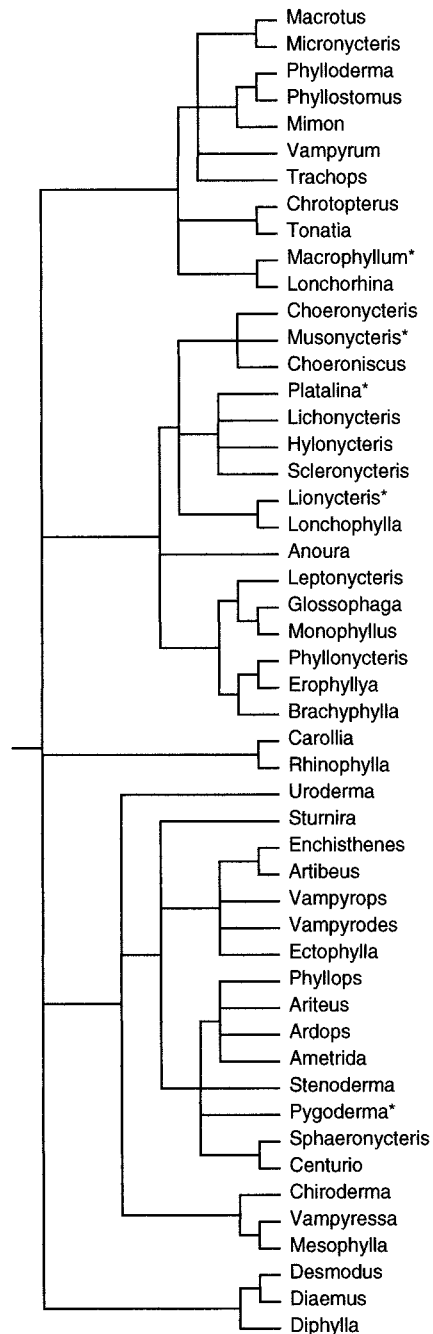


Fig. 6. Gardner's (1977a; redrawn from fig. 8) "arbitrarily derived" tree of phyllostomid relationships based on chromosomal similarities. Asterisks indicate taxa that were karyotypically unknown and whose placement was conjectural.

*pyrum* formed a polytomy. Placement of *Macrophyllum* was conjectural because its karyotype was unknown at that time.

Gardner (1977a) recognized three monophyletic groups within his nectar-feeder clade: (1) Phyllonycterinae (s.l.), *Glossophaga*, *Leptonycteris*, and *Monophyllus*; (2) *Anoura*; and (3) all remaining glossophagine genera. Within the first group, *Glossophaga* and *Monophyllus* were sister taxa and formed a clade with *Leptonycteris*. Also within this group, *Brachyphylla* appeared as the sister taxon of *Erophylla* and *Phyllonycteris*. Gardner (1977a) identified three clades within his third group: (1) *Choeroniscus*, *Choeronycteris*, and *Musonycteris*; (2) *Hylonycteris*, *Lichonycteris*, *Platalina*, and *Scleronycteris*; and (3) *Lionycteris* and *Lonchophylla*. Karyotypes of *Lionycteris*, *Musonycteris*, *Platalina*, and *Scleronycteris* were unknown at this time and their placement was conjectural.

Within Stenoderminae, Gardner (1977a) left the position of *Uroderma* unresolved. *Chiroderma*, *Mesophylla*, and *Vampyressa* formed a clade, and the latter two genera were sister taxa. Within the group formed by the remaining stenodermatine genera, Gardner (1977a) left the position of *Sturnira* unresolved. The sister taxa *Artibeus* and *Enchisthenes* formed a clade with *Ectophylla*, *Vampyrodes*, and *Vampyrops*. The final group consisted of ''short-faced'' stenodermatines. The positions of *Stenoderma* and *Pygoderma* (which was karyologically unknown) were unresolved, but *Ametrida*, *Ardops*, *Ariteus*, and *Phyllops* formed a clade, as did *Centurio* and *Sphaeronycteris*.

Bass' (1978) examination of G-banded karyotypes suggested that Desmodontinae, Phyllonycterinae, and Glossophaginae (s.l.) formed a clade, with Phyllostominae as the sister group. Bass (1978) found that the phyllonycterines and glossophagines included in her study have identical karyotypes and was therefore unable to draw conclusions concerning their relationships. However, Bass (1978) was able to resolve relationships among the desmodontine genera, and found that karyologically, *Desmodus* and *Diphylla* are more similar to each other than either is to *Diaemus*.

Using G-banded chromosomes and outgroup comparisons with noctilionids and mormoopids, Patton and Baker (1978) proposed that the karyotype of *Macrotus waterhousii* (FN = 60, 2n = 46) was primitive for phyllostomids. Patton and Baker (1978) identified two phyllostomine clades which differed from the more primitive *Macrotus waterhousii* karyotype: (1) *Micronycteris*, and (2) *Mimon*, *Phyllostomus*, and *Tonatia*. In the second clade, the former two genera appeared as sister taxa.

Johnson (1979) carried out additional karyological work and suggested that phyllostomines diverged before other subfamilies. This group was followed by desmodontines and stenodermatines, which split from a glossophagine-brachyphylline group before either of these latter subfamilies was distinct. Although G-banded chromosomes provided no resolution within much of the stenodermatine clade, Johnson (1979) did note that *Mesophylla* is karyologically very similar to *Vampyressa pusilla* (G-banded chromosomes of *Ectophylla* were not available).

Straney et al. (1979: 169) used allozyme data to produce a ''phylogenetic estimate'' of relationships among 13 phyllostomid genera. *Phyllostomus* and *Carollia* appeared as sister taxa in their tree. This group formed a clade with stenodermatines, except *Sturnira*. Within the stenodermatine clade, *Chiroderma* and *Uroderma* were sister taxa and grouped with *Artibeus* (*Dermanura*) *cinereus*, *Artibeus lituratus*, and *Vampyrops* (= *Platyrrhinus*). The last three taxa formed a clade; *Artibeus cinereus* and *Vampyrops* appeared to be more closely related to each other than to *A. lituratus*. *Artibeus jamaicensis* and *Ametrida* were successive sister taxa to this larger stenodermatine group.

The other large clade identified by Straney et al. (1979) included *Desmodus*, glossophagines, and *Sturnira*. *Desmodus* was nested within Glossophaginae, as the sister taxon of *Glossophaga*. This group formed a clade with *Anoura* and *Sturnira* as successive sister taxa. This assemblage and the phyllostomine group described above were sister taxa.

Straney (1980) used allozymic, karyological, immunological, and morphological data in separate component analyses designed to elucidate relationships among phyllostomines. Based on morphological data, Straney (1980) identified four groups of phyllosto-

mids defined by two or more derived character states (replicated components). These groups were: (1) *Lonchorhina*, *Macrophyllum*, and *Macrotus*; (2) *Lonchorhina* and *Macrophyllum*; (3) *Chrotopterus*, *Trachops*, and *Vampyrum*; and (4) *Chrotopterus* and *Vampyrum*. In addition to identifying the replicated components, Straney (1980) used subsets of his derived, "reliable" characters (i.e., adequately sampled characters that did not involve loss or reduction) that defined compatible groups to construct "compatible cladograms." In all but one of the 18 compatible cladograms that Straney (1980) identified, Desmodontinae was the sister taxon of the remaining phyllostomids. Another frequent grouping included *Lonchorhina*, *Macrophyllum*, *Macrotus*, and *Mimon bennettii*. Straney (1980) suggested that, based on his data set, the two subgenera of *Mimon* should not be considered congeneric; in 13 of the 18 cladograms Straney (1980) examined, these two taxa were not each other's closest relative.

Straney (1980) evaluated the compatibility of his morphologically based phylogenetic hypotheses with the data then available from chromosomes (e.g., Patton and Baker, 1978; Baker, 1979) and his own work in immunology. Although he did not find any congruence between the phylogenies based on karyology and his findings based on morphology, he did find that one of the clades he had identified using immunology appeared in his morphology tree. The base of Straney's (1980) immunology tree was a trichotomy. *Macrotus* was associated with *Desmodus*, whereas *Glossophaga*, *Carollia*, and *Artibeus* formed a clade with *Carollia* and *Artibeus* as sister taxa. The third group included two "tentatively" placed taxa, *Chrotopterus* and *Trachops*, which were united with *Vampyrum*. *Chrotopterus* and *Vampyrum* appeared as sister taxa. Based on all the available data, Straney (1980) concluded that the relationships of these three taxa, *Chrotopterus*, *Trachops*, and *Vampyrum*, were most likely to reflect phylogenetic relationships.

Finally, Straney (1980) conducted an allozyme analysis, using two methods, outgroup comparisons and component analysis, to produce trees. Although Straney (1980) did find several trees using the outgroup technique, each contained at least one group whose position was ambiguous. Straney (1980) felt unable to choose among these trees using only the allozyme data alone. His component analysis was more successful. Straney (1980) was able to identify three additional phyllostomid clades above the generic level: (1) *Macrophyllum* and *Phyllostomus*, (2) *Carollia* and *Rhinophylla*, and (3) *Desmodus* and *Diphylla*.

Corbet and Hill (1980, 1986; see table 2) presented a classification of the family, recognizing six subfamilies: Phyllostomatinae, Phyllonycterinae (which included *Brachyphylla*), Glossophaginae, Carolliinae, Sturnirinae, and Stenoderminae. Desmodontines appeared in a separate family.

Handley (1980) standardized nomenclature by correcting the misuse of certain familial and subfamilial names which were the result of improperly applied Greek and Latin word-formation rules. Handley (1980) noted that Phyllostomidae and Phyllostominae are correct, while Phyllostomatidae and Phyllostomatinae are not. Stenoderminae is an incorrect name for Stenodermatinae. Desmodidae (and hence Desmodinae) is an incorrect form of Desmodontidae (or Desmodontinae).

Baker and Lopez (1970) and Baker and Bass (1979) documented the similarity of the chromosomes in *Brachyphylla*, phyllonycterines, and glossophagines, but these authors were not able to clarify relationships among these taxa. Baker et al. (1981a) used electrophoretic and immunological data to address this question. Their results indicated that *Brachyphylla* was the sister taxon of *Erophylla* and *Phyllonycteris*. *Anoura*, *Choeroniscus*, *Hylonycteris*, and *Leptonycteris* were more closely related to *Glossophaga* and *Monophyllus* than to brachyphyllines. Finally, Baker et al. (1981a: 671) found that *Lionycteris* and *Lonchophylla* were "the most divergent of all the glossophagine and brachyphylline genera examined." However, the relationship between these two genera was described as "tenuous," and Baker et al. (1981a) were not able to determine whether *Lionycteris* and *Lonchophylla* were derived or primitive relative to other glossophagines.

Griffiths (1982) developed a hypothesis of relationships among nectar-feeding phyllos-
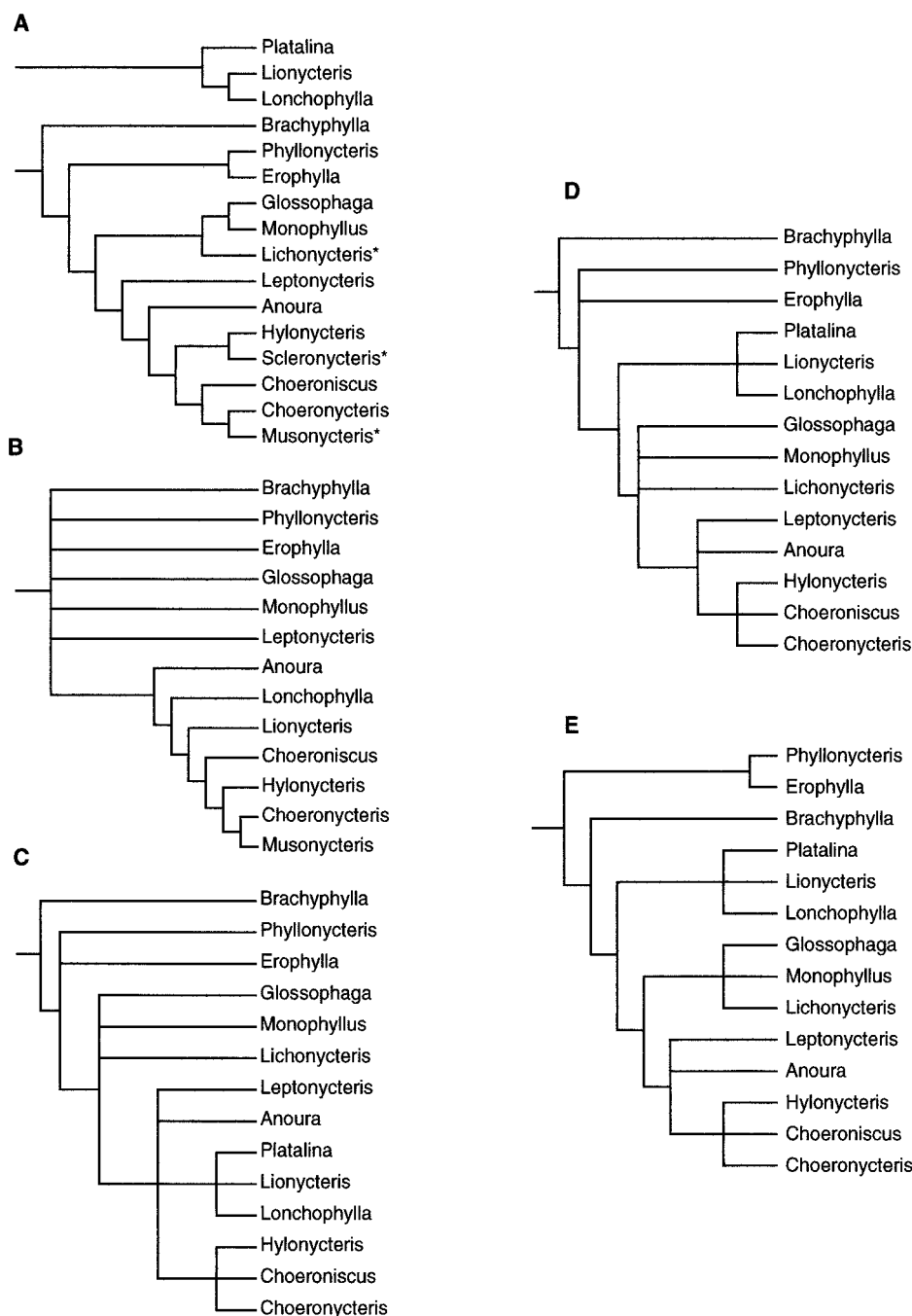
Fig. 7. **A.** Griffiths' (1982; redrawn from fig. 33) hypothesis of relationships among nectar-feeding phyllostomids based on hyoid and lingual data and additional consideration of karyological and dental data. The open base of the cladogram signifys the possible relationship of the lonchophylline clade to other nonnectar-feeding phyllostomids. Asterisks indicate taxa whose placement was based soley on craniodental data. **B.** Haiduk and Baker's (1982; redrawn from fig. 8) tree depicting relationships among nectar-feeding phyllostomids based on G-banded chromosome morphology. **C.** Haiduk and Baker's (1982; redrawn from fig. 9) reanalysis of Griffiths' (1982) original data, without consideration of char-

tomids based on a cladistic analysis of tongue and hyoid morphology, and some consideration of craniodental morphology and karyotypes (fig. 7A; see table 2). As many had before him, Griffiths (1982) proposed that glossophagines were not monophyletic. However, Griffiths (1982) ignited controversy by recognizing a new subfamily (Lonchophyllinae) for *Lionycteris*, *Lonchophylla*, and *Platalina* (see table 2), and by suggesting that Lonchophyllinae might be more closely related to nonnectar-feeding phyllostomids than to phyllonycterines, glossophagines (s.s.), or brachyphyllines. Winkelmann (1971) and Thomas (1903) had previously suggested a close relationship among these three genera. Winkelmann (1971: 90) indicated that *Lionycteris*, *Lonchophylla*, and *Platalina* formed a ''natural evolutionary unit,'' and suggested that this group was not closely related to other nectar feeders. Instead Winkelmann (1971) suggested that each group of nectar feeders had arisen from phyllostomine-like ancestors.

In Griffiths' (1982) tree (fig. 7A), *Lionycteris* and *Lonchophylla* were sister taxa and formed a clade with *Platalina*. The lonchophylline clade was not united with the rest of the cladogram to signify the possible close relationship of lonchophyllines to other nonnectar-feeding phyllostomids. *Brachyphylla* appeared as the sister taxon of the phyllonycterine-glossophagine clade, although Griffiths (1982) considered this placement tentative because he could identify only one potential synapomorphy uniting this group.

Subsequently, Griffiths (1985) changed his assessment of the relationship of *Brachyphylla* to Phyllonycterinae when he described several derived dental features of a brachyphylline (s.l.) clade. Griffiths (1985) further suggested that this group shared a common ancestor with Glossophaginae. However, in Griffiths' (1982) tree, Phyllonycterinae (s.s.) appeared as the sister taxon of glossopha-

gines. Within Glossophaginae, Griffiths (1982) found that *Hylonycteris*, *Anoura*, and *Leptonycteris* appeared to be successive sister taxa to *Choeroniscus* and *Choeronycteris*. The most basal glossophagine clade consisted of *Glossophaga* and *Monophyllus*. Based on characters of the teeth and basicranial region only, Griffiths (1982) placed *Musonycteris* with *Choeronycteris* and *Scleronycteris* with *Hylonycteris*. Griffiths (1982) placed *Lichonycteris* as the sister taxon of the *Glossophaga-Monophyllus* clade based on karyological and dental evidence.

Griffiths' (1982) conclusions drew criticism from several researchers. Haiduk and Baker (1982) performed a cladistic analysis of G-banded chromosome morphology in nectar-feeding phyllostomids, and their results did not support lonchophylline monophyly. In the tree based on G-band data (fig. 7B), the positions of *Brachyphylla*, *Erophylla*, *Phyllonycteris*, *Glossophaga*, *Leptonycteris*, and *Monophyllus* were unresolved. *Hylonycteris*, *Choeroniscus*, *Lionycteris*, *Lonchophylla*, and *Anoura* appeared as successive sister taxa to *Choeronycteris* and *Musonycteris*.

Although lonchophyllines did not appear to be monophyletic based on these results, Haiduk and Baker (1982) noted that standard karyotypes of *Lonchophylla robusta* appeared very similar to the standard karyotype of *Lionycteris spurelli*. Unfortunately, G-banded karyotypes of this species were unavailable, and *Lonchophylla thomasi*, which has a highly derived karyotype, was used. If the G-banded karyotype of *L. robusta* is more similar to that of *Lionycteris*, Haiduk and Baker (1982) suggested that it would indicate that these two genera had shared a common ancestor, with *L. thomasi* subsequently becoming more derived. Thus, lonchophyllines would be monophyletic.

Haiduk and Baker (1982) also presented the results of an unweighted parsimony analysis based on the original coding of Griffiths'

←

acter weights employed by Griffiths (1982) or karyological and dental data. **D.** Griffiths' (1983; redrawn from fig. 1) response to Haiduk and Baker (1982) was a cladogram based only on hyoid and lingual morphology. **E.** Smith and Hood's (1984; redrawn from fig. 3B) reanalysis of Griffiths' (1982) original data using an all zero outgroup and no character weights.

(1982) data. In this tree (fig. 7C), *Brachyphylla* appeared as the sister taxon of the remaining nectar feeders. *Erophylla*, *Phyllonycteris*, and glossophagines (s.l.) formed a polytomy. Within Glossophaginae (s.l.), the positions of *Glossophaga*, *Lichonycteris*, and *Monophyllus* were unresolved, but the remaining taxa formed a clade. The latter group was composed of a monophyletic Lonchophyllinae, *Anoura*, *Leptonycteris*, and a clade consisting of *Choeroniscus*, *Choeronycteris*, and *Hylonycteris*.

Griffiths (1983a) responded to Haiduk and Baker's (1982) critique with another cladogram (fig. 7D) based exclusively on hyoid and tongue data and constructed without the character weights used in his previous study (i.e., Griffiths, 1982). This tree was less resolved than that presented by Griffiths (1982), but was similar to the hyoid data tree presented by Haiduk and Baker (1982; fig. 7C). However, there was one important exception: in Griffiths' (1983a; fig. 6D) new tree, Lonchophyllinae appeared as the sister taxon of Glossophaginae (s.s.), rather than nesting within Glossophaginae as suggested by Haiduk and Baker (1982; fig. 7C). Griffiths (1982) had previously rejected a sister group relationship between glossophagines and lonchophyllines because he felt that brachyphyllines, phyllonycterines, and glossophagines shared more derived dental traits, and that some of the tongue and hyoid characters deserved more weight than others.

Warner (1983) favored the original Griffiths (1982) hypothesis, viewing Haiduk and Baker's (1982) G-banding study with skepticism due to problems with identifying homologous chromosome arms. Warner (1983) suggested that Griffiths' (1982) tree was supported by immunological data presented by Baker et al. (1981a, see above). Although Baker et al. (1981a: 671) had noted that *Lionycteris* and *Lonchophylla* were the most immunologically divergent among nectar feeders, they also noted that "the proposition that two or more glossophagine lineages arose independently from a non-nectar-feeding stock is highly suspect." Baker et al. (1981a) also added that they could not determine if *Lionycteris* and *Lonchophylla* had chromosomes that were derived or primitive relative to those of other glossophagines.

Smith and Hood (1984: 457) discussed observational inaccuracies and methodological flaws in Griffiths' (1982, 1983a) studies and presented several trees based on Griffiths' (1982) original coding of the data. Their most "diagnostically efficient" tree (fig. 7E), which was constructed using a hypothetical (all zero) outgroup, depicted slightly different relationships than those found by other authors (Smith and Hood, 1984: 456). *Erophylla* and *Phyllonycteris* appeared as sister taxa and formed a clade with all other nectar feeders. *Brachyphylla* was the sister taxon of a clade composed of glossophagines and lonchophyllines, which were each monophyletic. The only additional difference between this tree and that presented by Griffiths (1983a) is the recognition of a clade composed of *Glossophaga*, *Lichonycteris*, and *Monophyllus*.

Hood and Smith (1982, 1983; fig. 8) presented a cladistic analysis of phyllostomid subfamilial relationships using characters of the female reproductive tract. A monophyletic Stenoderminae, *Carollia*, and *Rhinophylla* formed a clade. This group formed a polytomy with brachyphylline (s.l.) and glossophagine (s.l.) genera. The genera of the "*Phyllostomus*-group" (*Phylloderma*, *Phyllostomus*) formed a polytomy with the nectar-feeder and fruit-feeder clade. Genera in the "*Macrotus*-group" (*Macrotus*, *Micronycteris*, and *Trachops*) formed a polytomy with the nectar-feeder, fruit-feeder, and *Phyllostomus*-group clade. *Desmodus* was the sister taxon to all other phyllostomids.

Koopman (1984) presented a classification of Phyllostomidae in which he recognized six subfamilies: Phyllostominae, Glossophaginae, Carolliinae, Stenoderminae, Brachyphyllinae (including *Brachyphylla* and phyllonycterines), and Desmodontinae.

Pierson (1986; fig. 9) used transferrin immunology to investigate relationships among phyllostomids. Pierson (1986) found that Phyllostominae was not monophyletic because *Brachyphylla* and the stenodermatines *Artibeus* and *Sturnira* appeared to be derived from within phyllostomines. Other results included: (1) *Mimon* and *Tonatia* were related to *Phyllostomus*; (2) *Chrotopterus*, *Trachops*, and *Vampyrum* formed a clade; (3) *Brachyphylla* and *Glossophaga* formed a monophy-
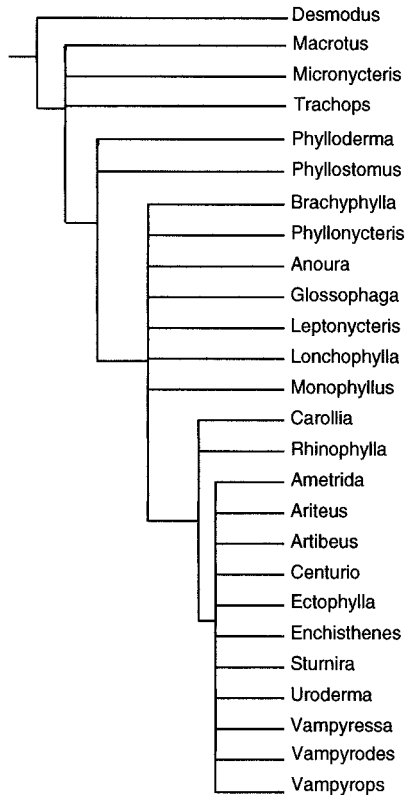
Fig. 8. Hood and Smith's (1982; redrawn from fig. 5) hypothesis of higher-level relationships among phyllostomid bats based on morphology of the female reproductive tract.
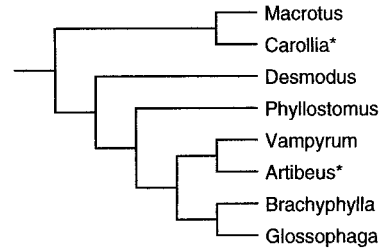


Fig. 9. Pierson's (1986; redrawn after fig. 35) proposed phylogeny of phyllostomid relationships based on transferrin immunology. This tree does not include all the taxa used by Pierson (1986); see the text for discussion of additional relationships. Asterisks indicate taxa for which antisera were unavailable.

letic group; (4) *Artibeus*, *Sturnira*, and possibly the *Brachyphylla-Glossophaga* clade were allied with the *Vampyrum* lineage. In some of the analyses, *Macrotus* formed the most basal phyllostomid branch, while in other analyses desmodontines were basal. Although Pierson (1986) found a relationship between *Macrotus* and *Carollia*, she noted that this finding was probably due to the conservative nature of the transferrin of *Carollia*.

Honeycutt (1981) and Honeycutt and Sarich (1987a) used albumin immunology to investigate phyllostomid relationships (fig. 10). These authors found that *Macrotus*, which was the most immunologically divergent phyllostomine, associated with desmodontines to form a basal phyllostomid lineage. Honeycutt (1981) and Honeycutt and Sarich (1987a) postulated that a slower rate of evo-

lution in desmodontines or equal yet independent divergence in albumins from those of other phyllostomids might have caused this unusual association. However, they found no conclusive evidence to support either possibility.

Honeycutt (1981) and Honeycutt and Sarich (1987a) also recognized a *Phyllostomus-Tonatia* group and a *Micronycteris-Vampyrum* group. The *Micronycteris-Vampyrum* group appeared as the sister taxon of a clade that included the *Phyllostomus-Tonatia* group, *Phyllonycteris*, *Brachyphylla*, *Glossophaga*, *Monophyllus, Carollia*. Using reciprocal comparisons between *Artibeus* anti-
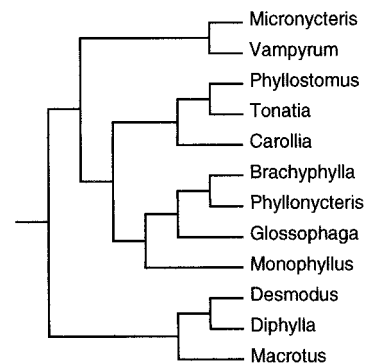


Fig. 10. Honeycutt's (1981; redrawn after fig. 2) and Honeycutt and Sarich's (1987a; redrawn after fig. 1) tree based on bidirectional immunological comparisons of albumins. The authors fit other taxa into this tree using unidirectional comparisons; placement of these taxa is described in the text.

sera and groups of antisera representing major lineages, these authors found that *Artibeus* associated with *Carollia*. Unidirectional comparisons were used to fit other taxa into this tree. *Chrotopterus* associated with the *Micronycteris-Vampyrum* group. *Lonchorhina*, *Macrophyllum*, and *Mimon* associated with the *Phyllostomus-Tonatia* group, but Honeycutt (1981) and Honeycutt and Sarich (1987a) noted that the association between *Lonchorhina* and the *Phyllostomus-Tonatia* clade was no closer than that seen between *Carollia* and this clade. Honeycutt (1981) found that *Phylloderma* associated with *Phyllostomus*.

Honeycutt's (1981) and Honeycutt and Sarich's (1987a) results indicated that the nectar-feeding taxa formed a clade. However, these authors found that Glossophaginae was paraphyletic because *Glossophaga* and *Monophyllus* were successive sister taxa to a clade containing *Brachyphylla* and *Phyllonycteris*. Honeycutt (1981) carried out unidirectional immunological comparisons with *Brachyphylla*, *Phyllonycteris*, *Glossophaga*, and *Monophyllus* to place *Erophylla*, *Anoura*, *Hylonycteris*, *Leptonycteris*, *Lionycteris*, and *Lonchophylla* in the tree. *Erophylla* associated with *Phyllonycteris*. *Leptonycteris* appeared closer to the *Glossophaga* lineage, whereas *Anoura* and *Choeroniscus* associated with the *Monophyllus* lineage. *Hylonycteris* could be placed at the base of either the *Glossophaga* or *Monophyllus* lineages. Honeycutt (1981) could not assess the relationships of *Lionycteris* and *Lonchophylla* because it appeared that these two genera represented independent lineages that had branched off prior to the brachyphylline-glossophagine common ancestor.

Honeycutt's (1981) and Honeycutt and Sarich's (1987a) results indicated that *Carollia* and *Artibeus* formed a clade that was the sister group of the *Phyllostomus-Tonatia* clade. Honeycutt's (1981) results also indicated that Carolliinae might not be monophyletic, since *Rhinophylla* associated with either *Carollia* or *Micronycteris*. However, Honeycutt (1981) used only unidirectional comparisons and could not resolve this question. Finally, Honeycutt (1981) and Honeycutt et al. (1981) reported that *Desmodus* and
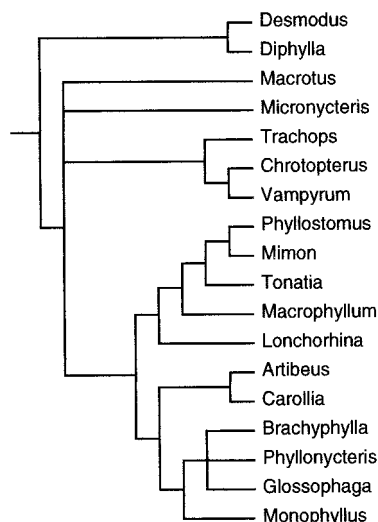


Fig. 11. Consensus tree from Honeycutt and Sarich (1987a; redrawn from fig. 3) based on immunological, chromosomal, and morphological data.

*Diaemus* were sister taxa within Desmodontinae.

Honeycutt and Sarich (1987a) also assessed congruence of their results with morphological data (from Griffiths, 1982; Hood and Smith, 1982; and Smith and Hood, 1984) and karyological data (from Patton and Baker, 1978; and Baker et al., 1979). A consensus tree based on these three data sets (fig. 11) suggested to Honeycutt and Sarich (1987a) that a major revision of Phyllostomidae was necessary. In the consensus tree, one clade was composed of a monophyletic group of nectar-feeding taxa and the fruit-feeding clade of *Carollia* and *Artibeus*. Within the nectar-feeding clade, *Brachyphylla*, *Phyllonycteris*, and *Glossophaga* formed a polytomy; *Monophyllus* appeared as the sister taxon of this group. The nectar- and fruit-feeder clade was the sister taxon of a group of phyllostomines (*Lonchorhina*, *Macrophyllum*, *Mimon*, *Phyllostomus*, and *Tonatia*; see fig. 11). This large clade and *Macrotus*, *Micronycteris*, and another phyllostomine clade (*Chrotopterus*, *Trachops*, and *Vampyrum*) formed a polytomy. Desmodontines occupied the basal branch within the family.

Owen (1987) conducted a parsimony analysis of relationships of stenodermatine bats

using discrete and continuous craniodental and external characters. Owen's (1987) ''best phylogenetic hypothesis'' (fig. 12A) indicated that *Artibeus* (s.l.) was not monophyletic. Owen (1987) suggested that small-bodied *Artibeus* species should be placed in a separate genus, *Dermanura*. He also suggested that, if *Vampyressa* is monophyletic, *Mesophylla* should be considered congeneric with it. The basal node of Owen's (1987) tree was a polytomy that included two clades of *Sturnira* and two larger clades (fig. 12A). The first of these latter groups consisted of a clade of ''short-faced'' stenodermatines, *Dermanura concolor* (= *Koopmania*; Owen, 1991), a clade of all remaining *Dermanura* species, and *Enchisthenes*. Within the ''short-faced'' stenodermatine group, the positions of *Centurio*, *Pygoderma*, and *Stenoderma* were unresolved, but *Ametrida* and *Sphaeronycteris* formed a clade, as did *Ardops*, *Ariteus*, and *Phyllops*. *Ardops* and *Ariteus* were sister taxa. Within the second large clade, Owen (1987) recognized five branches forming a polytomy: (1) *Vampyressa melissa*; (2) *V. bidens*, *V. brocki*, and *V. pusilla*; (3) *V. nymphaea* and *Mesophylla*; (4) *Chiroderma*, *Vampyrodes*, and *Vampyrops* (= *Platyrrhinus*); and (5) *Ectophylla*, a clade of all large *Artibeus*, and *Uroderma*.

Subsequently, Owen (1991) used selected discrete-state characters from his previous study in a parsimony analysis that included all species of *Dermanura* and all ''short-faced'' stenodermatines. Owen's (1991) ''proposed phylogeny'' (fig. 12B) was more resolved than his previous hypothesis (Owen, 1987; fig. 12A). *Dermanura concolor*, *Dermanura hartii*, and a clade composed of the remaining *Dermanura* species were successive sister taxa to the ''short-faced'' stenodermatines. Based on this outcome, Owen (1991) recommended recognizing *Enchisthenes* as a genus separate from *Artibeus*, and proposed that *Dermanura concolor* should be placed in a new genus, *Koopmania*. Owen (1991) did not make nomenclatural recommendations for the paraphyletic *Phyllops*, which included *Ardops* in his tree. *Stenoderma* was the sister taxon of *Ametrida* and *Sphaeronycteris* in this tree, and the positions of *Centurio* and *Pygoderma* were resolved (fig. 12B). *Ariteus*, previously a member of

the *Ardops-Phyllops* clade, became the sister taxon of *Centurio* and *Pygoderma*. The *Ardops* and *Centurio* clades were sister taxa in Owen's (1991) revised tree.

Lim (1993) recoded and reanalyzed the discrete-state craniodental and external characters from Owen's (1987, 1991) data sets, and added some new characters. The ''working hypothesis'' (fig. 12C) proposed by Lim (1993: 158) included two stenodermatine clades. The first clade included all ''short-faced'' genera. *Pygoderma* appeared as the sister taxon of all other ''short-faced'' stenodermatines. *Ametrida*, *Centurio*, and *Sphaeronycteris* formed a clade, with the latter two genera as sister taxa. *Ardops* and *Phyllops* were successive sister groups to a clade including *Ariteus* and *Stenoderma*. In the second stenodermatine group, two pairs of sister taxa formed a clade: (1) *Ectophylla* and *Mesophylla*, and (2) *Chiroderma* and *Vampyressa*. Successive sister taxa to this large clade were the sister genera *Platyrrhinus* and *Vampyrodes*, a clade consisting of *Artibeus* (s.l) and *Uroderma*, and *Sturnira*.

In Lim's (1993) analyses all members of the genus *Artibeus* were scored identically, and although he found no unique synapomorphy uniting this group, trees in which *Dermanura* was separated from *Artibeus* were two steps longer. Synonymy of *Mesophylla* with *Vampyressa* was also shown to be unwarranted, as these genera did not appear to be sister taxa in Lim's (1993) tree.

Lim (1993) also conducted a strict parsimony analysis of Owen's (1991) data set that used Owen's (1991) original character coding. The resulting tree (fig. 12D) was very different from Owen's (1991) analysis of the same data (fig. 12B). In Lim's (1993) tree (fig. 12D), *Artibeus* (s.s.) and *Dermanura* were sister taxa, further weakening Owen's (1987, 1991) contention that *Dermanura* should be recognized as a genus distinct from (and not particularly closely related to) *Artibeus*. Although *Enchisthenes* and *Koopmania* did not form a clade with *Artibeus* and *Dermanura* in Lim's (1993) reanalysis, Lim (1993: 152) suggested that Owen's (1991) results should be viewed with caution because of Lim's ''concerns about the discrete-state character set,'' rampant homoplasy, and violation of the assumption of ingroup mono-
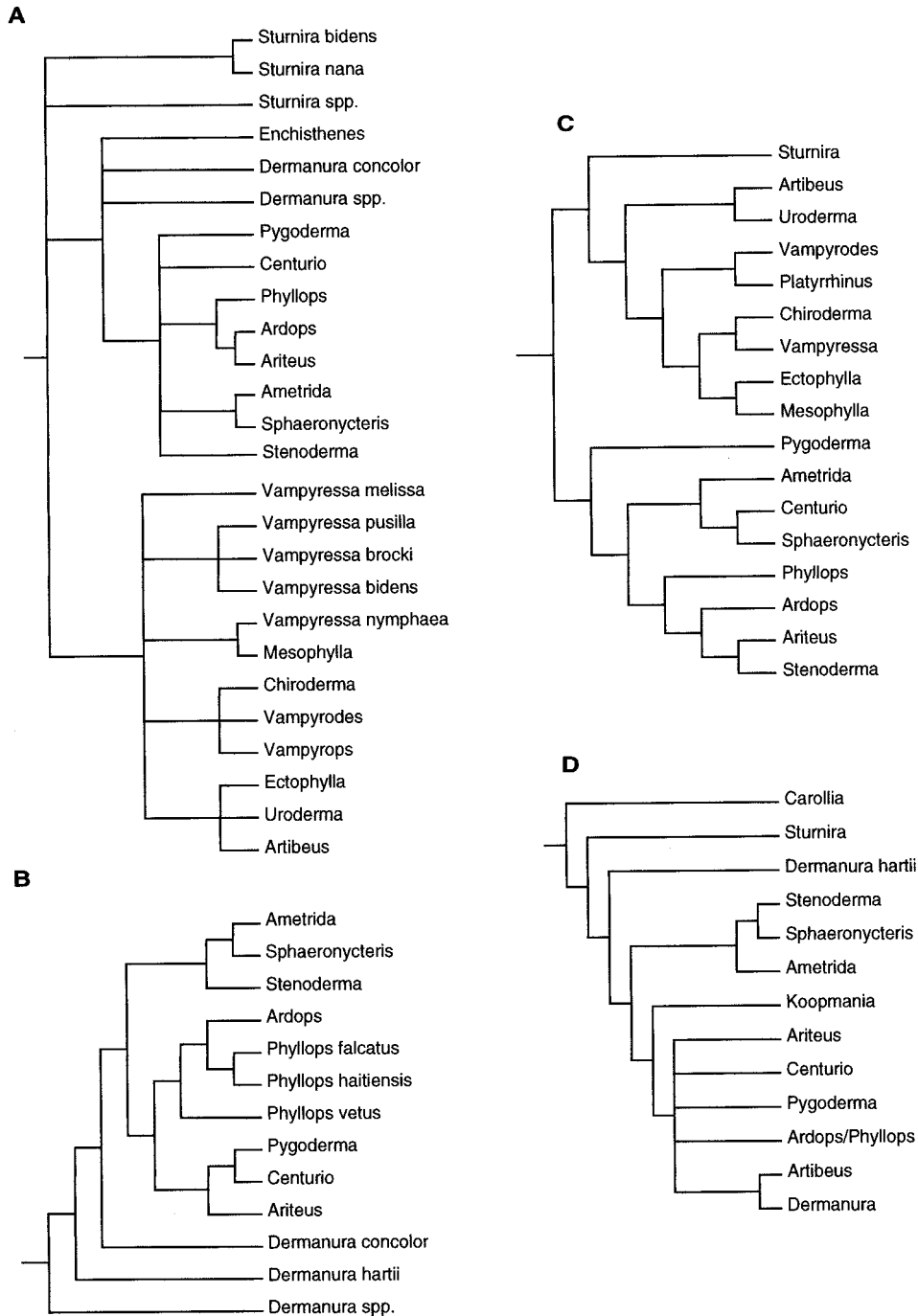
Fig. 12. **A.** Hypothesis of stenodermatine generic relationships proposed by Owen (1987) based on his study of continuous and discrete craniodental and external characters (redrawn from Owen, 1987: fig. 17). **B.** Result of Owen's (1991; redrawn from fig. 1) study designed to clarify relationships among *Dermanura*, *Enchisthenes*, and *Koopmania*, which was based on a reanalysis of selected characters from Owen (1987). **C.** Lim's (1993; redrawn from fig. 6) "working hypothesis" of stenodermatine relationships using discrete craniodental and external characters. Note that *Artibeus* includes *Dermanura*, *Enchisthenes*, and *Koopmania*. **D.** Lim's (1993; redrawn after fig. 3) reanalysis of Owen's (1991) data set.

phyly (i.e., *Artibeus*, an outgroup according to Owen [1991], grouped with *Dermanura*).

Baker et al. (1989) investigated higher-level phyllostomid relationships and produced a consensus tree (fig. 13A) that incorporated previous work in immunology (Baker et al., 1981a; Honeycutt et al, 1981; Arnold et al., 1982; Honeycutt and Sarich, 1987a; Honeycutt and Sarich, 1987b), karyology (Bass, 1978; Patton and Baker, 1978; Baker, 1979; Baker and Bass, 1979; Baker et al., 1979, 1981a, 1987, 1988a; Johnson, 1979; Haiduk and Baker, 1982; Baker, unpublished data cited in Baker et al., 1989), and morphology (Hood and Smith, 1982). The tree presented by Baker et al. (1989; fig. 13A) was similar to the consensus tree constructed by Honeycutt and Sarich (1987a; fig. 11) although it was less resolved. Unlike Honeycutt and Sarich (1987a), Baker et al. (1989) presented a revised classification based on their tree (see table 2). Desmodontinae was the only traditionally recognized subfamily that Baker et al. (1989) found to be monophyletic. Desmodontinae, *Macrotus*, *Micronycteris*, Vampyrinae (consisting of *Chrotopterus*, *Trachops*, and *Vampyrum*), and a redefined ''Phyllostominae'' formed a basal polytomy in their tree (fig. 13A). Phyllostominae included three tribes: Phyllostomini (the remaining phyllostomine genera), Glossophagini (brachyphyllines, phyllonycterines, glossophagines, and lonchophyllines), and Stenodermatini (carolliines and stenodermatines). Relationships among phyllostomine tribes were left unresolved. Baker et al. (1989) classified all genera in these higher-level groups as sedis mutabilis (taxonomic position unclear).

Van Den Bussche (1991) analyzed restriction site data from the ribosomal DNA gene complex, but found that the few informative characters and the large amount of homoplasy prevented the construction of a robust hypothesis on the basis of these data alone. To circumvent these problems, Van Den Bussche (1991) tested previously proposed phylogenies (from Smith [1976] and Baker et al. [1989]) for congruence with the restriction site data. The topology of the Baker et al. (1989) tree explained the restriction site data better than the Smith (1976) topology, requiring seven fewer steps (Van Den Bussche, 1991). Van Den Bussche (1992; fig. 13B)

subsequently mapped his restriction site characters on the cladogram proposed by Baker et al. (1989; see fig. 13A) to resolve relationships among genera. Results of this analysis indicated that *Micronycteris* was allied with Vampyrinae. Within Phyllostomini, *Macrophyllum* appeared as the sister taxon of the remaining genera. Within Stenodermatini, *Artibeus*, *Chiroderma*, and *Sturnira* formed a clade that was the sister taxon of a monophyletic group formed by the remaining stenodermatine genera, *Carollia*, and *Rhinophylla* (fig. 13B). Although the positions of many stenodermatines within the latter clade were unresolved, the restriction site data did diagnose two larger groups: (1) *Uroderma*, *Vampyrodes*, and *Vampyrops* (= *Platyrrhinus*); and (2) *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Pygoderma*, and *Stenoderma*. Van Den Bussche (1992) was unable to resolve relationships among three clades of nectar-feeding bats: (1) Brachyphyllinae (s.l.), (2) *Anoura*, *Glossophaga*, *Leptonycteris*, *Lionycteris*, *Lonchophylla*, and *Monophyllus*; and (3) *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris*. Based on the restriction site data, and consideration of immunological, karyological, and morphological evidence, Van Den Bussche (1992) proposed the recognition of Macrotinae and Micronycterinae as monogeneric subfamilies.

Van Den Bussche et al. (1993) examined 402 base pairs of the cytochrome *b* gene and an *Eco*RI-defined nuclear satellite DNA repeat. The satellite DNA repeat was found only in *Artibeus*, *Dermanura*, and *Koopmania*, suggesting that these three taxa formed a clade. Cytochrome *b* data also supported this hypothesis. *Enchisthenes* was found to lack the satellite DNA repeats seen in the other three taxa, and in a bootstrap tree of the cytochrome *b* data, *Enchisthenes* appeared as the sister taxon of *Centurio* rather than *Artibeus* (s.l.).

Van Den Bussche et al. (1998) examined the entire cytochrome *b* gene (1,140 bases) in 26 species of *Artibeus* (s.l.). This work supported the monophyly of a clade including *Artibeus*, *Dermanura*, and *Koopmania*. *Artibeus* and *Dermanura* appeared as sister taxa. Given these relationships, Van Den Bussche et al. (1998) retained *Koopmania* in
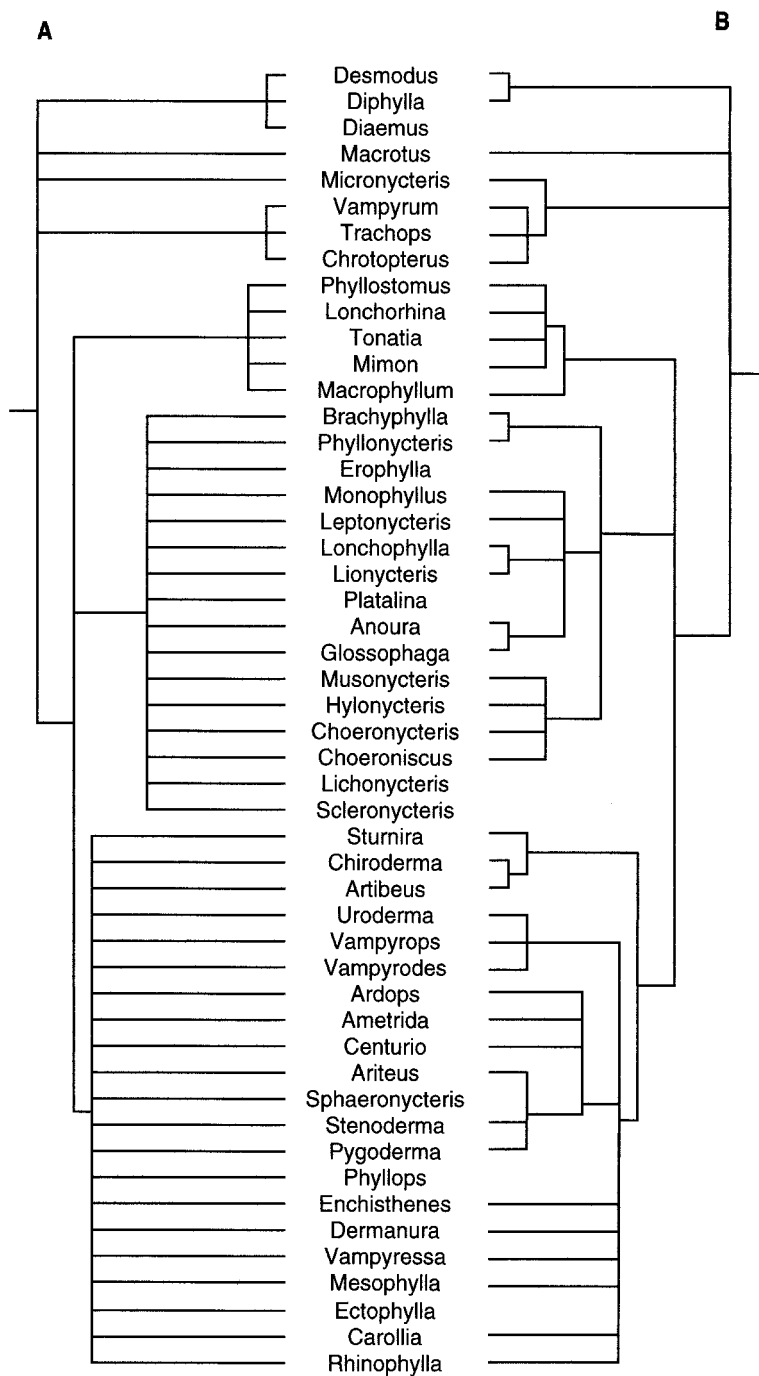
Fig. 13. **A.** Baker et al.'s (1989; redrawn after fig. 2) consensus tree based on morphology, immunology, and karyology. **B.** Van Den Bussche's (1992; redrawn from fig. 2) tree derived from mapping restriction sites onto the Baker et al. (1989) topology in an attempt to improve resolution of relationships within the clades identified by Baker et al. (1989).
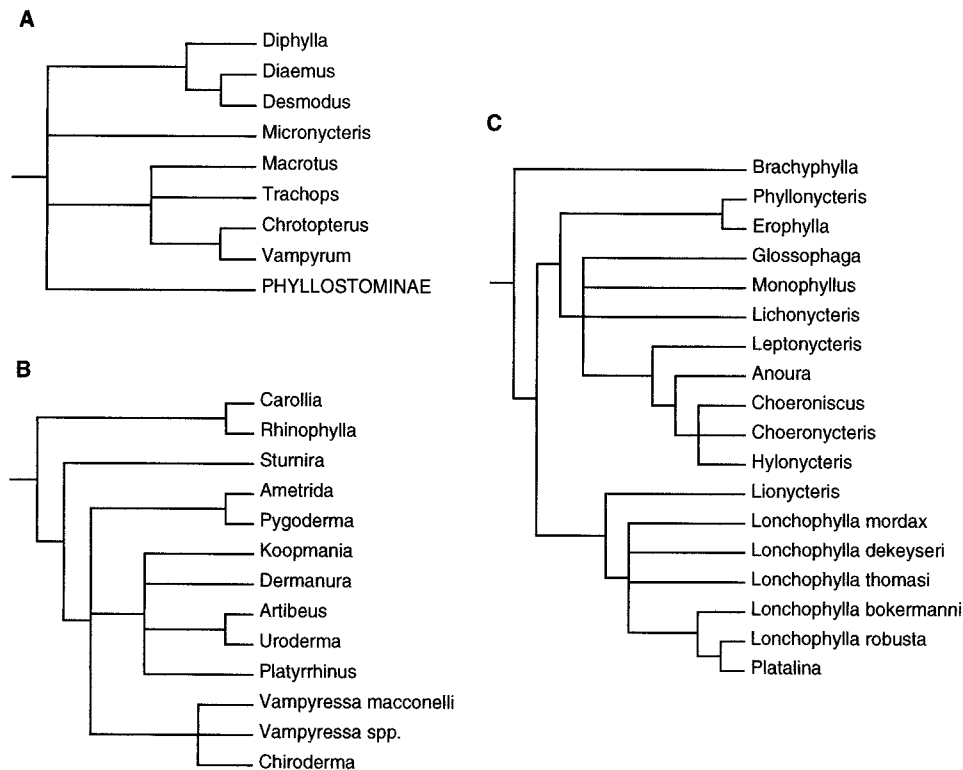
Fig. 14. Gimenez (1993) used the topology of Baker et al. (1989) to partition her analyses of lingual morphology. **A.** Cladogram of relationships from Gimenez's (1993; redrawn from fig. 22) analysis of desmodontines, vampyrines, *Macrotus*, *Micronycteris*, and Phyllostominae. **B.** Gimenez's (1993; redrawn from fig. 24) proposed relationships among Stenodermatini genera. **C.** Gimenez's (1993; redrawn from fig. 25) proposed relationships among Glossophagini genera.

*Artibeus*. Van Den Bussche et al. (1998) also supported the recognition of *Enchisthenes* as a genus distinct from *Artibeus* (s.l.) based on the results of the cytochrome *b* analysis and the earlier study of the nuclear satellite DNA repeat (Van Den Bussche et al., 1993).

Gimenez (1993) examined lingual morphology in phyllostomids and conducted several parsimony analyses designed to address intergeneric relationships within the higher-level taxa identified by Baker et al. (1989). Gimenez's (1993) first analysis (fig. 14A) included desmodontine genera, *Macrotus*, *Micronycteris*, vampyrine genera, Phyllostomini, Glossophagini, Stenodermatini, and the outgroups Noctilionidae and Mormoopidae. The last five taxa were scored as single OTUs in this analysis. Within desmodontines, *Desmodus* and *Diaemus* formed a clade with *Diphylla* as their sister group. The po-

sition of *Micronycteris* was unresolved, but Gimenez (1993) found that *Macrotus* grouped with Vampyrinae. *Macrotus*, *Trachops*, and the sister taxa *Chrotopterus* and *Vampyrum* formed a polytomy. Desmodontines, *Micronycteris*, the vampyrine group, and Phyllostominae (sensu Baker et al., 1989) formed a basal polytomy. Although included in her matrix, Gimenez (1993) did not depict relationships among Phyllostomatini, Glossophagini, and Stenodermatini in her tree.

Gimenez's (1993) second analysis examined relationships within Phyllostomini (sensu Baker et al., 1989). This analysis included Phyllostomini genera, Stenodermatini (a single OTU), and Glossophagini (a single OTU). Desmodontinae (a single OTU) and Vampyrinae (a single OTU) were used as outgroups. Gimenez (1993) found that lin-

gual characters were largely uninformative within Phyllostomatini. The three clades identified consisted of *Phylloderma* and *Phyllostomus*, *Mimon bennettii* and *Mimon crenulatum*, and Glossophagini and Stenodermatini.

Within Stenodermatini, lingual characters were more informative (fig. 14B). Stenodermatini genera and the outgroups *Micronycteris*, Phyllostomini (a single OTU) and Glossophagini (a single OTU) were used in this analysis. Carolliinae and Stenodermatinae were each monophyletic and appeared as sister taxa. *Sturnira* occupied the basal stenodermatine branch. Gimenez (1993) identified three clades among the remaining stenodermatine genera: (1) the "short-faced" taxa *Ametrida* and *Pygoderma*, (2) *Dermanura*, *Koopmania*, *Platyrrhinus*, and the sister taxa *Artibeus* and *Uroderma*, and (3) *Chiroderma*, *Vampyressa macconnelli* (= *Mesophylla*), and *Vampyressa*.

The final analysis conducted by Gimenez (1993) focused on relationships among nectar-feeding taxa (fig. 14C). *Micronycteris*, Phyllostomini (a single OTU), and Stenodermatini (a single OTU) were used as outgroups in this analysis. Gimenez (1993) corrected some observational inaccuracies in Griffiths' (1982) descriptions, but achieved results similar to his. Gimenez (1993) found that *Brachyphylla* appeared as the sister taxon of a clade consisting of all other nectar-feeders. Phyllonycterinae, Glossophaginae, and Lonchophyllinae were each monophyletic, and phyllonycterines and glossophagines formed a clade with lonchophyllines as their sister group. Within Glossophaginae (s.s.), the positions of *Glossophaga*, *Lichonycteris*, and *Monophyllus* were unresolved, but the remaining taxa formed a clade. Within the latter group, *Anoura* and *Leptonycteris* were successive sister taxa to the unresolved grouping of *Choeroniscus*, *Choeronycteris*, and *Hylonycteris*. Gimenez (1993) found that within Lonchophyllinae, *Lionycteris* was the sister taxon of a clade of *Lonchophylla* species. *Platalina* nested within the *Lonchophylla* species (fig. 14C).

Koopman (1993, 1994) presented a classification of phyllostomids that included seven subfamilies: Desmodontinae, Phyllostominae, Brachyphyllinae, Phyllonycterinae, Glossophaginae, Lonchophyllinae, and Stenodermatinae. Koopman (1994) also recognized two taxa within Stenodermatinae: Sturnirini included *Sturnira*, while Stenodermatini encompassed the remaining stenodermatine genera.

Based on a study of cranial characteristics and cranial allometry, Solmsen (1994) recognized four subfamilies of nectar-feeding phyllostomids: Phyllonycterinae, Brachyphyllinae, Glossophaginae, and Lonchophyllinae. Within Glossophaginae, Solmsen (1994) named the tribe Choeronycterini for the genera *Choeroniscus*, *Choeronycteris* (including *Musonycteris*), and *Hylonycteris*. In addition, Solmsen (1994) concluded that Lonchophyllinae was most closely related to Carolliinae, while other glossophagine genera seemed perhaps to share a closer evolutionary history (e.g., fig. 84 in Solmsen, 1994). Like Gimenez (1993), Solmsen (1994) found that *Platalina* appeared to nest within the genus *Lonchophylla*.

Gimenez et al. (1996; see fig. 15A) further evaluated relationships among the nectar-feeding phyllostomids. The tree derived from lingual morphology (Gimenez et al., 1996; fig. 15A) was similar to that presented by Gimenez (1993), but two previously partly resolved clades, including Lonchophyllinae, were completely unresolved. When Gimenez et al. (1996) combined their lingual data with Griffiths' (1982) hyoid data, resolution within the *Choeroniscus* group improved (fig. 15B). *Hylonycteris*, *Anoura*, and *Lichonycteris* appeared as successive sister taxa to *Choeroniscus* and *Choeronycteris*. Relationships among other taxa were identical to those in the tree based on lingual data only. Gimenez et al. (1996) also described a suboptimal tree (one step longer) in which Glossophaginae and Lonchophyllinae were sister taxa. When Desmodontinae was included in these analyses, desmodontines and *Brachyphylla* appeared as sister taxa.

In a classification of mammalian species, McKenna and Bell (1997), dramatically revised phyllostomid classification. These authors expanded the definition of Glossophaginae, which they recognized as including four tribes: Brachyphyllini, Phyllonycterini, Glossophagini, and Lonchophyllini. Similarly, Stenodermatinae was expanded to include
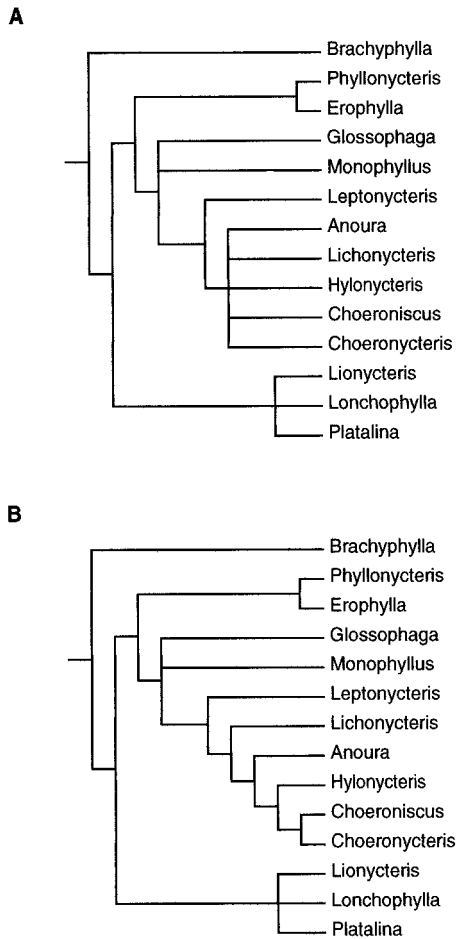
Fig. 15. **A.** Gimenez et al.'s (1996; redrawn from fig. 3) cladogram depicting relationships among nectar feeders based on lingual characters. **B.** Gimenez et al.'s (1996; redrawn from fig. 4) cladogram depicting relationships among nectar feeders based on lingual and hyoid characters.

the tribes Carolliini and Stenodermatini. *Sturnira* was placed in its own subtribe, Sturnirina, while the remaining Stenodermatini genera were placed in the subtribe Stenodermatina. Desmodontinae and Phyllostominae were recognized in their traditional form by these authors.

## SUMMARY

As was the case with taxonomy in general, phyllostomid classification was in a state of flux during the 18th and 19th centuries. Several authors made important contributions

that gradually added stability to classifications as their improvements were consistently used by other taxonomists. Goldfuss (1820) first divided Chiroptera into families, including a family Phyllostomata. However, it was Gervais (1854, 1856) who restricted the use of Phyllostomidae to New World leaf-nosed bats and applied names to the subdivisions of the family which have been used fairly consistently since his classification. After Miller's (1907) influential classification, which recognized hemidermines (= carollines) and phyllonycterines for the first time, phyllostomid taxonomy remained virtually unchanged until the 1960s. During this next period of change, mormoopids were recognized as a distinct family (Gerber, 1968; Gerber and Leone, 1971; Smith, 1972), desmodontines were recognized as phyllostomids (Machado-Allison, 1967; Forman et al., 1968; Gerber, 1968; Gerber and Leone, 1971), *Brachyphylla* was removed from Stenodermatinae and allied with nectar-feeders (Silva-Taboada and Pine, 1969; Baker and Lopez, 1970; Baker and Bass, 1979; Baker et al., 1981a), *Sturnira* was placed within Stenodermatinae (Baker, 1967; Gerber, 1968; Gerber and Leone, 1971), and a new subfamily, Lonchophyllinae, was recognized (Griffiths, 1982). These slight changes in taxonomy failed to reflect the controversies surrounding the evolutionary relationships of these bats. With the advent of cladistic methods, and research into many aspects of phyllostomid biology, both morphological and molecular, systematists have begun to evaluate the data supporting traditionally recognized groups.

Studies based on diverse types of data have supported monophyly of a number of higher-level phyllostomid taxa (see table 3) including Desmodontinae, Vampyrinae, Phyllostominae (sensu Baker et al. 1989), Phyllostomini, Stenodermatinae/Stenodermatini, Glossophagini, and Phyllonycterinae. However, several aspects of phyllostomid phylogeny remain controversial. Studies based on immunological and morphological data have indicated that Phyllostominae (sensu Koopman, 1993, 1994) is not monophyletic; however, there is no agreement on intergeneric relationships of phyllostomines because results of different studies did not

support congruent groups. Relationships among nectar-feeding genera have also proven difficult to resolve. Results of immunological and karyological studies have suggested that Lonchophyllinae might not be monophyletic, although analyses based on hyoid and lingual morphology have supported this grouping. Data from studies of allozymes, behavior, immunology, morphology, and parasitology support the placement of *Brachyphylla* as the sister taxon of Phyllonycterinae; however, hyoid and lingual data are not congruent with this interpretation. Monophyly of Carolliinae has been supported by some data sets (allozymes, lingual morphology), but immunological studies conflict with these results. Finally, intergeneric relationships within most higher-level groups of phyllostomids (e.g., stenodermatines, glossophagines) remain problematic.

Previous attempts to reach a phylogenetic consensus based on consideration of multiple data sets have produced trees that were either incomplete (lacking many taxa; e.g., Honeycutt and Sarich, 1987a) or not resolved at the generic level (e.g., Baker et al., 1989). These problems have apparently originated from the use of taxonomic congruence (see discussion of this method under Materials and Methods below). Because few taxa have been sampled for all relevant data sets, use of taxonomic congruence made full resolution of intergeneric relationships impossible. The studies presented by Honeycutt and Sarich (1987a) and Baker et al.(1989) excluded craniodental, external, hyoid, lingual, and morphology from formal consideration during tree-building. No previous study has used a character congruence approach applied to all available discrete data in a broad taxonomic sample. This approach, described in detail below, may help to resolve the branching pattern of genera within Phyllostomidae and permit evaluation of the monophyly of traditionally recognized subfamilies and other higher-level groups.

## MATERIALS AND METHODS

### SAMPLING AND CHARACTER CODING

We scored representatives of all currently recognized phyllostomid genera (see Koopman, 1993) for which specimens were available for most external, craniodental, lingual, and postcranial osteological characters listed under Character Descriptions below. Altogether, we examined more than 2,300 specimens (see appendix 1 for specimens examined). When available, we examined 10 individuals of each representative species (five males and five females) for each type of preparation used (e.g., skins). We used five or fewer specimens to score the tongue characters because of the destructive aspect of such dissections. We scored characters of the brain, chromosomes, digestive and reproductive tracts, hair microstructure, hyoid apparatus, postcranial musculature, and restriction sites based soley on published descriptions (see Character Descriptions below).

Numerous studies of phyllostomid relationships were based on morphology of the autosomal chromosomes (e.g., Baker, 1967, 1970, 1973, 1979; Gardner, 1977a; Patton and Baker, 1978), but we used none of these characters in our analysis. Identification of chromosomal synapomorphies has relied on assumptions of ingroup monophyly and direction of character change because most chromosomal characters can be understood only in the context of a reference taxon designated as primitive. For example, it is only by comparing karyotypes of *Micronycteris nicefori* to *Macrotus waterhousi* that we can say that *M. nicefori* has "Rearrangements of biarmed *waterhousi* chromsomes 1/2, 23/24, [and] 26/25 . . ." (Patton and Baker, 1978: 453). This approach may fail if the reference taxon has a derived morphology (see Discussion: Interpretation of Chromosomal Data, below). Because of this problem, and our inability to resolve it satisfactorily, we did not consider autosomal characters when constructing trees. However, once a tree is constructed using other data, chromosomal evolution may be evaluated in the context of the new tree. We adopted this a posteriori approach to investigate autosomal evolution.

We included three genera from other chi-

TABLE 3
**Data Sets Supporting Monophyly of Selected Higher-Level Clades of Phyllostomids**

| Clade | Type of data | Study |
|---|---|---|
| Carolliinae | allozymes | Straney (1980) |
| | morphology | Gimenez (1993) |
| Desmodontinae | allozymes | Straney (1980), Honeycutt et al. (1981) |
| | immunology | Honeycutt and Sarich (1987a), Honeycutt et al. (1981) |
| | karyology | Bass (1978), Baker et al. (1988b) |
| | morphology | Gimenez (1993) |
| Glossophaginae sensu stricto | morphology | Griffiths (1982), Gimenez (1993), Gimenez et al. (1996) |
| Glossophagini[a] | immunology | Baker et al. (1981a),[b] Pierson (1986), Honeycutt and Sarich (1987a) |
| | karyology | Baker and Lopez (1970), Bass (1978), Baker and Bass (1979), Haiduk and Baker (1982)[c] |
| Lonchophyllinae | morphology | Griffiths (1982), Gimenez (1993), Gimenez et al. (1996) |
| | restriction sites | Van Den Bussche (1992)[d] |
| Phyllonycterinae sensu stricto | allozymes | Baker et al. (1981a) |
| | immunology | Baker et al. (1981a) |
| | morphology | Griffiths (1982), Gimenez (1993), Gimenez et al. (1996) |
| | restriction sites | Van Den Bussche (1992)[d] |
| Phyllostominae sensu Baker et al. (1989) | immunology | Honeycutt and Sarich (1987a) |
| | karyology | unpublished data cited in Baker et al. (1989)[e] |
| | morphology | Hood and Smith (1982), Gimenez (1993) |
| | restriction sites | Van Den Bussche (1992)[d] |
| Phyllostomini[a] | immunology | Pierson (1986), Honeycutt and Sarich (1987a, 1987b) |
| | restriction sites | Van Den Bussche (1992)[d] |
| Stenodermatinae | immunology | Gerber (1968), Gerber and Leone (1971) |
| | morphology | Hood and Smith (1982), Gimenez (1993) |
| Stenodermatini[a] | immunology | Honeycutt and Sarich (1987a) |
| | morphology | Hood and Smith (1982) |
| Vampyrinae | immunology | Straney (1980), Pierson (1986), Honeycutt and Sarich (1987a) |
| | morphology | Straney (1980) |
| | restriction sites | Van Den Bussche (1992)[d] |

[a] Gimenez (1993) partitioned her analyses according to Baker et al.'s (1989) classification. Consequently, her results may not represent the globally optimal solution, and we do not consider her analyses tests of the monophyly of the tribes (e.g., Glossophagini) proposed by Baker et al. (1989).

[b] Baker et al. (1981a: 671) found that *Lionycteris* and *Lonchophylla* were "the most divergent of all the glossophagine and brachyphylline genera examined," but were unable to determine whether *Lionycteris* and *Lonchophylla* were derived or primitive relative to other glossophagines.

[c] Haiduk and Baker (1982) found that both *Lonchophylla* and *Lionycteris* have highly derived karyotypes in which few arms could be homologized to those primitive for the subfamily.

[d] Van Den Bussche (1992) mapped his restriction site characters onto the tree proposed by Baker et al. (1989). It is only in the context of the Baker et al. (1989) hypothesis that the restriction site characters support monophyly of these clades.

[e] Baker et al. (1989: 233) note that "three chromosomal arrangements . . . are found in some members of each tribe. . . . In other species the karyotypes are highly autapomorphic."

ropteran families as outgroups: *Pteronotus* and *Mormoops* (Mormoopidae), and *Noctilio* (Noctilionidae). Previous analyses of chiropteran interfamilial relationships have indicated that these families and Phyllostomidae form a well-supported clade, Noctilionoidea (Simmons, 1998; Simmons and Geisler, 1998). We assumed monophyly of each of these families based on previous work (Smith, 1972; Simmons, 1998) rather than directly investigating relationships among outgroup genera and phyllostomids, and con-

strained our analyses to reflect the most recent hypotheses of relationships among these taxa: ((Noctilionidae, Mormoopidae), Phyllostomidae). Accordingly, our data set includes only characters relevant to relationships among the ingroup taxa.

We assumed generic monophyly for most ingroup taxa. However, we assessed intrageneric variation for some characters by examining multiple species within a genus when we found previous reports of polymorphism, or when our own suspicions were raised. For some genera suspected of being nonmonophyletic, we sampled at the subgeneric and/or species level. For *Mimon*, we sampled the two monotypic subgenera: *M.* (*Anthorhina*) *crenulatum* and *M.* (*Mimon*) *bennettii*. We sampled representatives of four of the five subgenera of *Micronycteris*, including *M.* (*Lampronycteris*) *brachyotis*, and *M.* (*Trinycteris*) *nicefori*, which represent monotypic subgenera, and *M.* (*Glyphonycteris*) *sylvestris*, *M.* (*Micronycteris*) *hirsuta*, *M.* (*Micronycteris*) *minuta*, and *M.* (*Micronycteris*) *megalotis*. We included representatives of each of the three subgenera of *Vampyressa*: *V.* (*Vampyriscus*) *bidens*, which is monotypic; *V.* (*Metavampyressa*) *nymphaeae*; and *V.* (*Vampyressa*) *pusilla*. We separated *Artibeus* (s.l.) into the four currently recognized subgenera: *Enchisthenes* and *Koopmania*, which are monotypic, and *Artibeus* and *Dermanura*. In our character discussions, we use the species names for all of these taxa, except *Artibeus* (s.l.) where we consistently use the subgeneric names. We do this for convenience because both *Artibeus* and *Dermanura* are speciose and we often sampled broadly within them.

To examine tongue morphology, we dissected at least one individual of each taxon. The skin of the lower jaw was reflected over the mandible and muscles with origins or insertions on the mandible (e.g., m. mylohyoideus, and m. genioglossus) were cut, allowing the tongue to be separated from the mandible and reflected ventrally. This technique allowed us to view structures on the proximal tongue, which are difficult to see in most intact specimens. Unless necessary, additional specimens were not dissected; instead, we used individuals that were preserved with their mouths open, or specimens from which the skull had been previously removed. We examined all tongues using a Nikon microscope ($\times$0.66–$\times$4.0 plus doubling lens). To facilitate viewing of papillae, we dried tongues using canned air (e.g., Beseler Dust Gun) or paper towels. We illustrated tongue characters of selected specimens using a camera lucida.

We evaluated craniodental morphology using cleaned skeletons and skulls, and examined external characters using both fluid-preserved specimens and skins. We used a similar Nikon microscope in these examinations, and illustrated characters of selected specimens using a camera lucida. We occasionally took measurements for some characters (e.g., character 87: length of calcar) using digital calipers; discussion of methods used in these cases is provided in the character descriptions below.

We identified characters of potential phylogenetic significance based on comparisons among ingroup taxa. We utilized what Wilkinson (1995) has termed "reductive," as opposed to "composite," character coding. Reductive character coding breaks apparently independent attributes (e.g., shape and color pattern of a structure) into separate characters. In contrast, composite character coding combines such apparently independent features into single multistate characters. Reductive coding seems to have some benefits over composite coding. For example, Wilkinson (1995) noted that composite characters may conceal homoplasy and constrain reconstruction of ancestral states. Unless properly ordered, composite characters may not be analytically equivalent to reductive characters and may result in different trees (Wilkinson, 1995).

We also coded partly dependent characters in a hierarchical fashion where one character concerns the presence or absence of a trait, and subsequent dependent characters describe features of this trait (see Simmons, 1993). For example, degree of development of a hypocone on M3 is dependent on the presence of M3. Using hierarchical coding, taxa are first scored for the presence or absence of M3. Taxa possessing an M3 are then scored for the size of the hypocone in a second character. Taxa lacking an M3 are scored

"−" for the second character, indicating that this character does not apply to those taxa.

Unfortunately, computer algorithms do not distinguish between an inapplicable state ("−") and missing data ("?"). Thus, using hierarchical characters may result in impossible state reconstructions at internal nodes and for terminal taxa (Platnick et al., 1991), in the rejection of trees that would be more (or equally) parsimonious (Maddison, 1993), or in arbitrary resolutions (Wilkinson, 1995). It is possible to construct characters to handle hierarchical attributes in several alternative ways; however, some of these methods require that the absence of the character be scored more than once (Maddison, 1993; Pleijel, 1995). If absence of the complex trait is derived, this gives more weight to a single evolutionary event by counting it multiple times, which can bias searches for the most parsimonious trees. Another option is to use composite character coding (Maddison, 1993), which has other undesirable qualities (see above). Both methods affect character state reconstructions. Although imperfect, we prefer hierarchical coding because it best reflects our views on the logical independence of attributes (see above) and allows us to construct characters equivalent to our hypotheses of homology, without requiring that characters be weighted or ordered.

We constructed unique character states to accommodate intraspecific variation (polymorphism within a species). For example, if species A includes some individuals with yellow pelage (state 0) and others with brown (state 1) pelage, we erected state 2, which we described as "yellow or brown pelage; polymorphic within species." We used combinations of two or more character states to indicate taxonomic polymorphism in our composite terminal taxa. For example, if two species within the same genus exhibit different states (species A with state 0 and species B with state 1), we scored the genus 0/1 in the matrix. In addition to characters scored as inapplicable ("−"), we used "?" to indicate relevant data that had not been collected for a particular taxon. We recorded character states using MacClade version 3.0 (Maddison and Maddison, 1992), which we also used to examine character transformations and draft figures.

## ASSESSING CONGRUENCE AMONG DATA SETS

Systematists have used three approaches to assess congruence among data sets: taxonomic congruence, character congruence, and conditional combination. Taxonomic congruence involves separate analysis of data sets based on different character systems (e.g., molecular and morphological), and compares the results using consensus indices or consensus trees. Character congruence, or "total evidence" as it is often called, combines all available data sets in a single analysis. Conditional combination uses statistical tests for heterogeneity to determine if data sets should be combined in a character congruence analysis.

Hillis (1987) suggested that taxonomic and character congruence may be used to achieve different goals. Taxonomic congruence, which results in more conservative and stable topologies, might best be used to construct classifications, while character congruence, which results in more fully resolved but perhaps less stable hypotheses, might be used for character interpretation where the use of poorly resolved trees is problematic. Although stability is not necessarily a goal of systematics (Kluge, 1989; Kluge and Wolf, 1993), classificatory recommendations made on the basis of weakly supported topologies are clearly more likely to be overturned with the addition of new data. However, taxonomic congruence is not the only way to address the issue of stability. Bootstrapping and decay indices may be used to investigate support for clades produced in a character congruence analysis, allowing classificatory recommendations to be based on only the most strongly supported clades.

Lanyon (1993) and Miyamoto and Fitch (1995) have argued that data sets should be analyzed separately because each data set provides an independent test of the others. As Miyamoto and Fitch (1995: 69) noted:

> Independence is more likely for characters from different data sets than for characters from the same set (Swofford, 1991; Lanyon, 1993). As a result, characters from different data sets are less likely to support the same, and perhaps wrong, species phylogeny than are those from the same data sets (de Quieroz, 1993).

These authors have advocated use of consensus indices or trees to compare results of independent analyses.

Barrett et al. (1991) defended the use of taxonomic congruence in the following cases: to determine how much two data sets disagree with each other, how results might differ when applying different methods of analysis (e.g., phenetic vs. cladistic), and how results for different data sets compare if the data cannot be combined (e.g., discrete characters and distance data; also noted by Lanyon, 1993; Eernisse and Kluge, 1993).

In contrast, Kluge (1989) has advocated character congruence, and has advanced several criticisms of taxonomic congruence. Kluge (1989) and Kluge and Wolf (1993) noted that choice of consensus technique is arbitrary, and that different consensus techniques and indices may give different results. Kluge (1989), Eernisse and Kluge (1993), Kluge and Wolf (1993), and Simmons (1993) also criticized the notion that data sets can be partitioned into subsets that reflect ''real'' divisions.

Although data sets are typically equally weighted in taxonomic congruence, the characters in each data set are unequally weighted when the sizes of the data sets are different (Miyamoto, 1985). Miyamoto (1985) also criticized taxonomic congruence because it compares the topologies without reference to the strength of character data supporting them, resulting in trees that are less parsimonious than those taking all evidence into account. Lanyon (1993) suggested that only the most strongly supported clades be used to build taxonomic congruence consensus trees. However, these trees will still be less parsimonious than those taking all evidence into account.

Combining data seems to afford several benefits. Kluge (1989) and Barrett et al. (1991) have argued that any hypothesis must account for all evidence, and as Miyamoto (1985) noted, trees produced in a character congruence analysis more parsimoniously explain all the data. Furthermore, character conflicts are resolved in favor of the strongest evidence when data sets are combined (Hillis, 1987; Kluge and Wolf, 1993). Hillis (1987) and de Quieroz (1993) noted that because some data sets are informative in only some parts of the tree and not others, combining data may provide more resolution. Combining data may allow a weak phylogenetic signal to overwhelm noise that obscured this signal when the data are analyzed separately (Barrett et al., 1991; de Quieroz, 1993).

Recently, some authors (e.g., Bull et al., 1993; de Quieroz, 1993; Huelsenbeck et al. 1996) have suggested that it may be inappropriate to simply combine entire data sets that strongly support conflicting tree topologies because these conflicts may indicate that there are problems with either the data sets or method of analysis. This approach has been termed ''conditional combination.'' The chief concern of these authors (Bull et al., 1993; de Quieroz, 1993; Rodrigo et al., 1993; de Quieroz et al., 1995; Huelsenbeck et al., 1996) seems to be that a data set may be ''positively misleading'' in that it always recovers an incorrect phylogeny when a sufficiently large number of characters have been sampled (see Felsenstein, 1978). By combining a positively misleading data set with other data sets not afflicted with this problem, the entire analysis is compromised. As Bull et al. (1993: 385) noted ''it is better to obtain one right answer and one wrong answer from separate analyses than to get a single wrong answer in a combined analysis.''

Other problems that may lead to disagreement of two or more data sets include investigator error (e.g., in establishing character homology), computational error (e.g., failure to find the shortest tree; Cracraft and Mindell, 1989; Rodrigo et al., 1993), sampling error (Bull et al., 1993; Rodrigo et al., 1993; de Quieroz et al., 1995), violation of the assumptions of tree-building methods (e.g., rate of character change, or character independence; Hillis, 1987; Bull et al., 1993; Rodrigo et al., 1993; de Quieroz et al., 1995), and data sets that do not share the same history (e.g., horizontal transmission; Bull et al., 1993; Rodrigo et al., 1993; de Quieroz et al., 1995).

Several new statistical tests are being used to examine heterogeneity among data sets (e.g., Rodrigo et al., 1993; Farris et al., 1995) and provide information useful for deciding when data sets should be combined. In these tests, data may be combined if the disagree-

ment among the trees proves to be what one would expect from sampling error (Bull et al., 1993; de Quieroz et al., 1995; Huelsenbeck et al., 1996). But what happens when the null hypothesis (homogeneity) is rejected?

Although in practice it is not yet possible to identify the cause of disagreements among data sets, de Quieroz et al. (1995) advocated this approach. These authors suggested that when different stochastic processes (e.g., different rates of change) are involved, combined data sets may produce an incorrect solution (i.e., the data sets are positively misleading; Felsenstein, 1978; de Quieroz, 1993). In a maximum parsimony analysis, the solution to this problem may be differential character weighting (also proposed by Barrett et al. [1991], Bull et al. [1993], and Chippendale and Wiens [1994] for some or all situations when heterogenous data are combined). When the true tree topology is different for each data set (i.e., different histories), de Quieroz et al. (1995) and Bull et al. (1993) argued that data sets should not be combined and de Quieroz et al. (1995) advocated removing offending taxa or data sets from a combined analysis. Huelsenbeck et al. (1996) suggested that possible remedies might include using taxonomic congruence (previously proposed as a solution when two data sets strongly disagree by de Quieroz, 1993), reanalyzing the data using a different phylogenetic model, or simply leaving the relationships among the group in question unresolved.

Clearly, examining individual data sets for disagreement seems to be warranted before combining data in a character congruence analysis given the concerns of the authors advocating conditional combination. However, we are left with perhaps the most basic problem: how do we identify "real" data partitions? Although Bull et al. (1993) have championed "process partitions" as "real" classes of data because partitions evolve according to different rules (e.g., first, second, and third codon positions), the best examples of characters that might represent process partitions are molecular. Miyamoto and Fitch (1995: 66) suggested five other requirements that process partitions might meet (e.g., genes in a partition are not

linked and gene products from one parititon do not regulate gene expression in other partitions); however, our limited understanding of these types of genetic interactions make such conditions almost impossible to satisfy at the present time. Furthermore, we may fail to correctly identify "real" partitions, and tests for heterogeneity will indicate that data are homogeneous when they are not (Huelsenbeck et al., 1996). This appears to be a particular problem for morphological data sets, where the parameters governing the evolution of particular characters are virtually unknown.

We feel that all taxonomic congruence rests on an artificial division of evidence and has other associated problems (see above). Therefore, we use taxonomic congruence as a tool for identifying clades in which these character sets seem to be most informative and providing comparisons with previous work. We use character congruence for phylogenetic reconstruction and classification recommendations.

## PHYLOGENETIC ANALYSES

We conducted phylogenetic analyses using PAUP* (Swofford, 1998: version 4.0b1) on a Macintosh PowerBook 1400. To examine patterns of taxonomic congruence, we ran separate analyses of all data partitions. We chose three of our 11 partitions (pelage and integument; skull and dentition; postcranium) based on traditional anatomical divisions. The remaining eight partitions correspond to character sets examined in previously published papers that focused on specific anatomical systems (hyoid apparatus; tongue; digestive tract; brain; reproductive tract), types of chromosomes (sex chromosomes), mitochondrial DNA (restriction sites) and nuclear DNA (EcoRI-defined DNA repeat). Dividing the characters into partitions in this way facilitates comparison of our results with the results of previous studies. In other analyses, we combined all 150 characters in a character congruence analysis after testing the paritions for heterogenity.

We could not use exact search methods due to the size of the data matrix; instead, we used 1000 iterations of the heuristic

search algorithm with a random taxon addition sequence, although we modified this procedure when we found more than 30,000 most parsimonious trees (our MaxTrees setting), a common occurrence when we analyzed the separate partitions. In these cases, we first attempted to discover the shortest tree. We saved 30,000 most parsimonious trees from a single replicate that used a random taxon addition sequence. Then we ran two additional searches using 1000 iterations of the heuristic search algorithm with a random taxon addition sequence, but saved no more than 1000 trees that were longer than or equal to the length we discovered in our first search. In this manner, we attempted to sample different islands of most parsimonious trees. We compared the results of the three searches using strict consensus trees. When we ran searches for the data partitions, we eliminated those taxa for which no data were available (see table 4).

We used TBR branch swapping in most analyses, collapsed branches with a minimum length of zero, and interpreted multistate taxa as polymorphism (see Swofford and Begle, 1993 for discussion of these methods). We gave all characters equal weight in all analyses. We did not order characters in any analyses.

We used PAUP to construct consensus trees, calculate summary tree statistics, and perform bootstrap and decay analyses. We used both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) to optimize characters on trees. ACCTRAN forces state changes to a lower level (i.e., closer to the root) in the topology, favoring reversals. In contrast, DELTRAN places ambiguous character state changes higher in the topology thereby favoring parallel evolution of the feature under investigation. In the bootstrap analyses, we performed 100 replicates. For each bootstrap replicate, we conducted 5 iterations with a random taxon addition sequence, saving only 10,000 trees. In the decay analyses, we used the heuristic search option with a random addition sequence and 1000 repetitions to search for suboptimal trees. We performed these searches in one-step increments (i.e., if the shortest trees were of length X, our first decay analysis saved trees of length X and X + 1; the second analysis saved trees of length X, X + 1, and X + 2, etc.). We constructed strict consensus trees based on each analysis, and compared these to determine the number of additional steps required to collapse each clade that was present in the shortest trees (those of length X). For groups with a decay value of more than 2, we used monophyly constraint trees and searched for the shortest trees incompatible with the constraint tree. We performed only 10 iterations of these searches since the goal was not to find all the shortest trees, but simply to find one short tree that was incompatible with the constraint tree.

We use the following institutional abbreviations in this paper: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago, Illinois; MVZ, Museum of Vertebrate Zoology, Berkley, California; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

# CHARACTER DESCRIPTIONS

We use the classification of Koopman (1993) throughout the following sections to facilitate discussion of the taxonomic distribution of various features. In this context, use of traditional subfamilial names (e.g., ''phyllostomines'') is for convenience only and does not imply that these taxa are necessarily monophyletic.

For each character, we provide a summary of previous use in systematic studies.

Our study would never have been possible without these prior contributions. Nevertheless, we often encountered difficulty in comparing observations from the literature with our own work. To simplify such comparisons for future researchers, we include detailed discussion of the differences in observation, interpretation, and character construction that exist between previous studies and our own.

TABLE 4
**Genera Examined in Previous Phylogenetic Studies**[a]

| Genus | Baron et al. (1996a, b) | Benedict (1957) | Forman et al. (1979)[c] | Gimenez (1993)[d] | Griffiths (1982)[e] | Hood & Smith (1982, 1983) | Lim (1993) | McDaniel (1976) | Owen (1987)[f] | Sprague (1943) | Straney (1980)[g] | Strickler (1978) | Van Den Bussche (1991, 1992) | Vaughan & Bateman (1970)[h] | Wible & Bhatnager (1996)[i] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phyllostomidae | | | | | | | | | | | | | | | |
| Brachyphyllinae | | | | | | | | | | | | | | | |
| *Brachyphylla* | X | X | X | | X | X | | X | | | X | | X | | X |
| Carolliinae | | | | | | | | | | | | | | | |
| *Carollia* | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Rhinophylla* | X | X | | X | | X | X | X | X | | X | | X | | |
| Desmodontinae | | | | | | | | | | | | | | | |
| *Desmodus* | X | X | X | X | X | X | | X | | X | X | X | X | | X |
| *Diaemus* | X | X | X | X | | | | X | | | | | | | X |
| *Diphylla* | X | X | X | X | | | | X | | | X | X | X | | X |
| Glossophaginae | | | | | | | | | | | | | | | |
| *Anoura* | X | X | X | X | X | X | | X | | | X | | X | | X |
| *Choeroniscus* | X | X | X | X | X | | | X | | | X | | X | X | |
| *Choeronycteris* | X | X | | | X | | | X | | | X | X | X | X | |
| *Glossophaga* | X | X | X | X | X | X | | X | | X | X | X | X | X | X |
| *Hylonycteris* | X | X | X | | X | | | X | | | X | | X | | |
| *Leptonycteris* | X | X | X | | X | X | | X | | | X | X | X | X | X |
| *Lichonycteris* | X | X | X | X | X | | | X | | | | | X | | |
| *Monophyllus* | X | X | | | X | X | | | | | | | X | | |
| *Musonycteris* | | | | | | | | | | | | | X | | |
| *Scleronycteris* | | | | | | | | | | | | | | | |
| Lonchophyllinae | | | | | | | | | | | | | | | |
| *Lionycteris* | X | X | | X | X | | | | | | | | X | | |
| *Lonchophylla* | X | X | | X | X | X | | X | | | X | | X | | |
| *Platalina* | | X | | | X | | | | | | X | | | | |
| Phyllonycterinae | | | | | | | | | | | | | | | |
| *Erophylla* | X | X | | | X | | | X | | | | | | | |
| *Phyllonycteris* | X | X | | | X | X | | | | X | | | X | X | |

TABLE 4
Continued

| Genus | Baron et al. (1996a, b) | Benedict (1957) | Forman et al. (1979)c | Gimenez (1993)d | Griffiths (1982)e | Hood & Smith (1982, 1983) | Lim (1993) | McDaniel (1976) | Owen (1987)f | Sprague (1943) | Straney (1980)g | Strickler (1978) | Van Den Bussche (1991, 1992) | Vaughan & Bateman (1970)h | Wible & Bhatnager (1996)i |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Phyllostominae** | | | | | | | | | | | | | | | |
| Chrotopterus | X | X | X | X | | | | | | | X | | X | | |
| Lonchorhina | X | X | | X | | | | | | | X | | X | X | |
| Macrophyllum | X | X | X | | | | | X | | | X | | X | | |
| Macrotus | X | X | X | X | X | X | X | X | X | | X | | X | X | X |
| Micronycteris | X | X | X | X | X | X | | X | | | X | | X | X | |
| Mimon | X | X | | X | | | | X | | | X | | X | | |
| Phylloderma | X | X | X | X | | X | | X | | | X | | X | | |
| Phyllostomus | X | X | X | X | X | X | | X | | X | X | X | X | X | |
| Tonatia | X | X | X | X | | | | X | | X | X | X | X | | |
| Trachops | X | X | | X | | X | | X | | | X | | X | | |
| Vampyrum | X | X | X | X | | | | X | | | X | | X | | |
| **Stenodermatinae** | | | | | | | | | | | | | | | |
| Ametrida | X | X | | X | | X | X | X | X | | | | X | | |
| Ardops | X | X | | | | | X | | X | | | | X | | |
| Ariteus | X | X | | | | | X | | X | | | | X | | |
| Artibeus | X | X | X | X | X | X | X | X | X | X | X | | X | X | X |
| Centurio | X | X | X | | | X | X | X | X | | X | X | X | X | |
| Chiroderma | X | X | X | X | | | X | X | X | | X | | X | X | |
| Dermanura | X | X | X | X | | | X | X | X | | X | | X | X | |
| Ectophylla | | X | | | | X | X | | X | | X | | | | |
| Enchisthenes | X | X | | | | X | X | X | X | | X | | X | | |
| Koopmania | X | | | X | | | X | | X | | | | | | |
| Mesophylla | X | X | | X | | | X | X | X | | | | X | | |
| Phyllops | X | X | | | X | | X | | X | | | | | | |
| Platyrrhinus | X | X | X | X | X | X | X | X | X | | X | | X | | |
| Pygoderma | X | X | | X | X | | X | | X | | X | | X | | |
| Sphaeronycteris | X | X | | | | | X | | X | | | | X | | |
| Stenoderma | X | X | | | | | X | X | X | | | | X | | |
| Sturnira | X | X | X | X | | X | X | X | X | X | X | | X | X | |
| Uroderma | X | X | X | X | X | X | X | X | X | X | X | | X | X | |
| Vampyressa | X | X | X | X | X | X | X | X | X | | X | | X | | X |
| Vampyrodes | X | X | X | | | X | X | X | X | | X | | X | | |

TABLE 4
Continued

| Genus | Baron et al. (1996a, b) | Benedict (1957) | Forman et al. (1979)[c] | Gimenez (1993)[d] | Griffiths (1982)[e] | Hood & Smith (1982, 1983) | Lim (1993) | McDaniel (1976) | Owen (1987)[f] | Sprague (1943) | Straney (1980)[g] | Strickler (1978) | Van Den Bussche (1991, 1992) | Vaughan & Bateman (1970)[h] | Wible & Bhatnager (1996)[i] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Mormoopidae** | | | | | | | | | | | | | | | |
| *Mormoops* | X | X | | | | X | X | | | | X | X | X | X | X |
| *Pteronotus* | X | X | | X | | X | | | | X | X | X | | X | X |
| **Noctilionidae** | | | | | | | | | | | | | | | |
| *Noctilio* | X | X | | X | | X | X | | | | X | X | X | | X |

[a] Genera arranged in higher-level groupings after Koopman (1993), and alphabetically within subfamilies.

[b] In addition to studies listed in the table, we collected some data from: Altenbach (1979; for *Desmodus*); Vaughan (1959; for *Macrotus*); Van Den Bussche et al. (1993; for *Artibeus, Dermanura, Enchisthenes, Koopmania, Chiroderma, Uroderma, Platyrrhinus,* and *Sturnira*); Simmons (1996; for all *Micronycteris* species, except *M. behnii*).

[c] Some data summarized by Forman et al. (1979) appeared in earlier papers by Forman (1971, 1973), which examined mormoopids and noctilionids, respectively.

[d] Gimenez (1993) scored tongue characters for the following taxa based on previously published descriptions: *Macrotus, Brachyphylla, Phyllonycteris, Erophylla, Monophyllus, Leptonycteris, Choeronycteris, Hylonycteris,* and *Platalina*. Gimenez et al. (1996) restricted their focus to nectar-feeders and some outgroup taxa originally described by Gimenez (1993), and used previously published descriptions to code characters for *Platalina, Phyllonycteris, Erophylla, Monophyllus, Choeronycteris, Hylonycteris,* and *Platalina*. Gimenez et al. (1996) were able to examine *Macrotus, Brachyphylla,* and *Leptonycteris* for their study.

[e] Griffiths (1983b) described some of the musculature of the hyoid of *Pteronotus*.

[f] Owen (1991) analyzed relationships only among "short-faced" stenodermatines and *Dermanura* species, using *Artibeus, Sturnira,* and *Carollia* as outgroups.

[g] Straney (1980) compiled data from various sources as well as examining selected representatives for certain characters; thus, not all characters were scored for each taxon included in his study.

[h] Although Vaughan and Bateman (1970) list these taxa as specimens they dissected, they did not present data on each muscle for each representative.

[i] In addition to the taxa marked above, Wible and Bhatnager (1996) summarized data on the accessory olfactory bulb for *Macrophyllum, Micronycteris, Mimon, Phylloderma, Phyllostomus, Tonatia, Trachops, Vampyrum, Lonchophylla, Lionycteris, Monophyllus, Ardops, Dermanura, Enchisthenes, Koopmania, Chiroderma, Mesophylla, Platyrrhinus, Sphaeronycteris, Uroderma, Vampyressa,* and *Vampyrodes*.

## PELAGE AND INTEGUMENT

This section summarizes characters of the pelage, vibrissae, integument, and features of related structures including chin papillae, noseleaf, and pinnae. Many of these characters are described for the first time, but some are based on features originally described by Straney (1980: character numbers from appendix 1), Owen (1987: character numbers from appendix 2[3]; 1991: character numbers from the appendix), Lim (1993: character numbers from appendix 2), Marques-Aguiar (1994: characters from appendix 4), and Simmons (1996). We have modified their character descriptions in many cases, and have scored these characters for all taxa included in our analysis when possible (fluid specimens of *Musonycteris* and *Scleronycteris* were unavailable; see table 4 for taxa included in previous analyses). Characters related to hair structure (characters 1 to 4 below) are based on Benedict's (1957) descriptions (see table 4); we did not collect any new observational data for these four characters.

**Character 1:** *Pelage differentiated into over hair and under hair (0); or pelage uniform, over hairs apparently absent (1).* In most phyllostomids, the pelage is of uniform

[3] Character state numbers in Owen's (1987) appendix 2 do not correspond with those in the discrete character matrix he presented on pages 8–9. In appendix 2, the first assigned character state (presumably the primitive condition in most cases) is 1, whereas in the matrix the first character state assigned is 0, except for the first three characters where the character states in the matrix and those from appendix 2 agree. To avoid confusion, we choose to use the numbers in his matrix (i.e. beginning with state 0) in our discussions because they correspond with our method of scoring. Although Owen (1987) presented multistate characters and figures describing the manner in which these characters were ordered, he nevertheless appears to have recoded these characters using additive binary coding prior to running his analyses. These recoded characters were not present in his 1987 text, and we therefore direct our comments to the multistate characters presented in his appendix 2. However if Owen's (1987) additive binary characters were similar to those he presented in 1991, some of our criticisms of his characters might not be valid. For example, while Owen (1987) presented dental formulae in a multistate character—see our comments under character 48—Owen (1991) broke this character into several that described loss of individual teeth at specific loci (i.e., loss of a lower premolar).

length and density (Benedict, 1957) and the over hairs are apparently absent. In contrast, the pelage is clearly differentiated into fine, wavy under hairs and thicker, straighter, longer over hairs in *Desmodus*, *Diaemus*, *Phyllostomus*, *Phylloderma*, *Brachyphylla*, phyllonycterines, *Lionycteris*, *Ardops*, and *Sturnira* (Benedict 1957). The pelage is also differentiated into under hairs and over hairs in mormoopids and *Noctilio* (Benedict, 1957), suggesting that this is the primitive condition for phyllostomids.

Benedict (1957) described differentiation of the pelage and Straney (1980: character F2) first used this character in a component analysis. Our character states are equivalent to Straney's (1980) characters; however, we disagree with his characterization of desmodontines and brachyphyllines (s.l.). In his data matrix, Straney (1980) scored desmodontines "+", indicating that all desmodontines share the derived condition of differentiated pelage; however, *Diphylla* does not have differentiated pelage. Our scoring reflects Benedict's (1957) original descriptions. In addition, Straney (1980) scored brachyphyllines "++", indicating that not all members of the taxon have the derived state (pelage differentiated into under hairs and over hairs). However, according to Benedict (1957), *Brachyphylla*, *Erophylla*, and *Phyllonycteris* all have pelage that is differentiated into under and over hairs.

We based our conclusion that the over hairs are absent in bats with undifferentiated pelage on a comparison of cuticular scale types. In most bats with distinct over and under hair, the alternate annular arrangement of hair scales (see character 3) does not occur on the over hair; thus, it may be that in phyllostomids in which over and under hair cannot be distinguished, the over hair may be absent.

**Character 2:** *Basal bulb on hair shaft absent (0); or present (1).* In most phyllostomids, the proximal third of the hair filament is of roughly uniform diameter and there is no basal swelling, or bulb (Benedict, 1957). In contrast, a swollen basal bulb is present on the proximal third of the hairs in *Desmodus* and *Diaemus*, some phyllostomines (e.g., *Lonchorhina*, *Tonatia*), and some stenodermatines (e.g., *Ametrida*, *Vampyrodes*;
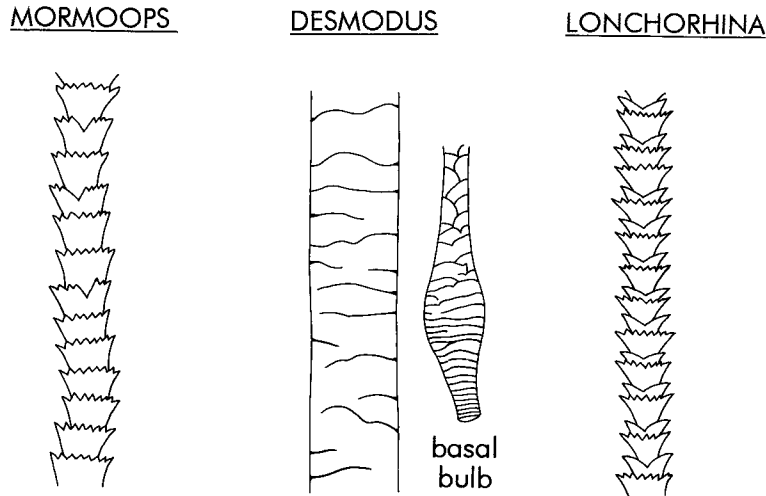
Fig. 16.   Magnified views (×100) of plastic impressions of hair shafts in the outgroup taxon *Mormoops* and two phyllostomids. The detail of the basal bulb is at 430× magnification and represents a "typical basal bulb" (Benedict, 1957: plate 24l) of the kind found in *Desmodus* (the drawing is of *Rhinolophus*). Note the "alternate annular" arrangement of the scales in *Lonchorhina* (see character 3; drawn after Benedict, 1957: plates 24l, 29v, 30a, v).

Benedict, 1957; fig. 16, detail). In mormoopids and *Noctilio*, the basal bulb is absent (Benedict, 1957), suggesting that this is the primitive condition for phyllostomids.

Straney (1980: character F1) first used this character in a component analysis. Our character states are identical to his, although our scoring of desmodontines is different. Benedict (1957) described *Diphylla* as lacking the basal bulb that is present in the other two desmodontine genera. Although Straney (1980: 35) accurately described the taxonomic distribution of this character in his text, he scored desmodontines "+" in his matrix, indicating that all desmodontines are derived in having a basal bulb. Our scoring reflects Benedict's (1957) description.

**Character 3:** *Consecutive cuticular scales appressed to hair shaft (0); or entire margin equally divergent (1); or consecutive scales with most divergent margins on alternate sides ("alternate annular" condition) (2).* In most phyllostomids, each cuticular scale encircles the entire hair shaft and the bodies of successive scales diverge most from the opposite sides of the filament (Benedict, 1957). This type of arrangement, known as "alternate annular," makes every other scale appear "hastate" (with a slight V-shaped emar-gination) on any given side of the filament, while the remaining scales appear to lack the V-shaped emargination (Benedict, 1957; see character 4 below; fig. 16). In contrast, the scales are completely appressed to the filament in the desmodontines (fig. 16); there is no difference in degree of divergence between the sides of each scale (Benedict, 1957). In *Mormoops*, consecutive cuticular scales have margins that are entirely divergent from the shaft; there is no difference in degree of divergence between the sides of each scale (Benedict, 1957; fig. 16). In *Pteronotus* and *Noctilio*, consecutive cuticular scales are appressed to the shaft (Benedict, 1957). This distribution of character states suggests that the appressed scale pattern seen in *Pteronotus* and *Noctilio* may be the primitive condition for phyllostomids.

Straney (1980: characters F3–F5) first used the divergence of the margin of the cuticular scales as a character in a component analysis, based on Benedict's (1957) descriptions. Straney (1980) defined three binary characters whose derived conditions are equivalent to our character states. However, Straney (1980) scored taxa for the alternate annular character (F5) as well as one of the other two characters (F3 or F4, scales either

divergent or appressed). Benedict (1957) characterized the degree of divergence of alternate annular scales from the shaft along what appears to be a continuum (appressed, slightly divergent, divergent, divaricate). Because of the continuous nature of this description, and the fact that the alternate annular condition describes a particular kind of divergence of the cuticular scales from the shaft of the hair, we did not include the additional information Straney (1980) used in his characters F3 and F4 in our version of this character.

Straney (1980) was not clear about which type of hair or which part of it he used to make his comparisons. Benedict (1957) noted that cuticular scale type changes over the length of the filament, and may be different on over hair and under hair, when these can be identified. Although Straney (1980) stated that all phyllostomids have entire, irregular emarginate, or denticulate scales alternating with hastate cuticular scales, this ''alternate annular'' condition occurs only on the middle part of the under hairs in *Phylloderma* (Benedict, 1957). On the over hairs and the tip of the under hairs, the cuticular scales are sinuate to erose coronal. Benedict (1957: 287) noted that only those scale types in the midregion of the hair shaft are deemed to be ''mature'' cuticular scale types. For this reason we used her descriptions of the midregion of all hairs, or the under hairs (when these could be identified; see character 1 above), to score this character and character 4.

**Character 4:** *Majority of scale margins on each hair entire (0); or irregular (1); or toothed (2); or entire and irregular (3); or entire and hastate (4).* In most phyllostomids, cuticular scale margins are entire (scales with a smooth straight margin; Benedict, 1957). However, in *Desmodus*, *Diaemus*, *Phylloderma*, *Phyllostomus*, and *Ardops*, the scale margins are irregular (Benedict, 1957; fig. 16). In *Lonchorhina*, *Macrophyllum*, *Anoura*, *Leptonycteris*, *Lionycteris*, and many stenodermatines (e.g., *Ariteus*, *Platyrrhinus*), the scales have toothed margins (Benedict, 1957; fig. 16). *Chrotopterus* seems to be unique among phyllostomids in consistently possessing scales of two different morphologies on a single filament: both entire and irregular shaped scales appear on

individual hairs (Benedict, 1957). We scored this taxon with state 3 in the matrix. *Phyllonycteris aphylla* has irregular scale margins while *Phyllonycteris poeyi* has entire scale margins. We scored the genus *Phyllonycteris* with states 0 and 1 in the matrix. In *Mormoops* and *Pteronotus quadridens*, the scale margins are toothed (Benedict, 1957), whereas *Pteronotus parnellii* has both entire and hastate scale margins on a single filament (Benedict, 1957; note that this is not the alternate annular condition described in character 3 above). In *Pteronotus gymnotus* and *Noctilio* the scale margins are entire (Benedict, 1957). We scored *Pteronotus* with states 0, 2, and 4 in the matrix. The primitive condition for phyllostomids cannot be assessed a priori given the distribution of these states in the outgroup taxa.

Benedict (1957) first described the morphology of the scale margins on bat hairs; this character has not appeared in previous phylogenetic analyses. Benedict (1957) described considerably more variation than we have recognized. For example, Benedict (1957) described our ''irregular'' scale margins (state 1) as being ''repand'' (slightly irregular at some points along the margin), ''sinuate'' (irregular along the entire scale margin with deeper notches), or ''erose'' (very irregular, with some sides of the scale being longer proximodistally than others). These scale types seem to illustrate states on a continuum. Thus, they may not represent discrete character states. For this reason, we decided to pool such states under the condition ''irregular.'' Similarly, we included both ''dentate'' and ''denticulate'' scale types within the character state ''toothed'' (state 2). We also scored taxa in which some scale margins occasionally differed from the most common margin type as having a single state because it seemed likely that occasional deviations may have resulted from damage to the scale margin (particularly because these deviations were almost always ''irregular'' in nature).

**Character 5:** *Dorsal fur unicolored (0); or distinctly bicolored, hairs with pale bases and dark tips (1); or tricolored, hairs with distinct dark bases, a pale median band, and dark tips (2).* In most phyllostomids, the dorsal fur is distinctly bicolored, with dark tips

and paler bases. Especially in phyllostomines with this feature, the pale bases of the hairs tend to be most evident over the shoulders and upper back and appear less distinct caudally. The white base may occupy more than one-half of the hair shaft (e.g., *Macrotus*) or be confined to a narrow stripe at the base of the fur (e.g., *Lonchorhina*). In contrast, *Micronycteris nicefori*, *M.sylvestris*, *Hylonycteris*, *Lichonycteris*, *Carollia*, and many stenodermatines (e.g., *Ametrida*, *Mesophylla*) have dorsal fur that is tricolored. A dark basal band is succeeded by a pale stripe and a dark tip. *Micronycteris brachyotis*, *Phyllostomus hastatus*, *Monophyllus*, and *Lionycteris* are the only phyllostomids that have unicolored fur (dark from tip to base). Because other species of *Phyllostomus* have bicolored fur, we scored this genus 0 and 1 in the matrix. The dorsal fur in *Mormoops* has a pale base and darker tip, but in *Pteronotus* and *Noctilio* the dorsal fur is unicolored. This distribution of character states leads us to conclude that unicolored fur is primitive for phyllostomids. Although we have not scored *Ectophylla* for most of the characters related to pelage color, we did score this taxon for this character. In *Ectophylla*, the posterior half of the dorsum is a grayish-brown color, and the individual hairs in this region have pale bases and a darker tip.

Owen (1987: character 3) used an ordered character with states identical to ours, later modifying it slightly when he restricted his analysis to a subset of original taxa surveyed (Owen, 1991: character 7). Our observations agree with those of Owen (1987) with a few exceptions. Owen (1987) described the dorsal pelage of *Platyrrhinus dorsalis*, which we observed to have a pale base and dark tip like other *Platyrrhinus* species, as tricolored. Owen (1987) also scored *Ectophylla* as having unicolored fur. *Ectophylla* is unique among phyllostomids in having a white head and shoulders and a brownish lower body. The hairs on the anterior of the dorsum are white from base to tip, while the brownish fur on the lower body has a brown tip and pale base. We suggest that the presence of "unicolored" white fur on the anterior of the dorsum of *Ectophylla alba* is an autapomorphy of this species, and that the hair on the lower body that has a pale base and dark tip

reflects a condition that *Ectophylla* may potentially share with other phyllostomids. Finally, Owen (1987) noted that *Chiroderma improvisum* has dorsal fur with a pale base and dark tip (in contrast to other *Chiroderma* species which have tricolored fur). We were unable to examine this species; however, Jones and Baker (1980: 1) described *Chiroderma improvisum* as having individual hairs that are "pale brownish gray throughout most of their length, slightly darker basally, and tipped with a dark, rich brown." A juvenile individual examined by the same authors had distinctly tricolored fur (Jones and Baker, 1980). We therefore score *Chiroderma* as possessing tricolored fur. Owen's (1991) observations are identical to those of Owen (1987). Both Simmons (1996: character 1) and Marques-Aguiar (1994: character 4) employed a similar character in their analyses of *Micronycteris* and large-bodied *Artibeus*, respectively; our observations agree with theirs.

**Character 6:** *Facial fur of uniform color (0); or facial stripes present (1).* In most phyllostomids, facial fur is of uniform color and no facial stripes are present. In contrast, many stenodermatines (e.g., *Artibeus*, *Uroderma*) have facial stripes. There are two stripes on each side of the face in most taxa: a more intensely colored dorsomedial stripe, and a lighter ventrolateral stripe. The dorsomedial stripe begins at the posterolateral edge of the noseleaf and runs superior to the eye, generally terminating at some point along the medial external surface of the pinna. The ventrolateral stripe begins along the corner of the mouth and generally runs toward the tragus, ending at its base. Stripes vary in length, width, and color intensity within and between genera. Although the presence of dorsomedial stripes is invariant in genera, ventrolateral stripes are not always present in all species of a genus. For example, *Chiroderma trinitatum* has two bright pairs of facial stripes, whereas *Chiroderma villosum* lacks the ventrolateral pair and has lightly colored bands in the region of the dorsomedial stripes. Nevertheless, all species of *Chiroderma* have at least dorsomedial stripes. Other taxa that exhibit similar variation in the presence of ventrolateral facial stripes are *Artibeus*, *Dermanura*, *Platyrrhin-*

*us*, *Uroderma*. Mormoopids and *Noctilio* lack facial stripes, suggesting that this is the primitive condition for phyllostomids. We scored *Ectophylla* ''−'' for this character (see below).

Owen (1987: character 4) used facial stripes as part of a complex multistate character that he termed ''pelage pattern.'' This character incorporated facial striping, dorsal striping (see character 7 below), shoulder patches (see character 8 below), and striping on the wing (an autapomorphy of *Centurio*). Owen (1987) ordered the character to preserve potential homologies. In general (see below) we agree with Owen's (1987, 1991) scoring of facial striping; however, Owen's (1987) description of character state 2 suggests that all taxa with facial stripes have paired stripes, rather than the situation we described above. One of our disagreements with Owen's (1987) scoring of facial stripes concerns *Artibeus*; Owen (1987) reported that *A. fuliginosus* (= *A. obscurus*) lacks facial stripes whereas we observed faint dorsomedial facial stripes in all *A. obscurus* we examined. We also scored *Ectophylla* as ''−'', whereas Owen (1987) regarded the pelage as uniformly colored. Owen (1991: character 8) considered facial stripes as a separate character for an analysis of a subset of stenodermatine taxa; however, scoring did not differ from his earlier work.

Lim (1993: character 1) used facial striping in his analysis of stenodermatine relationships. Although our descriptions of character states are identical to Lim's (1993), we do not agree with all his assessments concerning the taxonomic distribution of facial stripes. Lim (1993) noted that live specimens of *Koopmania* and *Mesophylla* have faint facial stripes similar to those in *Artibeus obscurus*. We could distinguish no trace of facial stripes in *Mesophylla*, either in color slides of live bats (AMNH 267281), or in well-preserved alcohol and skin preparations (e.g., AMNH 267281, AMNH 267563). Although our examinations of some color slides of live *Koopmania* suggested medial facial stripes were present in this genus, we believe that these ''stripes'' are the pale bases of the fur in this region, or frosted patches, because our examinations of skins of the bats appearing in these photos (e.g., AMNH 267193) did not reveal any facial striping. Frosted patches of fur are located on the forehead, face, neck, and shoulders of *Mesophylla*, and some specimens of *Koopmania* (e.g., AMNH 266267) also have frosted patches between the eyes, posterior to the noseleaf. These frosted patches may have been interpreted by Lim (1993) as facial stripes, but we do not believe they are homologous. Thus, we agree with Owen's (1987, 1991) assessment that *Mesophylla* and *Koopmania* lack facial stripes.

Lim (1993) scored *Ectophylla* as having facial and dorsal stripes and lacking a shoulder spot, whereas Owen (1987) scored the taxon as having uniformly colored pelage. We disagree with both scoring schemes. More than three quarters of the body of *Ectophylla* is grayish white; only the lower back is brown. Lim (1993) may have scored *Ectophylla* as possessing facial stripes because of a brown patch that extends from the lateral part of the noseleaf over the eye, but does not reach the ear. This brown fur visually separates the continuous white of the head into two parts that correspond to the areas in which the dorsomedial and ventrolateral stripes appear in other taxa. However, this color pattern is not strictly comparable to that seen in other phyllostomids with facial stripes, and we found it impossible to determine if stripes are unambiguously present. Accordingly, we scored *Ectophylla* ''−'' for this character.

**Character 7:** *Dorsal stripe absent (0); or always present (1); or sometimes present; polymorphic within species (2).* A pale dorsal stripe is present in the fur of one phyllostomine (*Mimon crenulatum*) and several stenodermatines (e.g., *Platyrrhinus*, *Uroderma*). In *Micronycteris nicefori*, a very pale dorsal stripe is present in most individuals (e.g., AMNH 266019) whereas it appears to be absent in the fur of others (e.g., AMNH 266015). We scored this species with state 2 in the matrix. Dorsal stripes usually begin at a point between the shoulder and the anterior margin of the medial pinnae, extend down the center of the back, and always reach the base of the tail. Length and color intensity of the dorsal stripe may vary among and within genera. For example, within *Vampyressa*, *V. pusilla* has no dorsal stripe, *V. brocki* has a

faint stripe present on the lower back to the base of the tail, and *V. bidens* has a distinct stripe present from a point between the pinnae to the base of the tail. Such differences also exist among species of *Chiroderma* and *Platyrrhinus*, although no species in the latter genus completely lacks a dorsal stripe. Because some species of *Chiroderma* lack a dorsal stripe, whereas in others this feature is present, this genus is scored 0 and 1 in the matrix. As noted above (see character 5), the fur of the lower back is brown in *Ectophylla* and would therefore be expected show evidence of dorsal striping (if present) since dorsal stripes always reach the base of the tail. There is no evidence of a dorsal stripe in *Ectophylla*. In mormoopids, dorsal stripes are absent; however, some individuals of both *Noctilio* species have a pale to strongly colored dorsal stripe. *Noctilio* is scored with state 2 in the matrix. The primitive state for phyllostomids cannot be assessed a priori.

Owen (1987: character 4) originally used this feature in his external character "pelage pattern," although he included several additional states to accommodate variation in stripe length. Because stripe length varies among species within genera, we choose to omit this information from our study. Our scoring of this character agrees with Owen's (1987) observations, with the exception of *Ectophylla*, which Owen (1987) scored as possessing unicolored fur.

**Character 8:** *Fur on shoulder of uniform color, no white shoulder spot (0); or distinct white shoulder spot present (1).* In most phyllostomids, the shoulder region is generally uniform in color and there is no distinct white spot. Although some specimens may appear to have pale patches on the shoulders, these patches do not have well-defined edges and are either extensions of the lighter ventral fur into the shoulder region (e.g., *Chrotopterus* AMNH 267131), or the pale bases of bicolored fur that are visible when the fur is slightly parted (e.g., *Tonatia silvicola* AMNH 267108). In *Sturnira*, many adults of both sexes have shoulder glands which produce a waxy secretion that may stain the fur in the shoulder region, producing what are termed "epaulettes" (Davis et al., 1964), but these patches are usually bright orange or brown, not white. In contrast, some stenodermatines (e.g., *Ametrida*, *Sphaeronycteris*) have a small, clearly defined patch of white fur on the shoulder. No white spot is present in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids. We scored *Ectophylla* "−" for this character because the shoulders in this species are completely white (see discussion under character 5 above).

Owen (1987: character 4; 1991: character 9) included shoulder spots in his phylogenetic analyses. Our character states and scoring are identical to those of Owen (1991) and Lim (1993: character 2).

**Character 9:** *Fur on neck of uniform color, no white neck spot (0); or distinct white spot sometimes or always present on neck (1).* In most phyllostomids, the area of the neck ventral and caudal to the lateral part of the pinna is roughly the same color as the fur on the neck and shoulders, and no white spot is present. In contrast, a white spot is present in *Ametrida*, *Centurio*, *Phyllops*, *Pygoderma*, *Stenoderma*, and *Sphaeronycteris*. In *Pygoderma*, the spot appears to be absent in some specimens (e.g., AMNH 234296). In *Centurio*, the spot is present on the face mask (see character 38 below). In the outgroups, mormoopids and *Noctilio*, no neck spot is present, suggesting that this is the primitive condition for phyllostomids. We scored *Ectophylla*, which has a completely white neck, "−" (see character 5 above).

This character has not been used in previous studies. We have chosen to treat polymorphism in this character conservatively (i.e., the derived condition is sometimes or always present) because Peterson (1965: 8), who was able to examine many more representatives of *Ametrida* than we did, found that this spot is not always present in this species. Our observations indicate that the spot varies in intensity, leading us to suspect that the spot may be polymorphic in more taxa than we report here.

**Character 10:** *Uropatagium without fringe of hair along trailing edge (0); or with distinct fringe of hair along trailing edge (1).* The phyllostomid uropatagium usually does not have a distinct fringe of hair that extends beyond the trailing edge of membrane. In contrast, a distinct fringe is present along most of the caudal edge of the uropatagium

in desmodontines, *Macrophyllum*, *Mimon crenulatum*, *Anoura*, *Leptonycteris*, and many stenodermatines (e.g., *Ardops*, *Platyrrhinus*). In *Rhinophylla fischerae*, *Artibeus hirsutus*, *Dermanura azteca*, and *D. tolteca*, distinct fringes are present, whereas other species in these genera lack a fringe. We scored these genera with states 0 and 1 in the matrix. The uropatagium lacks a fringe in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

Lim (1993: character 13) used the presence of a fringe on the uropatagium as a character, erecting two states: "Edge of uropatagium naked or sparsely and irregularly haired (0); edge of uropatagium densely and evenly haired (1)." Only *Platyrrhinus* and *Vampyrodes* were scored with the derived condition. In contrast, we found dense and evenly haired fringes in many additional stenodermatine taxa.

**Character 11**: *Superciliary vibrissae absent (0); or always present (1).* Most phyllostomids lack superciliary (= supraorbital) vibrissae (fig. 17D–E), a group of one or more vibrissae that occurs above each eye in most mammalian groups (Pocock, 1914; Brown, 1971; fig. 17A). However, a single superciliary vibrissa is present above each eye in *Desmodus* (fig. 17B), *Diaemus*, some phyllostomines (e.g., *Micronycteris megalotis*, *Vampyrum*; fig. 17C), and one stenodermatine (*Centurio*). Taxonomic polymorphism exists in two genera: *Lonchorhina* (present in *L. marinkellei*, absent in other species), and *Tonatia* (present in *T. silvicola* and *T. schulzi*, absent in other species). We scored these genera with states 0 and 1 in the matrix. In one specimen of *Chrotopterus* (AMNH 267443), the superciliary vibrissae are absent, but these vibrissae are present in all other specimens of *Chrotopterus* we examined. We consider this an anomaly and score *Chrotopterus* with state 1 in the matrix. In some taxa (e.g., *Micronycteris megalotis*, *Tonatia silvicola*) the superciliary vibrissae are anterior to their position in other species. Rather than directly superior to the eye, they are anterior and superior to it. However, they occur in the same position relative to the other groups of facial vibrissae (fig. 17C). We therefore consider these vibrissae to be ho-

mologous to the superciliary vibrissae of other taxa. Superciliary vibrissae are absent in mormoopids, but present in *Noctilio* (fig. 17F); accordingly the primitive condition for phyllostomids cannot be reconstructed a priori.

Although this character has not been used in previous phylogenetic analyses, there is much evidence to suggest that homologies may be drawn among vibrissal groups, and potentially among individual vibrissae. The locations of various groups of vibrissae on the face is highly conservative among mammals, and presumably homologous groups or individual vibrissae may be identified on the basis of their relative position (Pocock, 1914; Brown, 1971; Wineski, 1985). Many and perhaps all facial vibrissae have individual representations in both the spinal trigeminal nucleus and the somatosensory cortex (Zucker and Welker, 1969; Waite, 1973a, 1973b, Woolsey, 1978), further supporting the idea that homologies may be drawn among individual vibrissae and vibrissal clusters in different taxa, as we do here.

**Character 12:** *Genal vibrissae absent (0); or one vibrissa present in each cluster (1); or two genal vibrissae present in each cluster (2).* Genal vibrissae occur on the sides of the face ventral and/or posterior to the eye (Pocock, 1914; Brown, 1971; fig. 17A). Genal vibrissae are present in most phyllostomids (fig. 17B–C, E). However, these vibrissae are absent in some phyllostomines (e.g., *Macrophyllum*, *Mimon*), *Platalina*, and several glossophagines (e.g., *Glossophaga*, *Monophyllus*). In most phyllostomids with genal vibrissae, two occur in each cluster. However, *Brachyphylla*, *Erophylla*, most glossophagines, some lonchophyllines, and *Pygoderma* have a single genal vibrissa on each cheek. Taxonomic polymorphism occurs in *Lonchorhina* (absent in *L. fernandezi*, two in *L. aurita*), *Lonchophylla* (fig. 17D; absent in *L. mordax* and *L. thomasi*, two in *L. robusta*), *Anoura* (one in *A. caudifer* and *A. cultrata*, two in *A. geoffroyi*), *Choeroniscus* (absent in *C. minor* [= *C. intermedius*], one in *C. periosus*), *Carollia* (absent in *C. perspicillata*, one in *C. subrufa*), and *Sturnira* (absent in *S. bidens*, one in *S. bogotensis*, two in other species we examined). We scored these taxa with the appropriate combinations
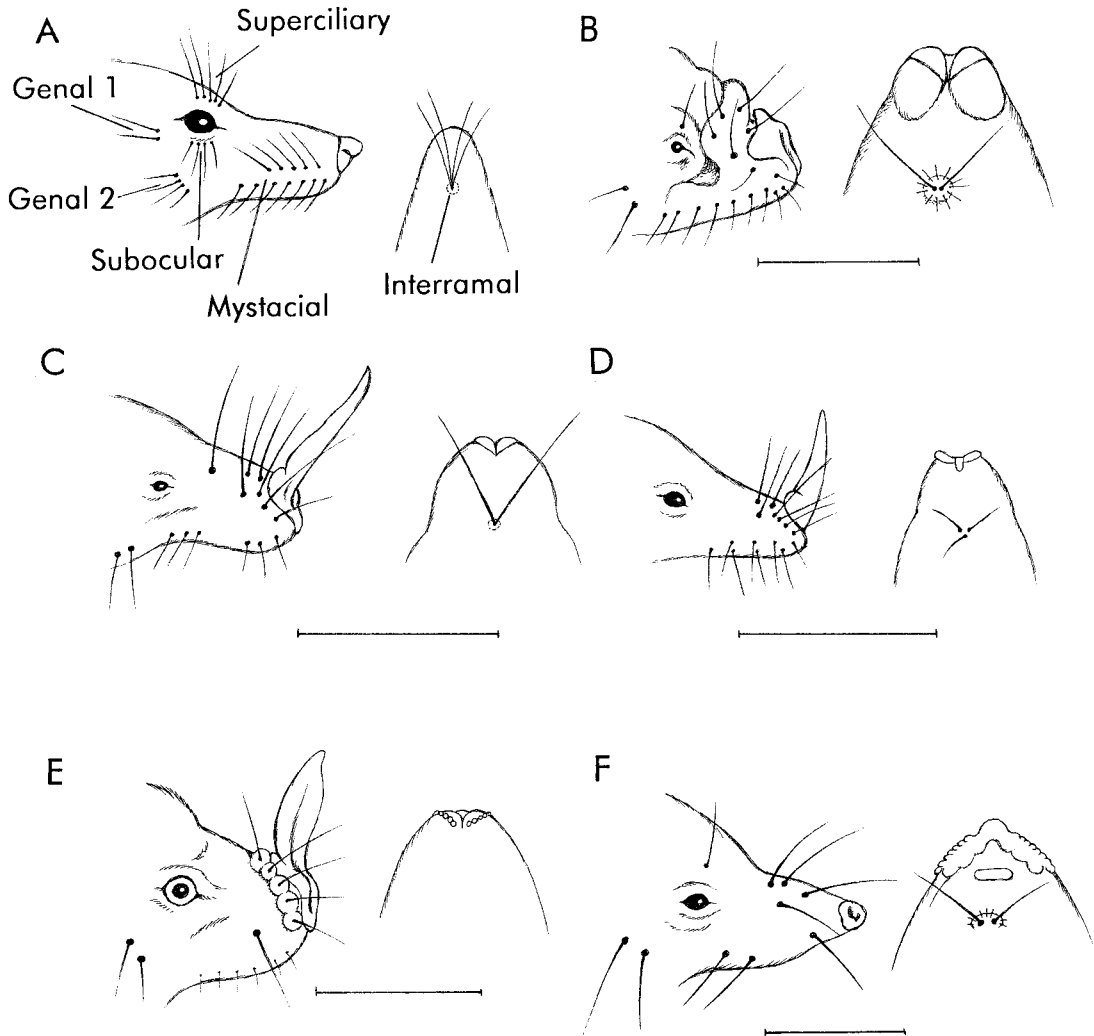
Fig. 17. Lateral view of the head (left) and ventral view of the chin (right) of selected taxa illustrating the position and number of vibrissae found in clusters. **A.** Generalized mammal (after Brown, 1971: fig. 6) **B.** *Desmodus rotundus* (AMNH 267503). **C.** *Micronycteris megalotis* (AMNH 267411). **D.** *Lonchophylla thomasi* (AMNH 266107). **E.** *Uroderma bilobatum* (AMNH 268564). **F.** *Noctilio leporinus* (AMNH 267408). Scale bar = 10 mm.

of character states in the matrix (e.g., *Lonchorhina* is scored 0 and 2). In one specimen of *Vampyrodes caraccioli* (AMNH 239254), we found three genal vibrissae present in each cluster, whereas all other individuals we examined had two. We view this as an anomaly as all other phyllostomids we examined had no more than two of these vibrissae; consequently, we score *Vampyrodes* with state 2 in the matrix. The genal vibrissae are absent in *Mormoops*, whereas *Pteronotus* has a single vibrissa on each cheek and *Noctilio* has two genal vibrissae in each cluster (fig. 17F). The primitive state for phyllostomids cannot be reconstructed a priori.

This character has not appeared in previous phylogenetic analyses.

**Character 13:** *Interramal vibrissae always absent (0); or none or one interramal vibrissa present, polymorphic within species (1); or one interramal vibrissa always present (2); or one or two interramal vibrissae*

*present, polymorphic within species (3); or two interramal vibrissae always present (4); or none or two interramal vibrissae present, polymorphic within species (5); or three interramal vibrissae always present (6).* Interramal vibrissae occur between the rami of the lower jaws well posterior to the mandibular symphysis in most mammals (Pocock, 1914; Brown, 1971; fig. 17A). Two interramal vibrissae are present in most phyllostomids (fig. 17B–C). However, interramal vibrissae are apparently uniformly absent in some phyllostomines (e.g., *Chrotopterus*, *Vampyrum*) and many stenodermatines (e.g., *Pygoderma*, *Uroderma*; fig. 17E). The three lonchophylline genera appear to be unique among phyllostomids in possessing three interramal vibrissae (fig. 17D). *Choeronycteris* and *Musonycteris* have a single interramal vibrissa. Among other genera, there is a large amount of both taxonomic and intraspecific polymorphism. Several species exhibit intraspecific variation: *Lonchorhina aurita* (absent or two), *Macrophyllum macrophyllum* (absent or one), *Phyllostomus hastatus* (absent or one), *Trachops cirrhosus* (absent or one interramal vibrissa), *Choeroniscus intermedius* (absent or one), *Chiroderma villosum* (absent or one), and *Koopmania concolor* (one or two), *Platyrrhinus aurarius* (absent or one). Taxonomic polymorphism occurs frequently; interramal vibrissae appear to be uniformly absent in *Tonatia saurophila*, *Sturnira bidens*, *S. nana*, and *S. tildae* whereas the congeners of these species have two interramal vibrissae. We scored these two genera with states 0 and 4 in the matrix. In *Phyllostomus discolor*, *Chiroderma trinitatum*, *Platyrrhinus dorsalis* and *P. helleri*, the interramal vibrissae are absent whereas other species in these genera are polymorphic (absent or one vibrissa). We scored these three genera with states 0 and 1 in the matrix. In *Lonchorhina*, *L. fernandezi* has two interramal vibrissae, whereas *L. aurita* is polymorphic (absent or two). We scored this genus with states 4 and 5 in the matrix. In *Choeroniscus minor* these vibrissae are either absent or a single vibrissa is present, whereas in *C. periosus* a single vibrissa is present. We scored the genus *Choeroniscus* with states 1 and 2 in the matrix. In *Dermanura* the interramal vibrissae are ab-

sent in *D. cinerea*, whereas *D. anderseni* has one and *D. tolteca* has two. We scored this genus with states 0, 2, and 4 in the matrix. Two interramal vibrissae are present in *Mormoops* and *Noctilio* (fig. 17F), whereas *Pteronotus* has one. This distribution of character states suggests that two interramal vibrissae are primitive for phyllostomids.

This character has not been used in previous phylogenetic analyses.

**Character 14:** *Vibrissae lateral to nose/noseleaf arranged in two columns; medial column with three or more vibrissae, lateral column with two vibrissae (0); or single column with three or more vibrissae present, lateral column absent (1).* In desmodontines, many phyllostomines (e.g., *Chrotopterus*, *Phylloderma*), *Brachyphylla*, phyllonycterines, glossophagines, and lonchophyllines, the vibrissae lateral to the noseleaf are arranged in two columns: a medial column (nearest the noseleaf), consisting of three or more vibrissae (see character 15), and a lateral column, composed of only two vibrissae (fig. 17B–D). The two vibrissae in the lateral column occur on the dorsum of the snout more or less posterior to the first and second vibrissae in the medial column (numbering from dorsal to ventral). The lateral column of vibrissae is absent in several phyllostomines (e.g., *Macrophyllum*, *Phyllostomus*), carolliines, and stenodermatines (figs. 17E, 18A–C). The lateral column is present in mormoopids and *Noctilio* (figs. 17F, 18D), suggesting that this is the primitive condition for phyllostomids.

This character has not appeared in previous phylogenetic analyses.

**Character 15:** *Vibrissae in column adjacent to noseleaf/nose number two (0); or three (1); or more than 3 (2).* In most phyllostomids there are more than three vibrissae in the column immediately adjacent to the noseleaf. These vibrissae are extremely long and well developed, with swollen bases (or pads as described in character 16 below; fig. 18A–B). In contrast, in *Ametrida*, *Centurio*, and *Sphaeronycteris* there are only three of these well-developed vibrissae surrounding the noseleaf (fig. 18C). In mormoopids and *Noctilio*, there are two vibrissae in this column surrounding the nose (due to the morphology of the face in mormoopids these vi-
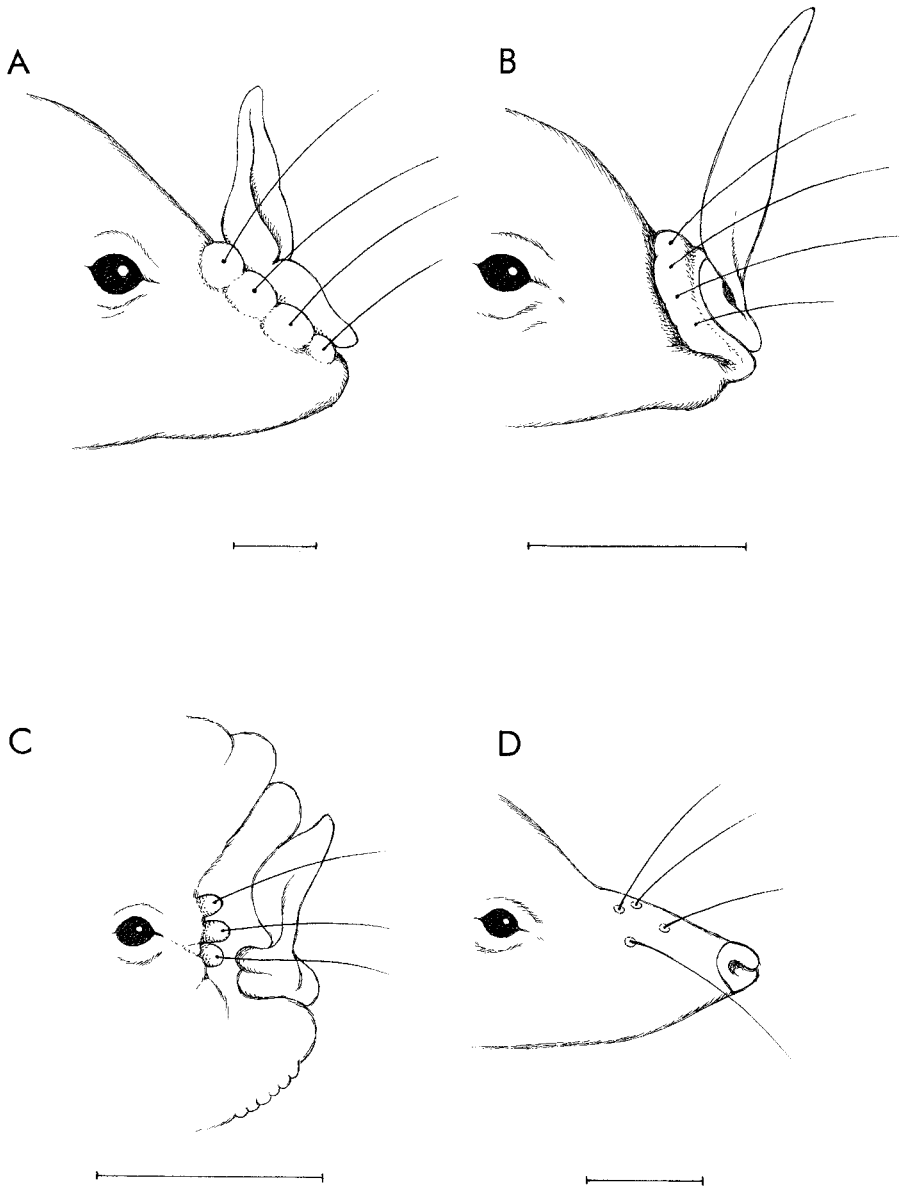
Fig. 18. Close-up view of the lateral column(s) of vibrissae and vibrissal papillae in **A.** *Phyllostomus hastatus* (AMNH 202308). **B**. *Rhinophylla pumilio* (AMNH 267163). **C**. *Sphaeronycteris toxophyllum* (AMNH 194213). **D.** *Noctilio leporinus* (AMNH 267408). Scale bar = 5 mm.

brissae are posterolateral to the nose; fig. 18D). The presence of two vibrissae in the column lateral to the noseleaf appears to be primitive for phyllostomids.

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

**Character 16:** *Vibrissae surrounding the nose/noseleaf arise from small, separate vi-brissal papillae (0); or vibrissal papillae connected, form padlike structure (1); or vi-brissal papillae connected, form free skin flap (2); or vibrissal papillae separate, form elongate, fleshy, cylindrical projections (3).* In most phyllostomids, the papillae of the in-dividual vibrissae located immediately adja-cent to the noseleaf are connected with each

other, forming two padlike structures, one on each side of the noseleaf (fig. 18A). These pads incorporate the vibrissal papillae in the medial and, when present, the lateral columns described in character 14. In contrast, the vibrissal papillae form fleshy skin flaps in a several taxa: *Rhinophylla*, *Ametrida*, *Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma* (fig. 18B). In *Centurio* and *Sphaeronycteris*, the vibrissal papillae are not connected with each other, and the papillae instead form elongate, fleshy cylinders that protrude from the face (fig. 18C). *Chrotopterus*, *Tonatia*, *Trachops*, and *Vampyrum* also have separate vibrissal papillae, but although these are often swollen, they are never elongate and cylindrical, nor do they form pads. In mormoopids and *Noctilio*, the vibrissal papillae are small and do not form padlike, flaplike, or cylindrical structures (fig. 18D); this distribution of character states suggests that the presence of small, separate vibrissal papillae is the primitive condition for phyllostomids.

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

**Character 17:** *Padlike or flaplike vibrissal papillae not in contact across dorsum of snout (0); or pads touch, or are confluent across dorsum of snout (1).* Most taxa with padlike or flaplike vibrissal papillae have two discrete, clearly separated, pads or flaps on either side of the noseleaf. These structures are not in contact, nor are they continuous, across the dorsum of the snout. In contrast, in *Brachyphylla*, *Erophylla*, and *Phyllonycteris* the padlike structures meet, or are continuous, posterior to the noseleaf. In these three genera, the vibrissae that are generally more laterally placed in other phyllostomids due to the wider separation of these pads, are located somewhat more posteriorly. Mormoopids and *Noctilio* do not have padlike or flaplike like vibrissal papillae; therefore, we scored these taxa ''−'' for this character. The primitive condition for phyllostomids cannot be reconstructed a priori. Taxa scored 0 and 3 in character 16 are also scored ''−'' for this character.

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

**Character 18:** *Noseleaf pale cream to dark brown, not strongly bicolored (0); or noseleaf yellow (1); or noseleaf bicolored,*

*well-defined cream patches present on proximal parts of the lateral lobes and edges of horseshoe, center of horseshoe and spear brown (2).* In most phyllostomids the skin of the noseleaf is a shade of pale to dark brown, generally the same color as the lips and face. Although the noseleaf appears lighter in color in some taxa (e.g., *Chrotopterus*), the range of colors seen in different species and within populations of a single species varies to such a degree that they cannot be coded as discrete character states. *Mimon crenulatum* presents an excellent example of the range of variation seen within species. The noseleaf in AMNH 267112 is a pale, creamy pink color; however, other individuals from the same locality have noseleaves that range from light brown around the edges of the spear with pale creamy pink in the center and on the horseshoe (AMNH 267883) to entirely brown (AMNH 267888). We thus recognize ''pale cream to dark brown'' as a single character state. *Ectophylla* and *Mesophylla* are unique among phyllostomids in having a noseleaf that is yellow in life (this generally fades to a much paler yellow color in preserved specimens). *Uroderma*, *Vampyressa bidens*, *V. nymphaea*, *V. pusilla*, and *Vampyrodes* exhibit yet another pattern, a consistently bicolored noseleaf. In these taxa the central rib of the noseleaf is always brown, but the lateral lobes and horseshoe edges have distinct patches of cream or yellow. In some species of *Chiroderma* (e.g., *C. trinitatum*), *Dermanura* (e.g., *D. cinereus*), and *Platyrrhinus* (e.g., *P. helleri*) the noseleaf is also distinctly bicolored, but congeners of these species have a brown or cream noseleaf. Thus, these three genera are scored 0 and 2 in the matrix. We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, ''−'' for this character; thus, the primitive state for phyllostomids cannot be assessed a priori. We also scored *Centurio* ''−'' for this character (see below).

This is the first use of this character in a phylogenetic analysis. Although one might imagine that state 2 might be correlated with presence of strong facial striping (see character 6), our observations suggest that this is not the case. In *Artibeus lituratus*, for example, strong facial stripes are present but the noseleaf is uniformly brown. However,

we did not use Lim's (1993: character 9) character for yellow coloration of the thumb because it has an identical distribution with the yellow noseleaf (found only in *Ectophylla* and *Mesophylla*); this suggests that these characters may not be independent.

Although presence of a noseleaf is generally regarded as a diagnostic feature of Phyllostomidae, a noseleaf with a well-defined horseshoe and spear may not be present in all phyllostomids. Although some authors have indicated that a noseleaf is present in *Centurio* (e.g., Hill and Smith, 1984; Lim, 1993), others have suggested that this taxon lacks a true noseleaf (Miller, 1907; Paradiso, 1967; Snow et al., 1980). We found that a spearlike structure is present between the nostrils in *Centurio*, but it is not confluent internarially with a horseshoe. Instead, this structure forms the medial part of the upper lip. The horseshoe portion of the noseleaf (if present) surrounds only the lateral portions of the nostrils. One way to settle the question of the homology of these structures might be to examine ontogeny of the narial region, but this has not yet been attempted. Pending such a study, we chose to score *Centurio* ''−'' for all characters related to the noseleaf.

**Character 19:** *Noseleaf spear long, greater than twice the height of the horseshoe (0); or spear truncated, equal to or less than the height of the horseshoe (1).* The phyllostomid noseleaf is divided into two parts, the horseshoe and the spear. The horseshoe surrounds the lateral and inferior aspects of the nostrils. The spear is a fleshy protuberance that rises off the surface of the snout from the superior aspect of the nostrils. The spear, which is continuous with the horseshoe both internarially and laterally, is generally delineated in some way from the alae of the horseshoe. The spear of the noseleaf is long and tapers to a point in most phyllostomids. In terms of relative proportions, the spear (as measured from the inferior margin of the nostril to the tip of the spear) is greater than twice the height of the horseshoe (as measured from inferior to superior horseshoe border; e.g., fig. 19B). In contrast, the spear is much shorter (truncated) in desmodontines, *Brachyphylla*, and phyllonycterines (figs. 19A, 20A). In these taxa, relative height of the spear ranges from equal to less

than half the height of the horseshoe. We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, ''−'' for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* ''−'' for this character.

Owen (1987: character 2, 1991: characters 3–5) and Marques-Aguiar (1994: character 9) both described the length of the noseleaf in relation to its width, within stenodermatines and *Artibeus* (*Artibeus*), respectively. We have redefined this character to account for the variation we observed among all phyllostomids.

**Character 20:** *Spear of noseleaf with pointed or rounded distal tip (0); or with* U-*shaped notch in distal tip (1).* The spear of the noseleaf has a pointed or rounded distal tip in most phyllostomids (figs. 19B–C, 20A–C, 21A–C). In contrast, a U-shaped notch is present in the distal tip of the noseleaf in desmodontines and *Brachyphylla* (fig. 19A). Presence of this notch may be dependent upon truncation of the spear (see character 19 above), but these features are not fully correlated. Phyllonycterines, which have a truncated spear, lack a notch in the distal tip (fig. 20A). We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, ''−'' for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* ''−'' for this character.

This character has not appeared in previous phylogenetic analyses.

**Character 21:** *Central rib absent (0); or rib restricted to proximal part of spear (1); or rib extends to distal tip of spear (2).* A thick, fleshy central rib is a prominent feature of the noseleaf of many phyllostomids. However, the central rib is absent and the noseleaf is flat in desmodontines, *Macrotus*, *Brachyphylla*, phyllonycterines, *Platalina*, and all glossophagines (figs., 19A, 20A, 20C). When the rib is present, it originates between the nostrils and extends distally into the spear. The rib extends into the proximal part of the spear but does not reach the tip in species of *Micronycteris*, *Lionycteris*, *Lonchophylla*, carolliines, *Sphaeronycteris*, and *Sturnira* (figs., 20B, 21A). In these taxa, the rib is well defined laterally but not distally, where it loses thickness and grades into the proxi-
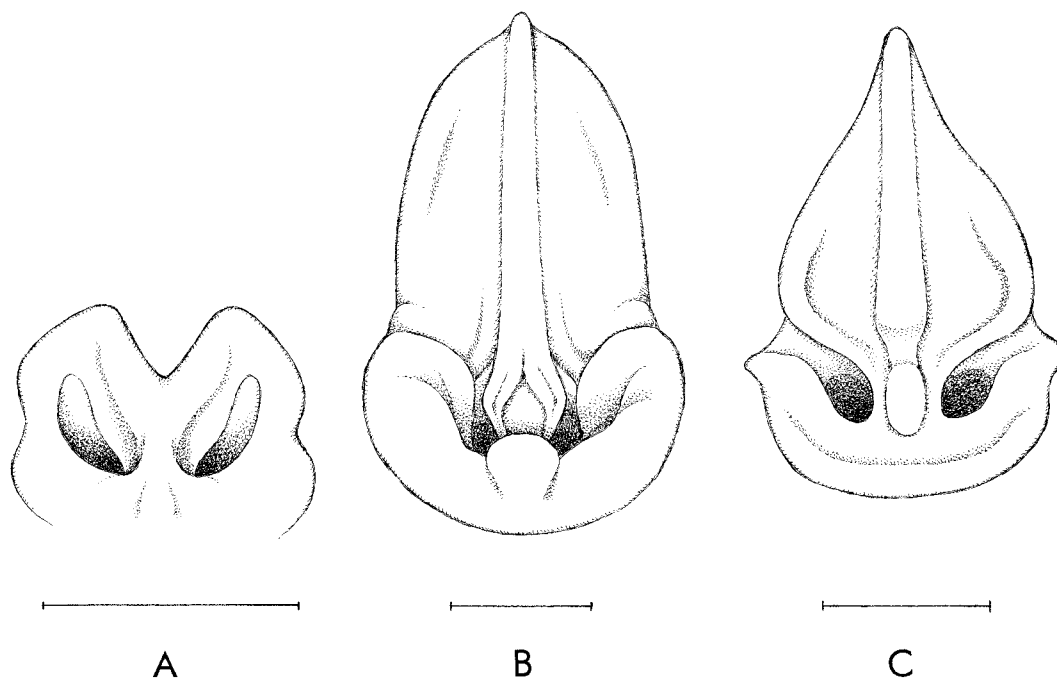
Fig. 19.    Anterior view of the noseleaf in **A.** *Desmodus rotundus* (AMNH 267503). **B.** *Vampyrum spectrum* (AMNH 202292). **C.** *Phyllostomus hastatus* (AMNH 233176). Scale bar = 5 mm.
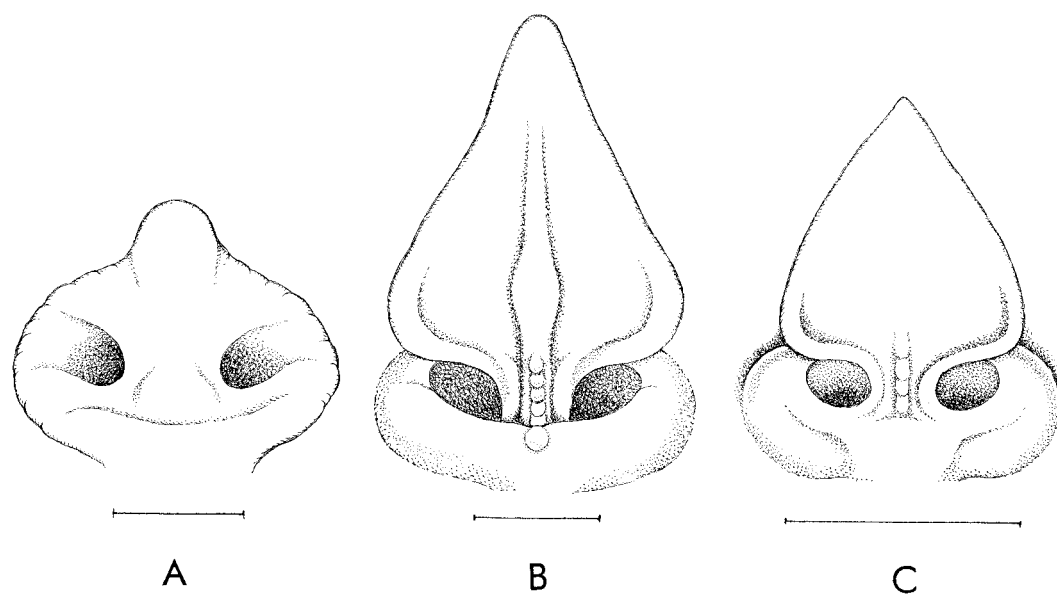


Fig. 20.    Anterior view of the noseleaf in **A.** *Erophylla sezekorni* (AMNH 194202) **B.** *Lonchophylla robusta* (AMNH 267452) **C.** *Choeroniscus intermedius* (AMNH 266122). Scale bar = 5 mm.
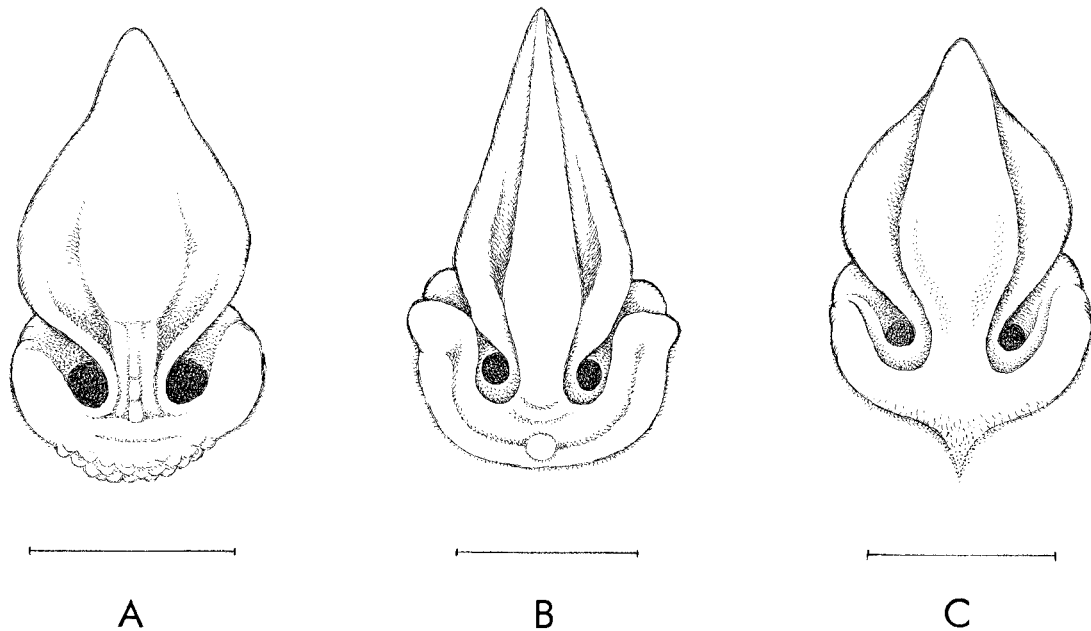
A        B        C

Fig. 21. Anterior view of the noseleaf in **A.** *Carollia perspicillata* (AMNH 266144) **B.** *Uroderma bilobatum* (AMNH 268564) **C.** *Ariteus flavescens* (AMNH 214944). Scale bar = 2 mm.

mal surface of the spear. In contrast, the rib extends to the tip of the spear in most stenodermatines and phyllostomines (figs. 19B–C, 21B–C). We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, ''−'' for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* ''−'' for this character.

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

**Character 22:** *Internarial region smooth, no midsagittal ridge or papillae (0); or narrow fleshy ridge or line of papillae always present along midsagittal line (1); or internarial ridge or papillae variably present, polymorphic within species (2).* A variety of structures occur between the nostrils in phyllostomids. The central rib of the spear continues into the internarial region in all taxa that have a rib (see character 21 above; figs., 19B–C, 20B, 21A–C). In most, the rib is the only structure present between the nostrils and it presents a smooth, slightly convex surface in this region. The internarial region is generally smooth (although flatter) in taxa that lack a rib on the spear (desmodontines, *Macrotus*, brachyphyllines, phyllonycterines,

*Platalina*). In contrast, a well-delineated, narrow, fleshy ridge or line of papillae is consistently present along the midsagittal line of the internarial region in some phyllostomines (e.g., *Lonchorhina*, *Vampyrum*), *Lionycteris*, *Lonchophylla*, glossophagines, and *Carollia* (figs. 19B, 20B–C, 21A). In one phyllostomine species that we examined (*Micronycteris hirsuta*), two out of 10 specimens exhibited an internarial ridge; consequently, we score this taxon with state 2 in the matrix. We did not detect any other within-species polymorphism in any other taxon. We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, ''−'' for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* ''−'' for this character.

Presence/absence of an internarial ridge or line of papillae is not correlated with presence/absence of the central rib; both are present in some taxa (e.g., *Vampyrum*) and absent in others (e.g., *Platalina*), whereas only a rib is present in some forms (e.g., *Phyllostomus*) and only an internarial ridge or line of papillae is present in others (e.g., *Glossophaga*). When both rib and ridge are present, the former is distinguished by its great-

er width and continuity with the rib of the spear; the internarial ridge is located on the rib between the nostrils in these taxa (e.g., *Vampyrum*).

The form of the internarial structures varies among taxa in which they are present (taxa scored 1 and 2 for this character). For example, *Chrotopterus* and *Vampyrum* always have a narrow, undivided internarial ridge, whereas a line of distinct papillae is present in the same location in other taxa (e.g., *Macrotus*, *Trachops*). Although we initially considered these to represent distinct conditions, further examination of glossophagines and lonchophyllines led us to discover a series of intermediates between the "ridge" and "papillae" conditions. Many glossophagines have a ridge that is subdivided by small grooves (e.g., *Glossophaga*), whereas in others the internarial structure more closely resembles a series of partly fused papillae (e.g., *Lionycteris*). The latter condition is also seen in some phyllostomines (e.g., *Micronycteris hirsuta*). Morphology of internarial structures also appears to vary within species. For example, within *Lonchophylla robusta*, some individuals (e.g., AMNH 235760) have a solid internarial ridge, whereas others (e.g., AMNH 235761) have an internarial ridge that consists of segments (three in this case) that appear to be elongate papillae. This type of variation leads us to conclude that the ridge and line of papillae represent endpoints of a continuum. As a result, we have not scored "ridge" and "papillae" as separate character states.

This character has not been used by other authors.

**Character 23:** *Sella absent (0); or present (1).* The sella (sensu Hernandez and Cadena, 1978) is a fleshy globular or trilobed structure that occurs on the horseshoe just inferior (or anterior) to the proximal end of the internarial ridge or line of papillae, with which it is continuous. Most phyllostomids lack a sella; it is present only in *Chrotopterus*, *Lonchorhina*, and *Vampyrum*. In *Chrotopterus* and *Vampyrum* (fig. 22A), the sella is a simple spherical structure. In contrast, in *Lonchorhina* the sella is a complex, trilobed structure with one anterior and two lateral lobes. It is located just inferior to the nostrils

on the edge of the horseshoe (fig. 22B). Because the horseshoe is completely bounded inferiorly by an extensive flap of skin in *Chrotopterus* and *Vampyrum* (see characters 25 and 26), the sella appears to occur in the middle of the horseshoe; however, it maintains the same position relative to the nostrils as seen in *Lonchorhina*. We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, "−" for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* and those phyllostomids that are scored with state 0 of character 22 (no internarial ridge or line of papillae) with "−" for this character.

Straney (1980: character G15) described the morphology of the noseleaf in *Lonchorhina* and *Macrophyllum* as having "lateral and medial projections on basal plate." However, our observations of this region in *Macrophyllum* indicate that most individuals do not have a trilobed structure (e.g., AMNH 222040). Therefore we do not consider differences in sella morphology as a separate character because we observed the trilobed sella in only one taxon.

**Character 24:** *Lateral edges of horseshoe thin and free (0); or superior portion of swollen edge of horseshoe forms free, flap-like edge (1); or swollen lateral edges of horseshoe ridgelike, fused to face along entire length with no free edge (2).* The lateral edges of the horseshoe consist of thin, free flaps of skin in most phyllostomids (figs. 19A–C, 20A, 21 A–C). In contrast, in some glossophagines (e.g., *Choeronycteris*, *Hylonycteris*) only the superior part of the lateral edge of the horseshoe forms a free, thickened flap, while the inferior part of the horseshoe is fused to the face (fig. 20C). In lonchophyllines and some glossophagines (e.g., *Anoura*, *Glossophaga*), both the superior and inferior parts of the horseshoe are fused to the face and there is no free edge (fig. 20B). In some species of *Tonatia* (e.g., *T. silvicola*), both the superior and inferior portions of the horseshoe are fused to the face, whereas in other species (e.g., *T. saurophila*) the entire lateral edge of the horseshoe is a thin, free flap. Consequently, we score *Tonatia* with states 0 and 2 in the matrix. We scored mormoopids and *Noctilio*, which clearly lack
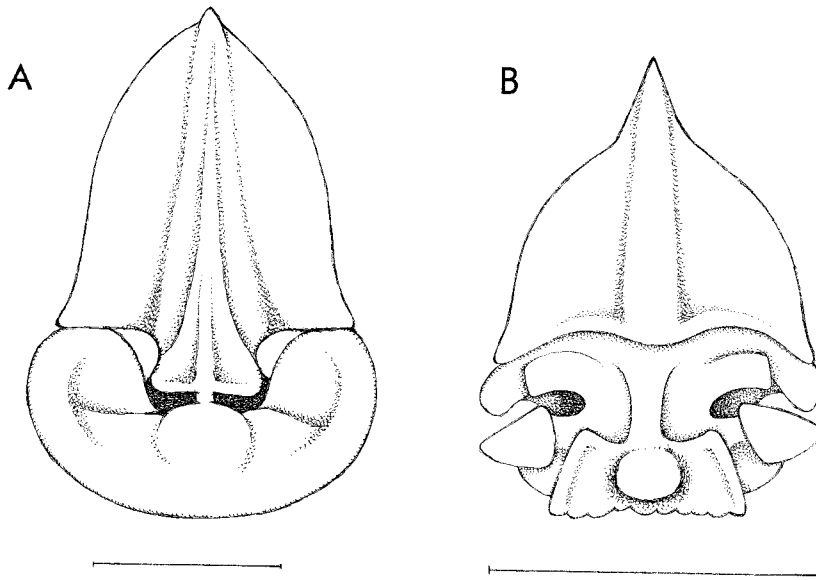
Fig. 22.    Anterodorsal view of the sella in **A.** *Vampyrum spectrum* (AMNH 202292) and **B.** *Lonchorhina aurita* (AMNH 199218). Note the position of this structure relative to the nostrils in both taxa. Scale bar = 5 mm.

a noseleaf, "−" for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* "−" for this character.

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

**Character 25:** *Inferior border of horseshoe is thin, free flap of skin (0); or inferior horseshoe is thickened ridge with no free edge (1); or inferior horseshoe grades smoothly into upper lip, no distinct boundary between lip and horseshoe (2).* The inferior border of the horseshoe is defined by a thin, free flap of skin in many phyllostomines (e.g., *Phyllostomus*, *Vampyrum*) and most stenodermatines (e.g., *Ametrida*, *Uroderma*; figs. 19B -C, 21B). In other phyllostomines (e.g., *Micronycteris megalotis*, *Mimon benettii*) and stenodermatines (e.g., *Ardops*, *Pygoderma*), the inferior border of horseshoe is formed by thickened ridge with no free edge (fig. 21C). In contrast, the inferior border of the horseshoe grades smoothly into the upper lip in desmodontines, some phyllostomines (e.g., *Phylloderma*, *Tonatia*, *Trachops*), *Brachyphylla*, phyllonycterines, glossophagines, lonchophyllines, carolliines, *Enchisthenes*, *Sphaeronycteris*, and *Sturnira* (figs.

19A, 20A–C, 21A). There is no clear boundary between the horseshoe and the upper lip in these taxa. We scored mormoopids and *Noctilio*, which clearly lack a noseleaf, "−" for this character; thus, the primitive condition for phyllostomids cannot be determined a priori. We also scored *Centurio* "−" for this character.

Straney (1980: characters G16–17) described two alternative conditions for the labial part of the horseshoe: fused to the upper lip (G16) or free (G17). We disagree with Straney's (1980) assessments of the labial horseshoe in *Mimon bennettii*, *Phylloderma*, glossophagines, and carolliines. Straney reported that in all of these taxa the ventral margin of the horseshoe is a free flap, contra our observations. Simmons (1996: character 7) also used a character similar to this one, although she did not consider our state 0 because it did not occur among members of the genus *Micronycteris*. Our scoring of this character in *Micronycteris* species is identical to hers. Marques-Aguiar (1994: character 10) also used this character, describing three conditions of the labial horseshoe (free, bound down and rimmed, and bound down and not rimmed), which she ordered 0 ↔ 1

↔ 2. Although we agree with her observations concerning most species, we found that the conditions she described for both *Artibeus fimbriatus* (bound down and rimmed) and *Artibeus amplus* (bound down and not rimmed) appeared very similar to the conditions we observed in all other species of *Artibeus* (s.s.; flaplike: character state 0); thus we do not score *Artibeus* as polymorphic for this character.

**Character 26:** *Thin, free edge of inferior horseshoe lies flat over upper lip (0); or forms upright cup around nostrils (1).* Among those phyllostomids that have a horseshoe with a thin, free inferior edge (most phyllostomines and stenodermatines; see character 25), this flap lies flat over the upper lip (figs. 19C, 21B). In contrast, the flap forms an upright cup around the nostrils in *Chrotopterus* and *Vampyrum* (fig. 19B). We scored mormoopids and *Noctilio*, which lack a noseleaf, "−" for this character. The primitive condition for phyllostomids thus cannot be determined a priori. We also scored *Centurio* and those phyllostomids that lack a thin, free flap of skin along the inferior border of the horseshoe (states 1 and 2 of character 25) "−" for this character.

This character has not been used in previous phylogenetic analyses.

**Character 27:** *Inferior border of thickened horseshoe smoothly curved or straight, no V-shaped notch or projection (0); V-shaped notch sometimes present (1); or V-shaped notch always present (2); or long, broad, V-shaped projection present (3).* The form of the inferior edge of the horseshoe varies among those taxa with a thickened labial border (see character 25 above). The inferior edge of the horseshoe generally forms a smoothly rounded U-shape or a straight line under the nostrils. However, a V-shaped notch is sometimes present in the center of the inferior border of the horseshoe in *Micronycteris megalotis* (e.g., AMNH 267411) and *Micronycteris minuta* (e.g., AMNH 233221) and is always present in *Micronycteris hirsuta*. An alternative condition is seen in *Ardops* and *Ariteus*, which have a long, broad, V-shaped projection that extends toward the lip from the center of the labial border of the horseshoe and gradually grades into the upper lip (fig. 21C). We scored mor-

moopids and *Noctilio*, which lack a noseleaf, "−" for this character. The primitive condition for phyllostomids thus cannot be determined a priori. We scored *Centurio* and those phyllostomids that do not have a thickened labial border (states 0 and 2 for character 25) "−" for this character.

This character has not been used in previous phylogenetic analyses.

**Character 28:** *Ridge of skin absent on dorsum of snout (0); or present (1).* No special structures occur behind the spear of the noseleaf in most phyllostomids (although see characters 17 and 29). However, in desmodontines a simple ridge of skin runs across the dorsum of the snout just posterior to the spear. The ridge extends between the superior margins of the lines of vibrissae described in character 14, but is not associated with any vibrissae. In *Desmodus* and *Diaemus*, this ridge of skin is connected to the posterior part of the noseleaf by two thin ridges, one from each of the lateral edges of the U-shaped notch of the spear. However, this connection is usually absent in *Diphylla* (one individual, AMNH 91283, had a single central connection running between the noseleaf and the ridge). In *Diaemus* and *Diphylla*, the ridge is generally relatively thin, and in *Desmodus* it is typically thicker and somewhat higher. However, there is significant within-species variation in ridge morphology, and the conditions seen in former taxa overlap that seen *Desmodus*. In *Mormoops* and *Noctilio*, there is no ridge of skin on the dorsum of the snout; however, in *Pteronotus*, a ridge is present on the dorsum of the snout. Based on this distribution of character states, it seems that absence of the ridge is the primitive condition for phyllostomids.

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

**Character 29:** *No outgrowth from posterior spear (0); or small scalloped outgrowth present, connected to base of spear by small ridge (1); or large sexually dimorphic outgrowth from base of spear present (2).* Although most phyllostomids do not have structures directly posterior to the spear (but see characters 17 and 28), an outgrowth of the posterior base of the rib is present in *Mesophylla* and *Vampyressa pusilla*. There is within-species variation in morphology of

this flap, which always has a scalloped appearance, but may appear bifid or trifid in different individuals. This outgrowth is connected to the posterior base of the rib by a small central connective ridge. The only other stenodermatine which has an outgrowth from the posterior spear is *Sphaeronycteris*. In this taxon, the outgrowth is large and sexually dimorphic (better developed in males). In *Sphaeronycteris*, there are also two parts to the outgrowth. The first is directly posterior to the spear, and attaches to almost the entire posterior face of spear, leaving a free border around the spear's edge. This primary attachment is a small, rounded ridge that connects the spear with the larger outgrowth, commonly termed the ''visor'' due to its appearance in male *Sphaeronycteris*. The ''visor'' connects with the entire posterior face of the first ridge in both sexes, but has a different morphology in each. In female *Sphaeronycteris*, the ''visor'' is small and has its origin over the center of each eye. In males, the origin is from the lateral corner of the eye and the structure is about four times the size of that present in females. We scored mormoopids and *Noctilio*, which lack a noseleaf, ''−'' for this character. Therefore, the primitive state for phyllostomids cannot be assessed a priori. We also scored *Centurio* ''−'' for this character.

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

**Character 30:** *Chin with pair of dermal pads, one present on each side of midline (0); or chin with multiple, well-developed dermal papillae (1); or chin smooth or with a few poorly developed papillae (2); or chin partly or completely covered with skin flaps (3).* In desmodontines, many phyllostomines (e.g., *Macrotus*, *Vampyrum*), phyllonycterines, glossophagines, lonchophyllines, and *Rhinophylla*, a pair of naked dermal pads are present on the chin (figs. 23A, 23C–E). These pads are typically oblong and are arranged in a U or V pattern just ventral to the lower lip. The space between the pads is always hairless and may lack other dermal structures, although small or large dermal papillae may be present in this region (e.g., *Rhinophylla*, see character 33 below).

The chin morphology of phyllonycterines and glossophagines is superficially different

from that of other phyllostomids with chin pads (fig. 23D). The chin in these genera is slightly (e.g., *Erophylla*) to deeply cleft (e.g., *Choeroniscus*) at the midline and the surfaces of the cleft are lined with smooth, hairless skin. The anterior borders of the cleft are fleshy and scalloped; these small projections resemble papillae when the cleft is closed and the bat is viewed anteriorly. Muscular action apparently keeps the cleft closed much of the time in living bats (personal obs.), but the cleft is often open in preserved specimens. In such cases, the fleshy walls of the cleft can be seen to resemble the chin pads typical of other bats with these structures, leading us to conclude that they are homologous. This hypothesis is further supported by the morphology of the chin in lonchophyllines, which is not cleft. In some individuals, only the superior margins of the pads appear to be scalloped as in glossophagines and phyllonycterines (e.g., *Lionycteris* AMNH 145504); however, substantial variation in edge ornamentation exists and the entire edge is scalloped in many individuals (e.g., *Lionycteris* AMNH 202295). The chin pads in lonchophyllines are arranged in the same U- or V-shaped pattern seen in desmodontines, phyllostomines, and *Rhinophylla*. Based on these observations, we score phyllonycterines, glossophagines, and lonchophyllines as having a pair of chin pads; differences in chin morphology among taxa with chin pads are treated separately in characters 31 and 32.

Many phyllostomines, *Brachyphylla*, *Carollia*, and most stenodermatines exhibit a markedly different pattern in which a U- or V-shaped row of small dermal papillae occurs in place of paired chin pads (figs. 23B, F). These papillae differ from the padlike structures described above because they arise from the flat anterior surface of the chin rather than the scalloping of the free edge of a chin pad. The space between the two arms of the U or V may be bare, or may contain some small papillae whose position and development varies from individual to individual. However, one large central papilla is consistently present in some taxa (e.g., most stenodermatines; see character 33). *Centurio* lacks chin papillae and pads altogether, and instead has a smooth chin. Most specimens
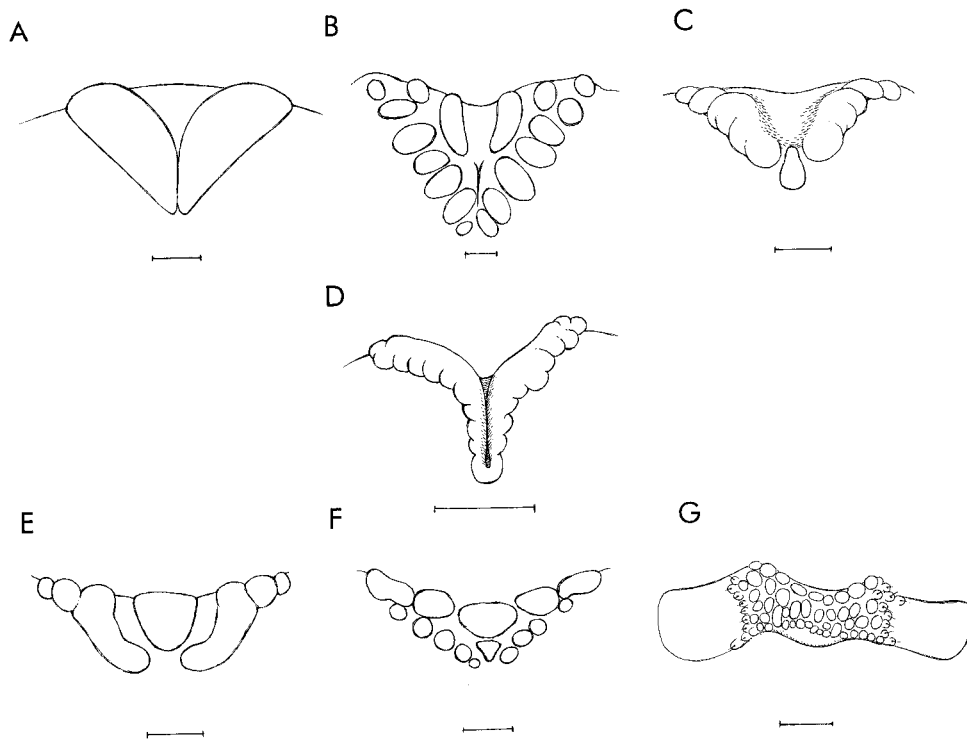
Fig. 23. Anterior views of the chins of representative phyllostomids and outgroup taxa. **A.** *Desmodus rotundus* (AMNH 267503). **B.** *Phyllostomus hastatus* (AMNH 202308). **C.** *Lonchophylla robusta* (AMNH 267452). **D.** *Choeroniscus intermedius* (AMNH 266122). **E.** *Rhinophylla pumilio* (AMNH 267163). **F.** *Uroderma bilobatum* (AMNH 268564). **G**. *Pteronotus davyi* (AMNH 214413). Scale bar = 1 mm.

of *Sphaeronycteris* also have a completely smooth chin, but one individual (USNM 494538) that we examined has an incomplete row of very small, poorly developed papillae on the chin. However, we consider the condition in both *Centurio* and *Sphaeronycteris* to be potentially homologous and score both with state 2 in the matrix.

*Mormoops*, *Pteronotus*, and *Noctilio* have chins that are partly or completely covered with complex folds of skin (fig. 23G). These flaps and folds do not appear to be comparable with the chin pads or papillae seen in phyllostomids, but instead seem to be outgrowths of the lower lip. *Pteronotus* has a papillated lip pad that covers the area along the lip and is continuous with the pinnae. The papillation is confined to the broader central area of the lip pad. The labial border of the pad is arched, and the mental border has a U-shaped notch. At the lateral corner of the mouth there is a low ridge of skin that is continuous with the pinna and with the lip pad. On the ventral surface of the chin, caudal to the lip pad is a caudal chin flap—a simple skin flap that encompasses the area between the canines. In *Mormoops*, the lip pad and caudal chin flap are similar to those in *Pteronotus*, although they are slightly smaller, but there are more complicated foliations connecting these elements. Two sets of lip flaps are present. The superior lip flaps are broad, ruffled foliations that course almost from the corner of the mouth to the posterior face of the lip pad, which they join. The caudal chin flap runs between the posterior surfaces of the superior lip flaps, encompassing the area just below the lip pad. Narrower inferior lip flaps, which are connected to the pinnae, course to just lateral of the point of attachment of the caudal flap to the superior lip flaps, where they too join the

posterior surface of the superior lip flaps. *Noctilio* lacks many of the foliations seen in mormoopids. A caudal chin flap runs between the flaplike lips. There are no additional foliations on surface of the chin. Because the unique conditions in the outgroup taxa do not occur among the ingroup, the primitive condition for phyllostomids cannot be assessed a priori.

Straney (1980: characters G18–19) used this character, describing two conditions: presence of simple chin pads (derived state of G18), roughly equivalent to our state 0, or complex chin pads (derived state of G19), roughly equivalent to our state 1. Our character is not identical to Straney's (1980), as he considered the chin flaps of mormoopids and noctilionids to be similar to chin papillae. Also, Straney (1980) scored *Lonchorhina*, *Brachyphylla*, and *Rhinophylla* as possessing multiple papillae on the chin, whereas we consider these taxa to have chin pads. This difference may be due to the presence of a large central papilla on the chins of these genera and others. We consider the presence of this papilla as a separate character (see character 33).

**Character 31:** *Chin pads simple, not scalloped (0); or chin pads with scalloped lateral edges (1).* As described above, the chin pads, when present, are simple (not scalloped) in desmodontines, phyllostomines, and *Rhinophylla* (figs., 23A, E). The lateral edges of the pads are smooth in these taxa. In contrast, the lateral edges of the chin pads are partly or completely scalloped in phyllonycterines, glossophagines, and lonchophyllines giving the pad edge a papillated appearance (see character 30 above; figs. 23C–D). We scored mormoopids and *Noctilio*, which lack paired chin pads, ''−'' for this character. The primitive condition for phyllostomids thus cannot be determined a priori. We scored phyllostomids that have either multiple chin papillae or smooth chins (states 1 and 2 of character 30 above) ''−'' for this character.

This character has not been used in previous phylogenetic analyses.

**Character 32:** *Chin without central cleft (0); or with slight to deep central cleft (1).* As described above (see character 30), the chin is relatively flat (not cleft) in most phyllostomids (fig., 23A–C, E–F). In contrast, the chin is slightly to deeply cleft at the midline in phyllonycterines and glossophagines (fig., 23D). Depth of the cleft appears to vary continuously however, and is therefore not considered as a separate character. Mormoopids and *Noctilio* have a chin that lacks a central cleft, suggesting that this is the primitive condition for phyllostomids.

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

**Character 33:** *Central papilla absent from chin (0); or central dermal papilla present on chin just ventral to midline of lower lip (1).* A central papilla is absent from the chin in desmodontines, most phyllostomines, *Brachyphylla*, and lonchophyllines (fig., 23A–C). In contrast, this papilla is present just ventral to the midline of the lower lip in *Macrophyllum*, carolliines, and stenodermatines (fig., 23E–F). The central papilla is surrounded laterally and inferiorly by either chin pads (e.g., *Rhinophylla*) or rows of dermal papillae (e.g., *Carollia*). We scored mormoopids and *Noctilio*, which have a unique chin morphology involving chin flaps (see character 30), ''−'' for this character. Thus, the primitive condition for phyllostomids cannot be determined a priori. We scored taxa with smooth chins (state 2 in character 30) and those with a chin cleft (state 1 of character 32) ''−'' for this character.

Although Straney (1980) discussed the distribution of the central papilla in phyllostomids, he did not use this as a character in his analysis. Our observations are largely in agreement with Straney (1980), with the exception of *Phylloderma*, *Phyllostomus*, and *Brachyphylla*. Straney (1980) described the central pad as doubled in *Phylloderma* and *Phyllostomus*. We did not observe a doubled central pad in these taxa, rather we found that these two genera, and many others, showed evidence of having two lateral central pads (see fig. 23B, F). However, due to marked within- and between-species differences, we were unable to use this as a character at this hierarchical level. In *Brachyphylla*, we did not observe a central papilla, while Straney (1980) indicated that this papilla was present.

**Character 34:** *Internal labial papillae absent (0); or internal labial papillae limited to lip line (1); or internal labial papillae more widely distributed, cover most of inside*

*of cheeks (2).* In most phyllostomids, the inner surface of the lips and cheek are smooth, but in stenodermatines these areas are studded with numerous small projections which Silva-Taboada and Pine (1969) called ''internal labial papillae.'' These fleshy papillae range in shape from somewhat flat, triangular projections to more conical structures. The extent to which internal labial papillae cover the inside of the mouth varies among taxa in which these structures are present. All stenodermatines have internal labial papillae along the upper lip, but the pattern of distribution is variable within species and no clear distinctions can be made among taxa. This is not true of the lower lip and cheeks, where the internal labial papillae are distributed in one of two patterns. Most stenodermatines have papillae located only along the lip line, and lack internal labial papillae on the inside of the cheeks. In contrast, *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Phyllops*, *Pygoderma*, *Sphaeronycteris*, and *Stenoderma* have internal labial papillae that more or less cover the inside of the cheeks. Mormoopids and *Noctilio* lack internal labial papillae, suggesting that absence of these structures is the primitive condition for phyllostomids.

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

**Character 35:** *Pinna margin not smoothly rounded, concavity located on lateral border (0); or pinna with smoothly rounded margin, no concavity on lateral border (1).* In most phyllostomids, a concavity is present at some point along the lateral margin of the pinna. However, in *Chrotopterus*, *Macrotus*, *Micronycteris hirsuta*, *M. megalotis*, *M. minuta*, *Tonatia*, *Trachops*, and *Vampyrum*, there is no concavity on the lateral margin of the pinna and the margin of the pinna is smoothly rounded. In mormoopids and *Noctilio*, a concavity is present on the lateral margin of the pinna, suggesting that this is the primitive condition for phyllostomids.

Owen (1987: character 1; 1991: characters 1–2) described the emargination of both the medial and lateral edges of the pinna. Although we agree with Owen (1987, 1991) that the pinna presents variation that may be useful in a phylogenetic context, our survey of this character suggests that Owen (1987) subdivided a continuous trait. Our character

has been designed to avoid dealing with the continuous nature of pinnal emargination while still describing relevant variation. Although we concur with Owen's (1987, 1991) observation of an emarginate lateral border in all stenodermatines and carollines, we disagree on the morphology of the pinna in *Macrotus*. Owen (1987: 58) described the pinna in *Macrotus* as ''Completely emarginated; pronounced indentation as in state 1.'' We did not use Owen's (1991: character 1) character ''Anterioproximal lobe on pinna,'' because this feature is an autapomorphy of *Centurio*. Simmons (1996) used presence or absence of a concavity in the lateral edge of the pinna in an analysis of relationships of *Micronycteris*, and our scoring agrees with hers.

**Character 36:** *Interauricular band absent (0); or present (1).* In most phyllostomids, the ears are not connected by an interauricular band. In contrast, a band of skin extends between the anterior external surfaces of the medial pinnae in *Macrotus*, *Micronycteris hirsuta*, *M. megalotis*, and *M. minuta*. All of these species have ears that, for phyllostomids, are large in proportion to the size of the skull: when folded forward they reach approximately to the end of the snout. The skin band in *Macrotus* and these species of *Micronycteris* is slightly less than one quarter the height of the ears. This band is flexible and is typically folded back against the braincase in preserved specimens. The band in each taxon originates from the external surface of each pinna just posterior to the medial edge, and runs transversely across the skull just anterior to the slope of the braincase. Although Koopman (1994) reported that *Tonatia silvicola* has these skin flaps, our examination of this species revealed that these structures do not appear similar to those present in *Macrotus* and *Micronycteris*. Instead, we interpret the ''flaps'' in *Tonatia* as slightly larger versions of the ridges of skin which cover the auricular muscles in all species (these are particularly visible if the pinna is pulled forward). We therefore score *Tonatia* as lacking an interauricular band. Although there are extensive foliations between the ears in *Mormoops* (see below), *Pteronotus* and *Noctilio* lack an interauricular band. The distribution of character states in the out-

group taxa suggests that absence of the interauricular band is primitive for phyllostomids.

In *Mormoops* the extensive foliations between the ears differ significantly from the morphologies described above. A flap of skin originates from each ear, but these flaps are much more extensive and complex than those described above. Each flap arises from the medial external surface of the pinna and courses anteromedially toward the midsagittal line. Near the midpoint, each flap divides, giving rise to a poorly defined branch that connects with its counterpart across the top of the cranium and a much larger flap that courses anteriorly until it terminates on the dorsum of the nose halfway between the tip of the snout and the slope of the braincase. These large right and left flaps are separated throughout their course along the rostrum. At the point of termination there is a roughly triangular lateral expansion in each of these flaps. Because of the differences between the simple skin band seen in some phyllostomids and the complex branched flaps found in *Mormoops*, we suspect that these structures are not homologous. *Pteronotus* and *Noctilio* lack skin flaps between the ears, and presence of these structures is generally interpreted as autapomorphy of the genus *Mormoops* (Smith, 1972). Accordingly, we score *Mormoops* "−" for this character.

Straney (1980: character G20) used presence of an interauricular band in his component analysis. However, he observed a band between the ears in *Lonchorhina* and several species of *Tonatia*. As we noted above, we interpret these flaps as being slightly larger versions of the ridges of the auricular muscles that connect the pinna with the fascia covering the skull. Simmons (1996: character 5) previously used presence of an interauricular band as a character in an analysis of relationships of *Micronycteris* species; our assessments agree with hers.

**Character 37:** *Notch in interauricular band shallow (0); or deep (1).* The interauricular band is characterized by a shallow, V-shaped midsagittal notch in *Micronycteris hirsuta* and *M. megalotis*. In contrast, the midsagittal notch is much deeper in *Macrotus* and *Micronycteris minuta*. In these taxa, the notch effectively divides the interauricular band into two triangular flaps, one associated with each ear. We scored mormoopids and *Noctilio*, which lack an interauricular band, "−" for this character. The primitive condition of this feature thus cannot be determined a priori. We scored other phyllostomids that lack an interauricular band (state 0 of character 36) "−" for this character.

Simmons (1996: character 6) previously used depth of the interauricular band as a character in an analysis of relationships of *Micronycteris* species. Due to the inclusion of several species of *Micronycteris* that do not appear in our analysis, Simmons (1996) subdivided the character more finely than we have done here, recognizing three states (shallow, moderate, and deep). However, our observations agree with hers.

**Character 38:** *Facial hood absent in both sexes (0); or present in males (1).* The skin of the neck is relatively taut and smooth in most phyllostomids. In contrast, folds of skin are present around the neck in *Centurio* and *Sphaeronycteris*. These skin bands are smaller in females than in males, and they reach their greatest development in male *Centurio*. In males of both *Centurio* and *Sphaeronycteris*, the throat folds apparently operate as a hood, or mask, which drops over the face when the bat is roosting (Hill and Smith, 1984; Paradiso, 1967; Goodwin and Greenhall, 1961; Nowak, 1991: photograph, p. 314). The facial hood is absent in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

Lim (1993: character 3) first used this character in a cladistic analysis. Our character states and scoring are identical to his.

## SKULL AND DENTITION

Characters described in this section are based largely on features originally noted by Straney (1980: character numbers from appendix 1), Owen (1987: character numbers from his appendix 2; 1991: character numbers from the appendix), Lim (1993: character numbers from appendix 2), Marques-Aguiar (1994: character numbers from appendix 4) and Wible and Bhatnagar (1996). Taxa examined in these studies are listed in table 4. We have revised many of the character descriptions given by these authors to

better describe variation within phyllostomids as a whole, and have scored most characters for all of the 63 taxa included in our analysis. In addition, we developed several new characters of potential phylogenetic significance; some of these first appeared in Simmons' (1996) analysis of relationships of *Micronycteris* species.

In the descriptions we present, we refer to paired structures (e.g., premaxillae) as singular (e.g., premaxilla), in effect describing half of the cranium or dentition. We do note cases where the two halves of the skull or dentition differ.

**Character 39:** *Vomeronasal tube well developed with neuroepithelium present (0); or rudimentary, neuroepithelium absent (1); or absent (2).* The vomeronasal epithelial tube (VET) is ''an elongate, cigar-shaped structure lined with epithelium'' that is associated with nerve fibers, vomeronasal glands, blood vessels, and venous sinuses (Wible and Bhatnagar, 1996: 294). In desmodontines, *Macrotus*, glossophagines, *Carollia*, and stenodermatines the VET is well-developed and has a neuroepithelial lining medially (Wible and Bhatnagar, 1996). In contrast, in *Brachyphylla* the VET occurs in a rudimentary form and lacks the neuroepithelium (Wible and Bhatnagar, 1996). In mormoopids, the VET is rudimentary in *Mormoops*, well developed in *Pteronotus parnellii*, and completely absent in *Pteronotus personatus* (Wible and Bhatnagar, 1996). We scored *Pteronotus* with states 0, and 2 in the matrix. The VET is absent in *Noctilio* (Wible and Bhatnagar, 1996). Thus, the primitive state for phyllostomids cannot be assessed a priori.

Based primarily on the work of Bhatnager and his colleagues (e.g., Bhatnager and Kallen, 1974; Cooper and Bhatnager, 1976; Bhatnager 1980, 1985; Frahm and Bhatnager, 1980; Frahm 1981; Bhatnager et al., 1982), Wible and Bhatnagar (1996) defined this character (and characters 40, 41, and 135), mapping it onto preexisting hypotheses of chiropteran relationships. Our character states and scoring are identical to theirs.

**Character 40:** *Vomeronasal cartilage bar-shaped (0); or curved,* J-*,* C-*,* U-*, or* O-*shaped in cross section (1).* The vomeronasal cartilage, which supports the VET, is present and J-, C-, U-, or O-shaped in cross section

in most phyllostomids (Wible and Bhatnagar, 1996). Because the curved vomeronasal cartilage changes shape over its length, more than one of these shapes may occur in a single individual. In contrast, *Brachyphylla* possesses a bar-shaped vomeronasal cartilage (Wible and Bhatnagar, 1996). Among the outgroup taxa, a curved vomeronasal cartilage is present in *Mormoops*, whereas a bar-shaped vomeronasal cartilage is present in *Pteronotus* and *Noctilio* (Wible and Bhatnagar, 1996). Given this distribution of character states, the presence of a bar-shaped vomeronasal cartilage appears to be primitive for phyllostomids.

Wible and Bhatnagar (1996) defined and mapped this character onto preexisting phylogenies of bats. Our scoring is identical to theirs. In the context of the phylogenies Wible and Bhatnager (1996) examined, they described the primitive state as our state 1. Their state 2 (vomeronasal cartilage absent) does not occur in any of our taxa and we therefore excluded it from consideration.

**Character 41:** *Nasopalatine duct present (0); or absent (1).* The nasopalatine duct, which connects the nasal and oral cavities through the incisive foramen in the palate, is present in most phyllostomids (Wible and Bhatnagar, 1996). In contrast, the nasopalatine duct is absent in *Macrotus* (Wible and Bhatnagar, 1996). The nasopalatine duct is present in *Mormoops* and *Pteronotus personatus*, but is absent in *Pteronotus parnellii* and *Noctilio* (Wible and Bhatnagar, 1996). We scored *Pteronotus* with states 0 and 1 in the matrix. Due to this distribution of character states among the outgroup taxa, the primitive state for phyllostomids cannot be reconstructed a priori.

Wible and Bhatnagar (1996) first used this character. Our character states and scoring are identical to theirs.

**Character 42:** *Zygomatic arch always complete (0); or always incomplete (1); or polymorphic within species (2).* Although most phyllostomids have a complete zygomatic arch, this structure is incomplete in *Phyllonycteris*, many glossophagines (e.g., *Choeroniscus*, *Lichonycteris*), lonchophyllines, and carolliines. In all taxa that lack the zygomatic arch, a distinct zygomatic process projects anteriorly from the lateral margin of

the mandibular fossa and posteriorly from dorsal or slightly posterior to the last molar. Both processes taper and have rounded tips. Among brachyphyllines, phyllonycterines, glossophagines, and lonchophyllines, a thin but complete arch is present only in *Brachyphylla*, *Erophylla*, *Glossophaga*, *Leptonycteris*, and *Monophyllus*. *Anoura* is the only phyllostomid that exhibits polymorphism in zygomatic development. Some specimens of *Anoura geoffroyi* have two complete zygomatic arches whereas others lack both, and one specimen (AMNH 78288) has a complete zygomatic arch on the right side and an incomplete arch (that does not appear to have been broken) on the left side. However, in *Anoura caudifera* it appears that both zygomatic arches may be complete in all individuals (Miller, 1907; personal obs.). Those specimens without a complete arch show clear evidence of breakage (e.g., AMNH 176347). Based on the states defined above, we scored *Anoura* with states 0 and 2. Mormoopids and *Noctilio* have a complete zygomatic arch, suggesting that this condition is primitive for phyllostomids.

Lim (1993: character 19) first used this character in a cladistic analysis. We have followed his character state definitions but have added state 2 (polymorphic). Although Koopman (1994: 81, 86) expressed some reservation about the status of the zygomatic arch in *Lichonycteris* (''more or less complete'') and in a subgenus of *Sturnira* (*Corvira*: ''weak or incomplete''), our examinations indicate that the zygomatic arch is never complete in *Lichonycteris*, but is always complete in *Sturnira* (*Corvira*).

**Character 43:** *Mastoid breadth less than zygomatic breadth (0); or greater than zygomatic breadth (1).* In most phyllostomids, breadth of the skull measured across the mastoid region is less than breadth measured across the zygoma. In contrast, mastoid breadth is greater than zygomatic breadth in *Lonchorhina*, *Micronycteris minuta*, and some species of *Tonatia* (e.g., *T. silvicola*, *T. evotis*). We scored *Tonatia* with states 0 and 1 in the matrix. We scored this character in some taxa with an incomplete zygomatic arch (see character 42) when the posterior process of the zygoma clearly extended laterally beyond the level of the mastoids (e.g.,

*Carollia*). However, in species where the posterior process of the zygoma does not extend past the level of the mastoid, we did not attempt to score this character; these taxa are scored ''−'' in the matrix. Mastoid breadth is less than zygomatic breadth in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

Simmons (1996: character 14) first used mastoid versus zygomatic breadth as a character in a phylogenetic analysis of relationships of *Micronycteris* species; our assessments agree with hers.

**Character 44:** *Hard palate long, extends into interpterygoid space (0); or no palatal extension or emargination (1); or palate with shallow posterior emargination that extends maximally to middle of upper second molar (2); or with deep emargination that extends minimally to posterior border of first molar (3).* The posterior part of the hard palate extends into the interpterygoid space in most phyllostomids (fig. 24A). In some taxa (e.g., *Pygoderma*) there is no extension of the hard palate into the interpterygoid space, nor is the palate emarginate (fig., 24B). However, in some stenodermatines the hard palate lacks a posterior extension and is emarginate. In *Centurio* and *Sphaeronycteris*, the palatal emargination is shallow, extending to approximately the middle of M2 measured at the labial margin of the tooth (one specimen [AMNH 175651] of *Centurio* in which the emargination appears deeper has clearly been damaged; fig. 24C). The emargination is deeper in *Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma* ending somewhere along the labial border of M1 (fig. 24D). In *Ametrida*, the pterygoids are very small (compressed in the anterior-posterior dimension) and the internal nasal aperture is reduced by bony laminae extending medially from the pterygoids in both the coronal and transverse planes (fig. 24E). This is a unique condition among phyllostomids (Miller, 1907; personal obs.), and does not appear to be homologous with other conditions described above; we therefore scored *Ametrida* ''−'' for this character. In *Mormoops blanvillii*, *Pteronotus*, and *Noctilio*, the hard palate extends into the interpterygoid space; however, there is no palatal emargination or extension in *Mormoops megalophylla*. This distribution of character
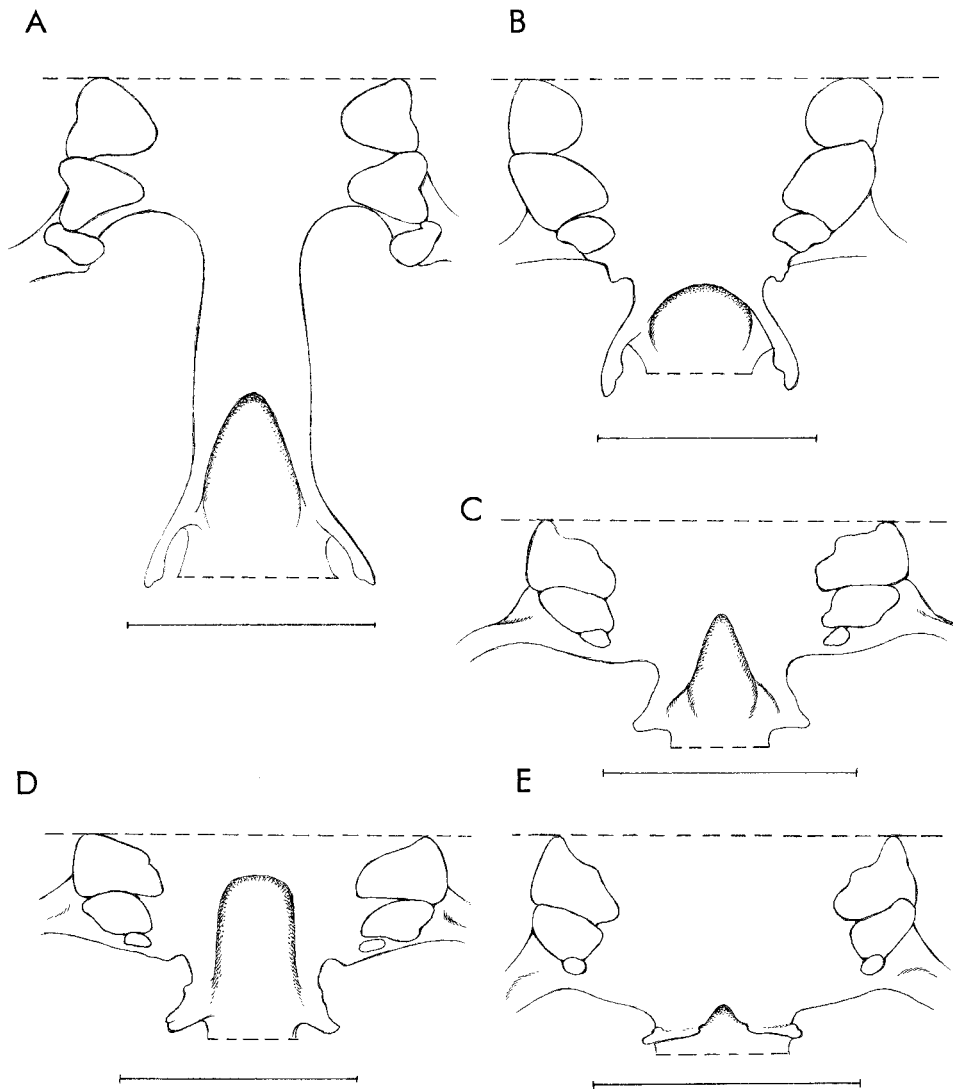
Fig. 24. Ventral view of the palate and mesopterygoid fossa in selected taxa illustrating palate length and shape of the palatal emargination. **A.** *Carollia perspicillata* (AMNH 130722) **B.** *Pygoderma bilobatum* (AMNH 248339) **C.** *Sphaeronycteris toxophyllum* (AMNH 209741) **D.** *Stenoderma rufum* (AMNH 208982) **E.** *Ametrida centurio* (AMNH 187224). Scale bar = 5 mm.

states suggests that possession of a hard palate that extends into the interpterygoid space may be primitive for phyllostomids.

Owen (1987: character 9) measured the length of the posterior margin of the hard palate from the anterior border of the orbit, and defined three states: "Extends farther caudad than least width of palate between orbits" (0), "Extends caudad to anterior border of orbits, but no farther than least width of palate" (1), "Does not extend caudad to anterior border of orbit" (2). This character was ordered (0 ↔ 1 ↔ 2). Subsequently, Owen (1991: characters 21–22) split his (1987) states 1 and 2 into separate characters. Although Owen's (1991) scoring remained unchanged, he transformed the multistate character he had previously described (Owen, 1987: appendix 2) into several characters using additive binary coding. We have de-

scribed this character in different terms than those used by Owen (1987, 1991) to accommodate some of the variation his character did not account for. Thus, our character is not directly comparable to his.

Lim (1993) recognized that Owen's (1987) state 2 encompassed more variation than Owen (1987) had described. Accordingly, Lim (1993) erected several states to account for this variation. However, Lim (1993: character 4) incorporated shape and size in a single ordered $(0 \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5)$ character: "Hard palate extending into interpterygoidal space (0); no palatal extension or emargination (1); palatal emargination shallow and V-shaped (2); palatal emargination moderate and converging anteriorly (3); palatal emargination deep and narrow (4); palatal emargination very deep and wide (5)." We have chosen to score shape separately from length (see character 45). In addition, we do not recognize moderate emargination (Lim's state 3) as a distinct character state. Lim (1993) stated that this condition appears in *Phyllops*, but our observations suggest that the "moderate" condition, which would be an autapomorphy of *Phyllops* and therefore uninformative in a phylogenetic analysis, more closely resembles the conditions seen in *Ardops*, *Ariteus*, and *Stenoderma*. We also do not score the palate of *Ametrida* for this character; Lim (1993) considered the palate in this genus to lack an extension or emargination.

**Character 45:** *Posterior border of hard palate always* U-*shaped (0); or always* V-*shaped (1).* The shape of the caudal border of the palate does not appear to be a useful character among phyllostomids with long palates (state 0 in character 44) because there is a continuous range of variation among the U-, V-, and W-shaped conditions both within genera and individual species. For example, *Lonchophylla thomasi* has a V-shaped emargination, whereas other *Lonchophylla* species, such as *L. robusta*, have a U shape (Koopman, 1994; personal obs.). In *Carollia subrufa*, the posterior palate is V shaped in some specimens (e.g., AMNH 164023), but is U shaped in others (e.g., AMNH 186375). In those taxa that do not have a palatal extension or emargination (state 1 in character 44), the posterior edge of the palate is

straight to barely curved (fig. 24B). The shape of the medial posterior border of the hard palate appears to be potentially informative in stenodermatines with emarginate hard palates (states 2 and 3 in character 44). In *Ardops*, *Ariteus*, and *Stenoderma*, the palatal emargination is U-shaped (fig. 24D). The emargination is V-shaped in *Centurio*, *Phyllops* (we examined both *P. falcatus* and *P. haitiensis*; see below), and *Sphaeronycteris* (fig. 24C). The primitive condition for phyllostomids cannot be assessed a priori because mormoopids and noctilionids do not have emarginate palates. We scored taxa that do not have an emarginate palate (states 0 and 1 of character 44 above) "−" for this character.

Owen (1987: character 10) first described this character using four states, including the "U-" and "V-shaped" conditions we recognize. The other two states, "square" (his state 0) and "median projection" (his state 3) do not apply to taxa with an emarginate palate. Owen (1987) scored his palatal character for all taxa, including those with long palates, and ordered it in a complex fashion. Subsequently, Owen (1991: character 23) again used a similar character but only recognized two states: "square" and "V-shaped." Our observations often do not agree with those of Owen (1987, 1991). Owen (1987) considered *Ametrida* to have a V-shaped posterior border of the hard palate and described this border as U-shaped in *Pygoderma* and *Phyllops falcatus*. Owen (1991) grouped taxa into two categories. "Square" included *Ametrida*, *Centurio*, *Phyllops haitiensis*, and *Sphaeronycteris*. "V-shaped" included the remaining taxa with emarginate palates and *Pygoderma*.

Lim (1993: character 4) considered palatal shape and length as a single ordered character, but scored the shape of the caudal border only in taxa with palatal emargination. Marques-Aguiar (1994: character 21), who also considered whether the "mesopterygoid fossa" had U- or V-shaped borders, scored this character for taxa with long palates. We have followed Lim (1993), because posterior border shape is variable within species with long palates, and because the posterior border of the palate may not be homologous in taxa with emarginate palates and those with
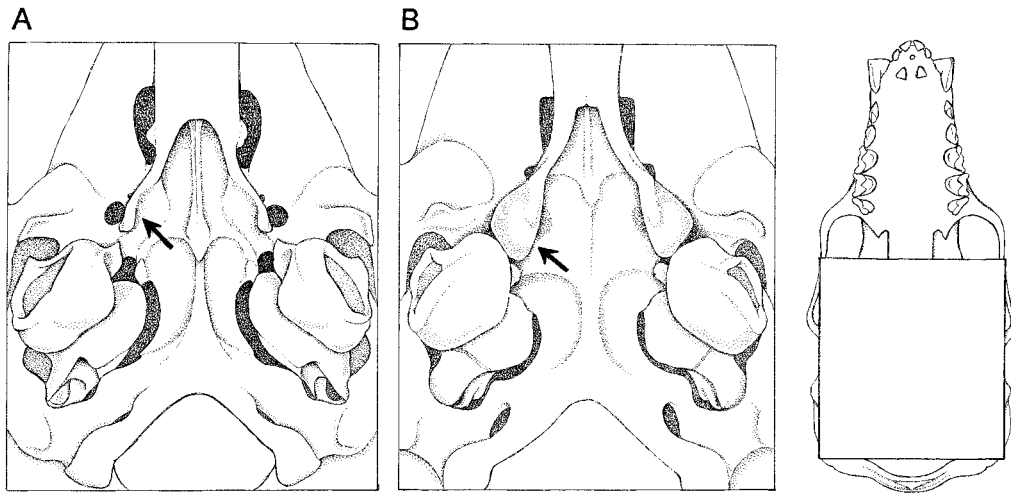
Fig. 25. Ventral view of the basicranium in **A.** *Glossophaga soricina* and **B.** *Choeroniscus intermedius*. The difference in inflation of the pterygoids is indicated by the arrows. Redrawn from Phillips (1971: fig. 45).

longer palates. We have described the states of this character in slightly different terms, recognizing only two general shape categories, "V-" and "U-shaped," rather than the four states Lim (1993) recognized (V-shaped; moderate and converging anteriorly; deep and narrow; very deep and wide). Two of the four conditions Lim (1993) identified are autapomorphies. *Phyllops* was the only genus Lim (1993) scored with the "moderate and converging anteriorly" condition, while only *Ardops* was scored as "palatal emargination very deep and wide." Because these are autapomorphies, they are not informative in a phylogenetic analysis at this level. In addition, we observed that these two taxa share more general conditions (either "V-" or "U-shaped") with other taxa. Consequently, we have recognized only these two conditions. We did not score genera with a palate that has no extension or emargination (state 1 in character 44) because a straight to slightly curved posterior border of the hard palate and state 1 in character 44 have identical distributions.

**Character 46:** *Pterygoid lamina sheetlike (0); or pterygoid lamina greatly inflated posterior to anterior margin of mandibular fossa (1).* The pterygoid lamina is a relatively thin sheet of bone that projects ventrally from the

basicranium. In most phyllostomids, the pterygoid may curve slightly at its posterior and distal end, but over most of its course it diverges from the midline of the basicranium. In most phyllostomids, the pterygoid lamina is not inflated or ballonlike (fig. 25A). In contrast, in *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, the pterygoid lamina is greatly inflated, ballooning laterally posterior to the anterior margin of the mandibular, or glenoid, fossa (fig. 25B). Anterior to this point, the pterygoid diverges from the midline of the basicranium. In mormoopids and *Noctilio* the pterygoid does not balloon laterally, suggesting that this is the primitive condition for phyllostomids.

This character has not been used in previous cladistic analyses, although it has been described by other authors (e.g., Miller, 1907; Phillips, 1971; Koopman, 1993).

**Character 47:** *Rostrum sloping; facial processes of premaxilla and maxilla above teeth lie perpendicular to palatal processes (0); or facial processes of premaxilla and maxilla oriented horizontally above teeth (1).* The rostrum slopes gently from the forehead to the external nares in most phyllostomids. Just above the teeth, the facial processes of the premaxilla and maxilla lie roughly perpendicular to the palatal processes of these
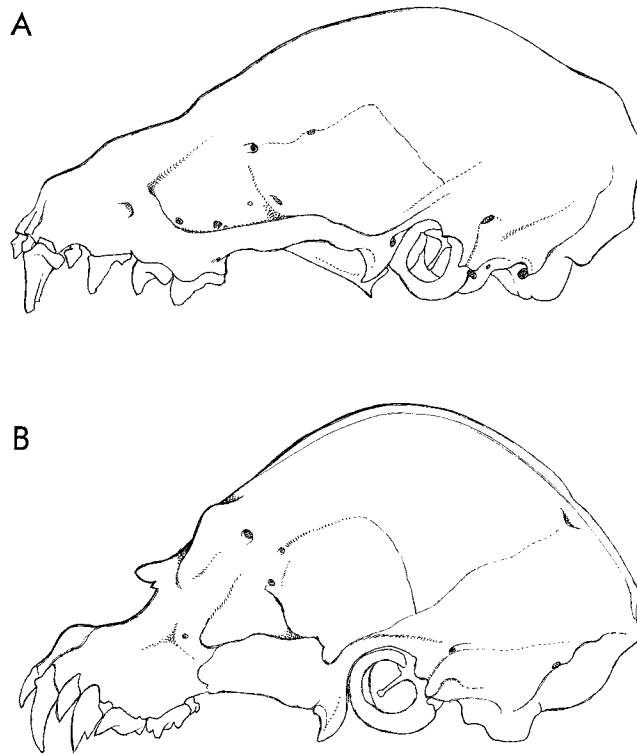
Fig. 26. Lateral view of skull contrasting the gently sloping rostrum of **A.** *Mesophylla macconnelli* (AMNH 268539) to the more foreshortened ''apelike'' rostrum in **B.** *Ametrida centurio* (AMNH 267274).

bones in these taxa (fig. 26A). In contrast, the facial bones that compose the normally sloping rostrum in most phyllostomids (nasal and maxilla) are upturned and largely oriented vertically in *Ametrida* and *Sphaeronycteris*. The nasal aperture in these two taxa is located at the base of the cranium, giving the skull a distinctly ''apelike'' appearance. Just above the teeth, the facial processes of the premaxilla and maxilla lie in roughly the same plane as the palatal processes (rather than being roughly perpendicular to the palatal processes), an arrangement that makes this area appear dorsoventrally compressed (fig. 26B). In mormoopids and *Noctilio*, the rostrum is gently sloping and the facial surfaces of the maxilla and premaxilla just above the teeth are roughly perpendicular to the palatal processes, suggesting that this arrangement represents the primitive condition for phyllostomids.

Lim (1993: character 7) originally scored this character with two states (''gradually sloping rostral profile'' and ''dorso-ventral compression of the rostrum''), which correspond to our character states; our observations agree with his.

**Character 48:** *I2 present (0); or absent (1).* No bat has more than two upper incisors (Slaughter, 1970). Although there has been some debate regarding the homologies of these teeth to those in other mammals, most workers agree that these teeth probably represent I1 and I2 (Thomas, 1908; Anderson, 1912; Slaughter, 1970). Most phyllostomids retain both I1 and I2. In contrast, *Desmodus* and *Diaemus* lack I2. Mormoopids and *Noctilio* retain I2, suggesting that this condition is primitive for phyllostomids.

Owen (1987: character 21) used complete dental formula as a character in his examination of stenodermatine relationships. Under Owen's (1987) coding scheme, different dental formulae were scored as different

character states and the transformation series was ordered in a complex fashion. The result of this coding was that homologies of individual teeth and tooth regions were not always preserved. For example, Owen's (1987) coding precluded the possibility that presence of a single lower incisor might be a shared, derived feature of two taxa with different overall dental formulae. Owen (1991) recoded these data, using characters considering specific tooth regions separately. Lim (1993) did not use dental formula in his analysis of stenodermatine relationships. We consider dental formula to be potentially informative, but prefer to score presence/absence of teeth at individual tooth loci to better preserve initial assessments of putative homologies.

**Character 49:** *I1 distinctly larger than I2 (0); or I1 and I2 approximately equal in size (1).* In most phyllostomids that retain both I1 and I2, the inner tooth (I1) is noticeably larger than the outer tooth (I2; fig. 27B, D–G). In contrast, I1 and I2 are approximately equal in size in glossophagines (fig. 27C). In mormoopids and *Noctilio*, I1 is noticeably larger than I2, suggesting that this is the primitive condition for phyllostomids. We scored taxa that lack I2 (state 1 in character 48) "−" for this character.

Lim (1993: character 10) described a single ordered character for size and shape of I1. The criterion Lim (1993) used to judge the size of I1 appears to have been arbitrary. Many of the taxa that Lim (1993) scored as possessing "reduced" teeth of various morphologies (his states 0, 2, and 3 of character 10) have an I1 roughly two times as large as I2 (e.g., *Ametrida*; fig. 27E). We prefer to define two characters that describe size and shape separately (this character and character 50) because this method allows clear definition of potential homologies. Phillips (1971: 26), who commented at length on the dentition of glossophagine (s.l.) bats, considered the I1 of *Lonchophylla* to be "about as large as" I2. The representatives of *Lonchophylla* we have examined (see appendix 1 for specimens) all possessed an I1 that was noticeably larger (often 2X as large) than I2.

**Character 50:** *I1 occlusal margin generally straight or slightly rounded (0); or occlusal margin concave, C-shaped (1); or oc-*clusal margin evenly bifid (2); or main cusp on occlusal margin pointed (3); or mesially and distally projecting lobes present (4).* I1 in most phyllostomids has a roughly straight or somewhat rounded occlusal margin (fig. 27B–C). In desmodontines, I1 has a strongly concave (C-shaped) occlusal margin (fig. 27A). Yet another pattern appears in some stenodermatines (e.g., *Artibeus*, *Uroderma*), which have an I1 with a well-developed notch in the occlusal margin near the center of the tooth (fig. 27D). Presence of this notch gives the tooth a bifid or bilobed appearance. Although the notch may be slightly offset from the center of the tooth, both lobes are approximately the same size. Finally, other stenodermatines (e.g., *Ametrida*, *Stenoderma*) have a pointed main cusp on I1 (fig. 27E–G). *Rhinophylla pumilio* appears to have a unique I1 morphology. In this species, the occlusal margin of the tooth has two projecting lobes, one which projects mesially and one distally, with a slight depression between them. However, both *R. alethina* and *R. fischerae* have a straight occlusal margin on I1; thus we have scored *Rhinophylla* with states 0 and 4 for this character. I1 is bifid in mormoopids, but has a straight or somewhat rounded occlusal margin in *Noctilio*. The primitive state for phyllostomids thus cannot be reconstructed a priori.

Lim (1993: character 10) described a multistate ordered character based on the size and shape of I1. We do not agree with Lim's (1993) coding of this character. *Mormoops* and *Pteronotus*, which both have a bifid I1, were coded solely on the basis of tooth size by Lim (1993), who apparently ignored the similarity between the condition in these taxa and those seen in other taxa with bifid incisors (e.g., *Artibeus*). Lim (1993) also described two conditions for I1 of the "short-faced" stenodermatines (see discussion in character 51). In this character, we have chosen to emphasize the similarity in the shape of the main cusps of I1 in all "short-faced" stenodermatines, while describing certain differences among them in the characters below (51 and 52). Dividing the characters in this way best reflects our hypotheses of homology.

Marques-Aguiar (1994: character 24), in her analysis of relationships among species
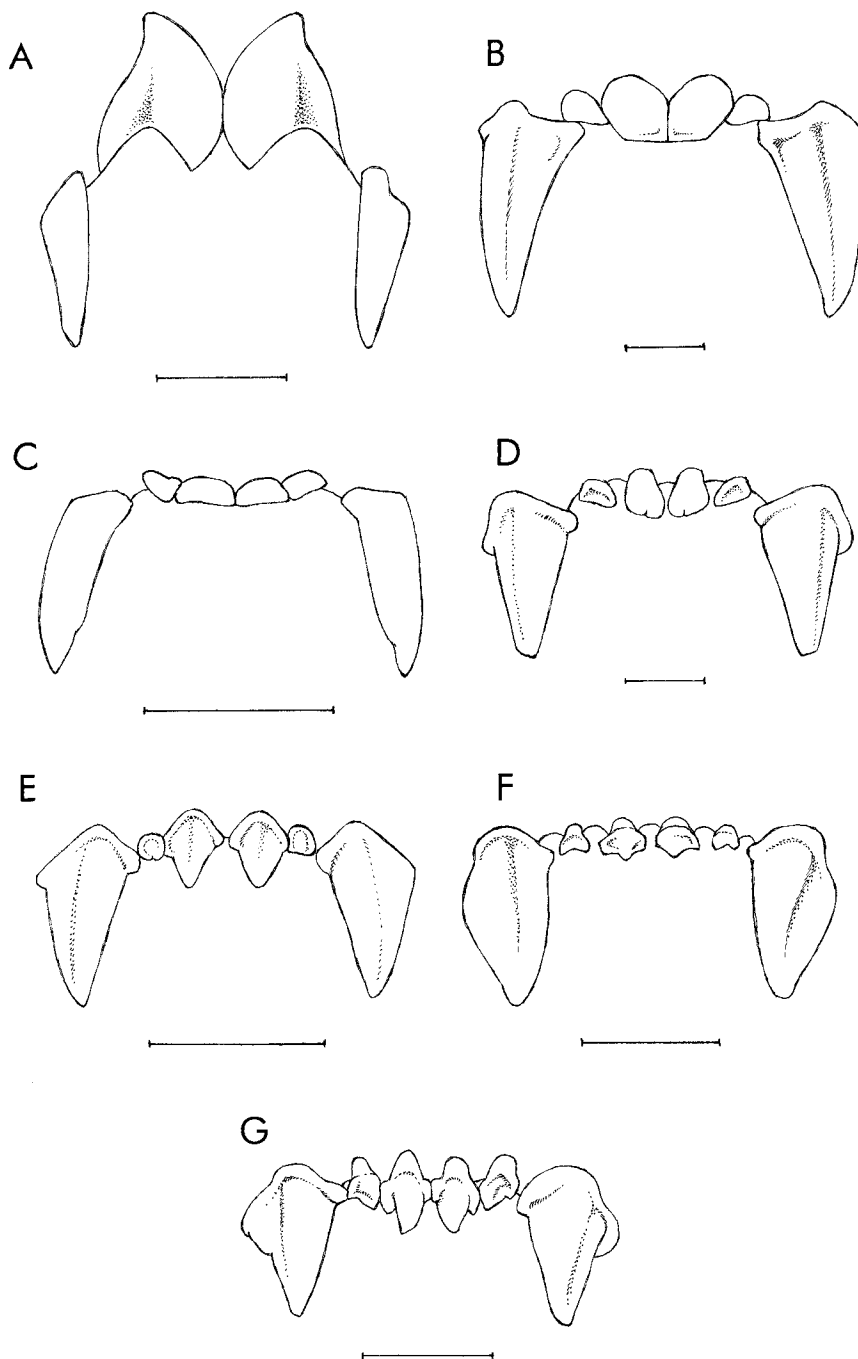
Fig. 27. Anterior view of the upper central and lateral incisors in **A.** *Desmodus rotundus* (AMNH 174303). *Desmodus* has only one pair of incisors. **B.** *Phyllostomus hastatus* (AMNH 267905). **C.** *Glossophaga soricina* (AMNH 209354). **D.** *Artibeus jamaicensis* (AMNH 266337). **E.** *Ametrida centurio* (AMNH 187225). **F.** *Centurio senex* (AMNH 256846) **G.** *Stenoderma rufum* (AMNH 208982). Scale bar = 5 mm.

of the subgenus *Artibeus*, described a character based on morphology of I1. The two character states were "(0) bilobed (bifid) and not pointed," and "(1) simple (not bifid) and pointed." Although we agree with her characterization of all members of the subgenus *Artibeus*, *Dermanura gnoma*, and *Koopmania* as possessing a bilobed I1, we do not agree that I1 in *Enchisthenes* is pointed.

**Character 51:** *I1 with pointed main cusp offset mesially, lateral part of tooth forms poorly to well-developed cusp (0); or, pointed cusp roughly in center of tooth (1).* Among those phyllostomids with a pointed main cusp on I1, there appear to be two distinct morphologies. In *Ardops*, *Ariteus*, *Centurio*, *Pygoderma*, *Phyllops*, and *Stenoderma*, the most well-developed part of I1 is the mesial part of the tooth. This part of the tooth forms a distinct, pointed cusp in all these taxa (figs. 27F–G). Thus, the main cusp appears offset from the center (longitudinal axis) of the tooth. The lateral part of the tooth may form a well-developed (e.g., *Ardops*) or poorly developed (e.g., *Pygoderma*) cusp. In contrast, the main cusp comes to a point in roughly the center of the tooth in *Ametrida* and *Sphaeronycteris* (fig. 27E). In one specimen (AMNH 187225) of *Ametrida* out of 10 we examined for this character, we found an exceptionally well-developed accessory cusp near the tip of the main cusp. We interpret this as an anomaly, and score *Ametrida* with state 1. Mormoopids and *Noctilio* do not have pointed inner upper incisors and are therefore scored "−" for this character, as are all other taxa lacking pointed incisors (states 0, 1, 2, and 4 in character 50). The primitive state for phyllostomids thus cannot be reconstructed a priori.

Lim (1993: character 10) originally scored morphology of the inner upper incisors in his analysis of stenodermatine relationships. He scored *Ametrida*, *Centurio*, *Pygoderma* and *Sphaeronycteris* as having an I1 that is triangular in shape. He described the remaining "short-faced" taxa as having an I1 with a small secondary outer cusp (we call this cusp the "lateral cusp" to avoid confusion with the "accessory cusp"; see below). We observed the lateral cusp in most "short-faced" taxa, including *Pygoderma*. In addition, we found it difficult to characterize the teeth of *Centurio* and *Pygoderma* as similar to those of *Ametrida* and *Sphaeronycteris*, when both *Centurio* and *Pygoderma* clearly had mesially offset main cusps.

Although Miller (1907) reported that the main cusp in *Centurio* is in the center of the tooth, our observations indicate that it is placed towards the mesial edge of the tooth. Finally, Miller (1907) observed, as we did, an often poorly developed accessory cusp toward the tip of the main cusp in *Pygoderma*. This condition appears to be an autapomorphy of this genus. In the other taxa with a lateral cusp, as in *Pygoderma*, the lateral cusp arises from the base of the tooth, it does not arise from the main cusp.

**Character 52:** *I1 with pointed main cusp only slightly longer than lateral cusp (0); or main cusp 2× the length of the lateral cusp (1).* In those stenodermatines with a lateral cusp, there are two patterns of main cusp development. In *Stenoderma* and *Pygoderma*, the main cusp is very long, roughly twice the size of the smaller lateral cusp (fig. 27G). In the remaining taxa with a mesially displaced main cusp, this cusp is only slightly longer than the lateral cusp (fig. 27F). We scored mormoopids and *Noctilio*, which do not have a pointed I1, "−" for this character. The primitive state for phyllostomids thus cannot be reconstructed a priori. We scored all other taxa lacking pointed incisors (states 0, 1, 2, and 4 in character 50) and well-developed mesial cusps (state 1 in character 51) "−" for this character.

Although this character has not appeared in previous cladistic analyses, this feature of the teeth was noted by previous authors (e.g., Miller, 1907).

**Character 53:** *i1 present (0); or absent (1).* Most phyllostomids have two lower incisors, which we identify as i1 and i2 following Slaughter (1970; although see Thomas, 1908 for a different view). However, i1 is absent in many glossophagines (e.g., *Anoura*, *Choeronycteris*, *Hylonycteris*). Mormoopids and *Noctilio* retain i1, suggesting that presence of i1 is the primitive condition for phyllostomids.

This character has not been used in previous phylogenetic analyses, although numerous authors have described dental for-

mulae of glossophagines (e.g., Miller, 1907; Phillips, 1971; Koopman 1994).

**Character 54:** *i2 present (0); or absent (1).* Although most phyllostomids retain i2, this tooth is absent in some phyllostomines (e.g., *Chrotopterus*, *Tonatia*), many glossophagines (e.g., *Anoura*, *Choeronycteris*), and some stenodermatines (*Sturnira bidens*, *S. nana*, and *Vampyressa bidens*). We scored *Sturnira* with states 0 and 1 in the matrix. Mormoopids retain both lower incisors, but i2 is absent in Noctilio. The primitive condition for phyllostomids cannot be assessed a priori.

Straney (1980: character K3) based a binary character on presence or absence of i2. Our character states are equivalent to his, as is our scoring with the exception of our observation that not all stenodermatines have i2. Owen (1991: character 44) defined a character for loss of a lower incisor (from two incisors to one) in some stenodermatines, but our observations are not consistent with his coding of this character. Owen's (1987) character for dental formula correctly scored the two *Sturnira* species and *Vampyressa bidens* as possessing a single lower incisor. However, Owen (1991) scored *Ariteus* and some species of *Dermanura* as having only one lower incisor; all specimens of these taxa that we examined retained both i1 and i2.

**Character 55:** *I1 and i1 in contact or separated by small gap when cheek teeth occlude (0); or I1 and i1 separated by marked gap (1); or I1 occludes with cingular shelf on lower canine well posterior to i1 (2); or I1 occludes posterior to i1 in mandibular fossae (3).* When the jaw is closed and the canines and postcanine teeth are in occlusion, the I1 and i1 contact each other in most phyllostomids, though in some taxa these teeth may be separated by a very small gap. In contrast, I1 and i1 are separated by an extremely large gap when the canines and postcanine teeth are in occlusion in most stenodermatines. The only stenodermatines with a ''normal'' occlusal pattern (state 0) are two of the three species of *Chiroderma* we examined (*C. salvini* and *C. trinitatum*), *Ectophylla*, *Mesophylla*, *Sturnira*, and *Vampyressa* species. We scored *Chiroderma* with states 0 and 3 in the matrix. Another pattern occurs in *Chrotopterus* and *Vampyrum*,

where I1 occludes with a broad cingular shelf that encircles the posterolingual base of the lower canine. Thus, I1 lies well posterior to i1 when the canines and postcanine teeth are in occlusion. Similarly, in desmodontines, the I1 lies posterior to the i1 when the canines and postcanine teeth occlude. However, in these taxa I1 rests in a fossa located in the mandible posterior to i1. In mormoopids and *Noctilio*, the I1 and i1 occlude or are separated by a very small gap when the canines and postcanine teeth occlude, suggesting that this is the primitive condition for phyllostomids. We scored taxa lacking both lower incisors (state 1 of characters 53 and 54) ''−'' for this character.

To our knowledge, patterns of incisor occlusion have not been previously used as characters in phylogenetic analyses of phyllostomid taxa, although the occlusal pattern and fossae of desmodontines have been described before (e.g., Miller, 1907).

**Character 56:** *P3 present (0); or absent (1).* No bat is known to have more than three upper premolars (Slaughter, 1970). Although there has been continuing debate regarding the homologies of these teeth to those in other mammals (e.g., Miller, 1907; Thomas, 1908; see review in Slaughter, 1970), most recent workers have settled on numbering the premolars ''P2-P3-P4'' in bats (e.g., Slaughter, 1970), and we follow this usage mainly for convenience[4]. Of the three upper premolars found primitively in bats, most phyllostomids retain two, which are apparently homologous to P3 and P4 of other bats (Slaughter, 1970). Only one noctilionoid, *Anoura*, has P2 in addition to P3 and P4; this appears to be an autapomorphy. In contrast, desmodontines have only one upper premolar, having lost P3 (Slaughter, 1970). Mormoopids retain both P3 and P4, whereas *Noctilio* has apparently lost P3. The primitive

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[4] Thomas (1908) argued that the missing premolar in both upper and lower jaws is the second. This argument has been accepted by some authors (e.g., Handley, 1959; Simmons and Handley, 1998). However, the identity of the missing tooth has no bearing on phyllostomid relationships. Given the widespread usage of P2-P3-P4, we adopt this system to avoid confusion, but recognize that P2 may be P1.

state for phyllostomids thus cannot be reconstructed a priori.

Straney (1980: character K6) described a binary character based on presence of P3; our character states and scoring are identical to his.

**Character 57:** *Second distal accessory cusp on P4 absent (0); or second distal accessory cusp sometimes present (1); or second distal cusp always present (2).* P4 lacks a second distal accessory cusp in most phyllostomids. In contrast, two distal accessory cusps are often present in the stenodermatines *Ardops*, *Ariteus*, *Artibeus*, *Dermanura*, *Phyllops*, *Platyrrhinus*, and *Pygoderma*. The second distal accessory cusp is always present only in *Uroderma* and *Vampyrodes*. Mormoopids and *Noctilio* do not have a second distal accessory cusp, suggesting that this is the primitive state for phyllostomids.

Lim (1993: character 6) first described this character; however, he scored only *Platyrrhinus* and *Uroderma* as having two distal accessory cusps, and did not note the polymorphism we have discovered in almost every species in which this feature is present. Despite our consideration of the ''sometimes present'' and ''always present'' conditions as separate character states, we suspect that the second distal accessory cusp is not uniformly present in any species (this suspicion is strengthened because Lim [1993] did not report the presence of this cusp in *Vampyrodes*).

**Character 58:** *p3 absent (0); or p3 greatly reduced, tooth peglike, cusps poorly or not developed (1); or moderately reduced compared to p2 and p4, cusps present and well developed (2); or p3 crown height roughly equivalent to p2 and p4 (3).* As with the upper premolar dentition (see above), the three lower premolars of bats are typically numbered ''p2-p3-p4'' (Slaughter, 1970), and we follow this usage. Only two premolars (presumed to be p2 and p4) are present in desmodontines, some phyllostomines (e.g., *Mimon*, *Phyllostomus*), *Brachyphylla*, phyllonycterines, carolliines, and stenodermatines. The hypothesis that p3 is absent in these taxa is supported by the observation that p3 is reduced in size relative to p2 and p4 in many phyllostomids. In these taxa (e.g., *Lonchorhina*, *Macrophyllum*), this tooth is extremely small (less than one quarter the overall size of p2 and p4) and peglike with cusps that are poorly developed or absent. In two specimens of *Lonchorhina* (AMNH 149233 and AMNH 183850) we suspect that p3 may be absent; however, dried tissue is present in this region, making it impossible for us to unambiguously determine whether p3 is present in these two individuals. We therefore score p3 as present in *Lonchorhina*. This tooth is absent from both sides in one specimen of *Macrophyllum* (AMNH 209320), but we consider this an anomaly, and score *Macrophyllum* with state 1. In some phyllostomines (e.g., *Phylloderma*, *Tonatia*), the crown of p3 is reduced in size, but the height of p3 is less than or equal to one third the height of p2 and p4. However, the tooth is still large and has well-developed cusps. In all remaining phyllostomids in which this tooth is present, the lower premolars have crowns that are subequal in height. In mormoopids, p3 is moderately reduced in *Mormoops* and is greatly reduced and peglike in *Pteronotus*. *Noctilio* has only two premolars. Although it is not clear which tooth has been lost, we score *Noctilio* as having state 0 to leave open the possibility that this is a derived trait shared with some phyllostomids. The primitive condition for phyllostomids thus cannot be reconstructed a priori.

Straney (1980: characters K8, 10–12) first used premolar loss and reduction in a phylogenetic analysis. His character K8 dealt with the presence or absence of this tooth. Our observations for this character are identical with his, although Straney (1980: 68) scored *Noctilio* as possessing p3. However, he noted that this tooth was absent in this taxon in his text. To evaluate degree of reduction of p3, Straney (1980) used the height of the cingula on p2 and p4; thus, our results are somewhat different from his. If we consider our character states 3, 2, and 1, equivalent to Straney's (1980) K10 (subequal), K11 (p3 lower than p2, 4 but above cingulum), and K12 (p3 lower than cingulum on p2,4), respectively, the only taxa that we disagree on are *Phylloderma*, *Tonatia*, and *Trachops*. Straney (1980) considered both *Phylloderma* and *Trachops* to have the derived state of K12 (p3 lower than cingula on p2, 4), and found that different species of

*Tonatia* had different states for this character (derived for K10, K11, and K12). Our disagreement with Straney (1980) may be due to the presence of a better developed lingual cingulum in these three genera. As noted above, we consider p3 to be moderately reduced in these three taxa.

Owen (1991: character 43) used a character whose derived state was defined as the loss of a lower premolar (reduction in number from three to two premolars). Among his outgroups, Owen (1987) correctly scored only *Macrotus* as possessing three lower premolars. However, in his 1991 paper, Owen incorrectly scored the following taxa as having three lower premolars (state 0 for character 43): *Carollia perspicillata*, *Ametrida*, *Ardops*, *Enchisthenes*, *Koopmania*, *Phyllops*, *Sphaeronycteris*, *Stenoderma*, and *Sturnira ludovici*.

Simmons (1996: character 18) described an ordered character similar to this in her analysis of relationships among *Micronycteris* species. Our character state 0, p3 absent, was not used by Simmons (1996) because all *Micronycteris* retain p3. We have further modified this character by comparing the crown heights of the premolar teeth, rather than the overall size of tooth. Consequently, our character is not directly comparable to hers.

**Character 59:** *Postcanine teeth including p3 aligned in row roughly parallel to long axis of mandible (0); or p3 sometimes lingually displaced from toothrow (1); or p3 always lingually displaced from toothrow (2).* In most phyllostomids, all of the postcanine teeth, including p3, are aligned in a row that runs roughly parallel to the long axis of the jaw. However, p3 is always lingually displaced from the toothrow in *Chrotopterus*. In *Lonchorhina*, *Macrophyllum*, and *Trachops*, some specimens retain p3 in the toothrow (e.g., *Lonchorhina*: AMNH 184701; *Macrophyllum*: AMNH 94551; *Trachops*: AMNH 266081), whereas in others p3 is lingually displaced (e.g., *Lonchorhina*: AMNH 230122; *Macrophyllum*: AMNH 262424; *Trachops*: AMNH 267442). In those specimens with lingually displaced p3s, p2 and p4 are in contact to the labial side of this tooth. This tooth is not reduced in *Mormoops*. *Pteronotus* retains p3 in the toothrow, conse-

quently p2 and p4 are not in contact in this genus. This tooth is absent in *Noctilio*. Thus the primitive state for phyllostomids cannot be reconstructed a priori. It seems likely that lingual displacement can only occur in taxa in which p3 is greatly reduced in size (e.g., taxa scored 1 for character 58). We are unaware of any examples from other microchiropteran families where a tooth of normal size is displaced, but there are examples of lingual displacement of greatly reduced teeth (e.g., *Myotis seabrai* and *M. lesueuri*; Koopman, 1994). Therefore, we score this character only in those taxa that have a greatly reduced p3; we scored genera in which p3 is either absent, slightly reduced, not reduced, or (states 0, 2, and 3 of character 58) "−" for this character.

Straney (1980: character K13) previously used this feature as a binary character and scored it in all phyllostomines in his analysis. Although we have found that this tooth is sometimes lingually displaced in *Lonchorhina*, our other observations agree with Straney's (1980) scoring of this character. However, we found that this feature is often variable, and have taken this into account in constructing our character states. We disagree with Smith (1972: 56) who stated that p3 is "markedly reduced to a small peg-like unicuspid tooth and is almost always excluded (lingually), or nearly so, from the toothrow" in the genus *Pteronotus*.

**Character 60:** W-*shaped ectoloph present on M1–M2 (0); or absent (1).* A W-shaped ectoloph is prominent on the upper molar teeth of most microchiropterans (Slaughter, 1970; Koopman and MacIntyre, 1980; Koopman, 1994), and many phyllostomids retain this characteristic (e.g., fig 28B, E). The W-shaped ectoloph is best developed on M1 and M2, but is generally present, although often altered, on M3 when this tooth is present (see character 64). However, desmodontines, brachyphyllines, phyllonycterines, several glossophagines (e.g., *Lichonycteris*, *Musonycteris*), *Platalina*, carollines, and stenodermatines do not have a W-shaped ectoloph on M1–M2 (fig. 28A, C–D, F). A W-shaped ectoloph is present on M1–M2 of mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

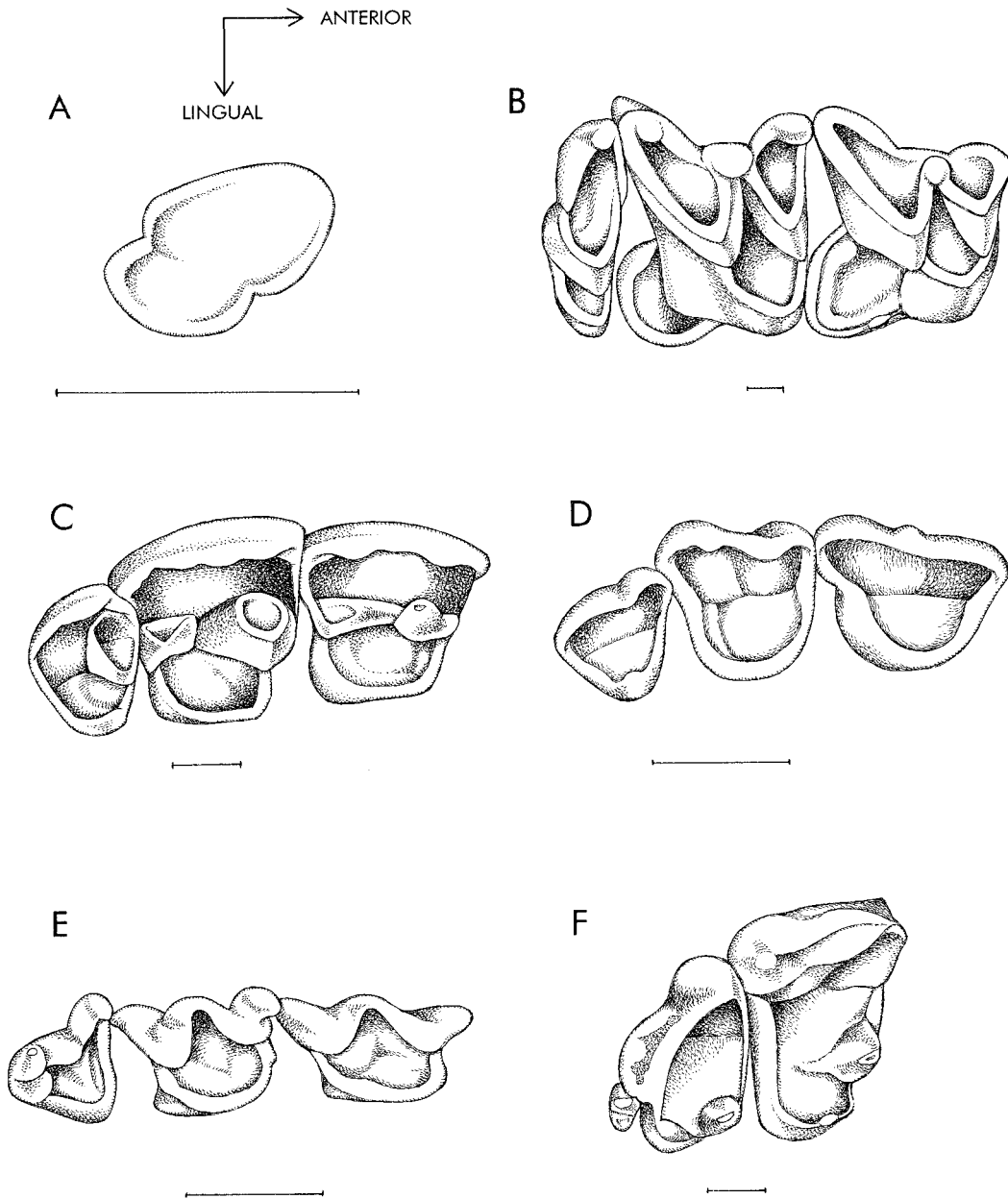Although the presence of a W-shaped ec-

Fig. 28. Occlusal view of M1-M3 in selected phyllostomids. **A.** *Desmodus rotundus* (AMNH 174303). Only M1 is present. **B.** *Chrotopterus auritus* (AMNH 267852). **C.** *Brachyphylla cavernarum* (AMNH 208181). **D.** *Phyllonycteris poeyi* (USNM 103542). **E.** *Monophyllus redmani* (AMNH 236662). **F.** *Artibeus jamaicensis* (AMNH 266331). Scale bar = 1 mm.

toloph has not been formally defined as a character in a cladistic analysis, the phylogenetic implications of the presence/absence of the W-shaped ectoloph in phyllostomids have been discussed by Slaughter (1970) and Phillips (1971). Slaughter (1970) viewed the primitive condition as retention of the W-shaped ectoloph and noted various conditions which evolved from a dilambdodont condition. Phillips (1971) divided glosso-

phagine (s.l.) bats into three groups based on molar morphology, primarily on the presence or absence of the W-shaped ectoloph, and noted that presence of a W-shaped ectoloph was more primitive. We agree with most of Phillips' (1971) observations, but have found that *Hylonycteris* has an ectoloph, whereas *Lichonycteris* does not, contra Phillips (1971). Finally, in considering the homologies of the cusps of the molar teeth of *Brachyphylla*, Griffiths (1985: 546) commented that "In every stenodermatine genus but two, the W-shaped ectoloph pattern was clearly evident . . . displaced laterally up against the stylar cusps of the tooth . . . ." We consider a strongly W-shaped ectoloph pattern to be absent in all stenodermatine genera. Although there are crests that are displaced laterally against the stylar cusps, these do not form a W shape (compare fig. 28B and F).

Although we are aware that we may be lumping several conditions together under our state 1 (i.e., the W-shaped ectoloph may have been lost in different taxa due to the loss or movement of different crests or cusps), we defined the character in this manner due to the problems associated with drawing homologies among the cusps of the upper molar teeth in taxa with unique molar morphologies. Often, homologies among cusps on the upper molars are drawn in consideration of the taxonomic affinities of the genus in question (e.g., Griffiths' [1985] interpretation of molar morphology in *Brachyphylla*), an approach that is not suited for cladistic analysis.

**Character 61:** *Hypocone basin distinct on M1, hypocone indistinct to well developed (0); or basin and cusp both indistinct or absent (1); or hypocone wing present (2).* The hypocone is conspicuously absent on the upper first molar of many phyllostomids, including desmodontines, brachyphyllines, phyllonycterines, glossophagines, lonchophyllines, carollines, and some stenodermatines (e.g., *Mesophylla*, *Platyrrhinus*; fig 28A, C–D). In most of these taxa, the hypocone basin is poorly developed and the tooth triangular, rather than square, in occlusal outline (some stenodermatines like *Platyrrhinus* and *Sturnira* are exceptions, but in these genera there is no cusp in the hypocone region). In all other genera, a variably de-

veloped hypocone is present in the well-developed hypocone basin. In many phyllostomines this cusp is incorporated into a crest that runs into the hypocone region and may encircle it; thus the cusp itself is often indistinct (fig. 28B). In stenodermatines, the cusp is usually not incorporated into a crest and is more distinctly conical than in the phyllostomines (fig. 28F). *Monophyllus* appears to be unique among phyllostomids in having what Phillips (1971) termed a hypoconal wing, a buttresslike structure that slopes towards the palate rather than connecting with the metacone (fig. 28E). In mormoopids and *Noctilio*, a distinct hypocone is present, suggesting that this is the primitive condition for phyllostomids.

Straney (1980: characters K19–23) scored hypocone development in what we interpret as two series of characters. The first series (character K19 and K20) dealt with whether this cusp was indistinct (the derived condition of character K19) or distinct (the derived condition of character K20). Straney (1980) scored most taxa, but not all, for these two characters. The second series (characters K21 to K23) dealt with the height of the hypocone: very low (derived condition of character K21), low (derived condition of character K22), or relatively high (derived condition of character K23). Straney scored all taxa for this second series of characters.

Owen (1987: character 14) described hypocone development on the first upper molar in a five-state ordered character. Marques-Aguiar (1994: character 26) also described the development of the hypocone on M1, defining three states. Although the fine grade distinction between a moderately developed hypocone and a well-developed hypocone might be appropriate for a species level analysis in some taxa (e.g., Marques-Aguiar, 1994), the character states defined by Owen (1987) appear to subdivide a continuous series of hypocone development. Our observations of the presence or absence of this cusp conflict with several of Owen's (1987) observations. Owen (1987) found that some species of *Chiroderma*, *Platyrrhinus*, *Sturnira*, and *Vampyrodes* have at least a moderately developed hypocone; our observations suggest that this cusp is absent in these taxa. Owen (1991: character 30, 31, 32)

transformed his original multistate character into three separate binary characters. One of Owen's (1991) characters (30) is equivalent to ours. Our observations of the presence/absence of this cusp agree with those of Owen (1991).

Lim (1993: character 5) redefined this character as a discrete state ordered (0 ← 1 → 2) character by scoring the presence of either three or four cusps on the first upper molar (the fourth cusp being the hypocone). Our states and scoring are identical to his with one exception. Lim (1993) described *Sturnira* as having an autapomorphic state in which the protocone and hypocone are obscured by a longitudinal groove. Although we observed a longitudinal trough in *Sturnira* between the buccal and lingual cusps, this trough does not obscure the protocone and hypocone regions. *Sturnira* appears to lack a hypocone; accordingly, we score this taxon 1.

Phillips (1971) considered a hypocone basin to be present on the upper molars of *Anoura*, *Glossophaga*, *Leptonycteris*, and *Lonchophylla*. Although this region of the tooth may be present in these taxa, it is more poorly developed in these genera than this region is in phyllostomines and stenodermatines. The outline of the first upper molar in these genera remains much more triangular in outline than those of the stenodermatines and phyllostomines we examined. We also disagree with Slaughter (1970), who observed that all stenodermatines have a hypocone.

Considerable disagreement exists concerning the presence and location of many cusps (especially the paracone and metacone) on the upper first molars of some taxa (e.g., *Brachyphylla*, *Erophylla*, and *Phyllonycteris*). However most authors (e.g., Miller, 1907; Slaughter, 1970; Koopman and MacIntyre, 1980; Griffiths, 1985) have considered the hypocone to be lacking in these genera. Our observations support this interpretation, consequently we have scored these taxa 1 for this character.

**Character 62:** *M1–M2 lacking extensive elongation in metastylar region (0); or with exceptionally long metastyle present (1).* In most phyllostomids, the metastylar region of the upper first two molars is poorly to moderately developed and is not exceptionally

elongate (fig 28A, C–F). In contrast, in *Chrotopterus*, *Trachops*, and *Vampyrum*, an exceptionally long metastyle is present at the distolabial border of these teeth (fig. 28B). Although the metastylar region of M1–M2 is elongate in some glossophagines (e.g., *Glossophaga*), the loph present on this region of the tooth (the postmetacrista) is approximately equal in length to the other lophs present on the tooth. This situation is unlike the condition seen in *Chrotopterus*, *Trachops*, and *Vampyrum*, where the postmetacrista is much longer than any other loph on the tooth. Thus we do not consider these two conditions homologous and score taxa like *Glossophaga* with state 0. The labial margin of M1–M2 in mormoopids and *Noctilio* does not have an exceptionally elongate metastylar region, suggesting that this is the primitive state for phyllostomids. We scored this character on the morphology of M1 alone in taxa lacking an M2 (e.g., *Desmodus*).

Straney (1980: character K26) used this character previously in a component analysis, and our scoring is identical to his. Slaughter (1970) also described this feature of the teeth in phyllostomids.

**Character 63:** *M3 present (0); or sometimes or always absent (1).* Most bats have three upper molars (''M1-M2-M3'') as do most other mammals. The third upper molar (M3) is present in most phyllostomids (fig. 28B–E). In contrast, M3 is absent in desmodontines, *Leptonycteris*, *Lichonycteris*, and many stenodermatines (e.g., *Centurio*, *Ectophylla*; fig 28A, F). In both *Artibeus* and *Chiroderma*, M3 is almost always absent in some species (e.g., *A. lituratus*, *C. villosum*), whereas it is consistently present in others (e.g., *A. obscurus*, *C. trinitatum*). Consequently, we scored these two taxa with both 0 and 1 in the matrix. In addition, we found that M3 was present on both sides in one specimen each of *Enchisthenes* (AMNH 233791; we examined 6 for this character), and *Mesophylla* (AMNH 262540; we examined 10). We scored these taxa with state 1. In *Sphaeronycteris*, we found that M3 was frequently absent from one side of the dentition (e.g., AMNH 24379), although all specimens we examined had M3 present on at least one side. Consequently, we scored *Sphaeronycteris* with state 0 for this char-

acter. Mormoopids and *Noctilio* have three upper molars, suggesting that presence of M3 is the primitive condition for phyllostomids.

Owen (1987: character 15) first used a character to describe the development of M3. In this character, Owen (1987) considered not only the presence or absence of this tooth but its size (well developed with cusps present 0; or poorly developed, small, and peg-like 1). Our observations of the size and cusp development of M3 suggest that there is no simple way to characterize tooth size and development in phyllostomids; these features appear to vary continuously. Subsequently Owen (1991: character 34) used a character identical to ours. Our observations of the presence/absence of this tooth agree with those of Owen (1987, 1991), with the exception of our observation that this tooth is sometimes present in *Artibeus jamaicensis*, *Enchisthenes*, and *Mesophylla*, and may be absent in *Sphaeronycteris*. Although Owen (1991: 19) noted that "the condition of both M3 and m3 was miscoded in the table [1987: table 1], even though properly coded in the analyses," our observations do not differ greatly from Owen's (1987) table 1.

Although we have usually erected a unique character state for polymorphic taxa, we have not done so here because we suspect that polymorphism is more widespread than we have reported, particularly with the very reduced teeth present in some stenodermatines. Thus, we have been conservative, pending further evaluation of polymorphism in these taxa.

**Character 64:** *Ectoloph on M3 W-shaped (0); or V-shaped (1).* Among phyllostomids that have a W-shaped ectoloph on M1 and M2 and a third upper molar (see characters 60 and 63), there are two distinct morphologies of the M3 ectoloph. In glossophagines and lonchophyllines with a W-shaped ectoloph on M3, a virtually complete W-shape is present (fig. 28E). In contrast, in phyllostomines the ectoloph appears V-shaped on M3 (fig. 28B). In mormoopids and *Noctilio*, a complete W-shaped ectoloph is present on M3, suggesting that this is the primitive condition for phyllostomids. We scored taxa lacking both a W-shaped ectoloph and an M3 (state 1 of character 60 and state 1 of character 63) "−" for this character.

Straney (1980: character K24) first used this character in a component analysis. Although our scoring and Straney's are identical, we have described this character differently. Straney (1980) described his character as the presence or absence of only the postmetacrista on M3. Although we suspect that the premetacrista, metacone, and postmetacrista have been lost, a view proposed by Slaughter (1970), we have avoided erecting any character (except see character 61) that would force us to draw homologies among the cusps on the upper molars. There is too much ongoing debate concerning the homology of the cusps on the upper molars in many genera (e.g., *Brachyphylla*, *Phyllonycteris*, and *Erophylla*).

Phillips (1971) indicated that the W-shaped ectoloph is absent from M3 in *Anoura*, *Glossophaga*, *Lonchophylla*, and *Monophyllus*, usually because one of the styles (e.g., mesostyle, metastyle) or cristae (e.g., metacrista = postmetacrista) are lacking. However, our observations of M3 in these taxa indicate that the W-shaped lophs are still distinctly visible on M3 in these taxa. Thus, our observations agree with Slaughter (1970: 68), who noted that "glossophagines have a well developed premetacrista and a short metacrista."

**Character 65:** *m2 present (0); or absent (1).* As in the upper dentition, most phyllostomids have three lower molars (designated "m1-m2-m3"). Most phyllostomids retain m2; however, this tooth is absent in *Desmodus* and *Diaemus*. Mormoopids and *Noctilio* have three lower molars, suggesting that presence of m2 is the primitive condition for phyllostomids.

This character has not been used in previous phylogenetic analyses, although numerous authors have described dental formulae in phyllostomids (e.g., Miller, 1907; Phillips, 1971; Owen, 1987; Koopman, 1994).

**Character 66:** *m3 present (0); or sometimes or always absent (1).* Most phyllostomids retain m3. In contrast, m3 is absent in desmodontines, *Leptonycteris*, *Lichonycteris*, and many stenodermatines (e.g., *Centurio*, *Ectophylla*). In *Chiroderma*, *Dermanura*, and *Sturnira*, m3 is present in some species (e.g., *C. doriae*, *D. glauca*, *S. lilium*) and is

absent in others (e.g., *C. villosum*, *D. cinerea*, *S. thomasi*). Consequently, we score these taxa with both 0 and 1 for this character. In *Pygoderma*, a single m3 is present on the left side in two individuals (AMNH 261761, AMNH 246408), one specimen has both the left and right m3 present (AMNH 234295), and the remaining individuals lack m3 entirely (a total of seven). We score *Pygoderma* with state 1. In *Sphaeronycteris*, we found that one m3 was frequently absent (e.g., AMNH 76251), although all specimens we examined had an m3 on at least one side. Consequently we score *Sphaeronycteris* with state 0 for this character. Mormoopids and *Noctilio* have three lower molars, suggesting that presence of m3 is the primitive condition for phyllostomids.

Owen (1987: character 22) first used a character to describe the development of m3. In this character Owen (1987) considered not only the presence or absence of this tooth but its size (well developed with cusps present 0; or poorly developed, small, and peglike 1). Our observations of the size and cusp development of m3 suggest that there is no simple way to characterize tooth size and development in phyllostomids; these features appear vary in a continuous fashion. Owen (1991: character 46) and Marques-Aguiar (1994: character 29) both used the presence of the third lower molar as a character. With the exception of our observations of the variability of this feature in *Pygoderma* and *Sphaeronycteris*, we agree with Owen (1987, 1991) and Marques-Aguiar (1994).

Although absence of M3 (see character 63 above) and absence of m3 are clearly correlated in some taxa, this is not true of all taxa. For example, some species of *Artibeus*, *Ariteus*, some species of *Dermanura*, *Mesophylla*, *Vampyressa bidens*, and *Vampyrodes* lack M3 but retain m3. Accordingly, we score presence/absence of upper and lower third molars as separate characters. We also score polymorphism in this character conservatively (see discussion in character 61).

**Character 67:** *m1 does not form high shearing ridge, lingual aspect of tooth well developed (0); or m1 laterally compressed, lingual aspect of tooth poorly developed, tooth incorporated into continuous shearing ridge with anterior cheek teeth (1).* Like most bats, most phyllostomids have lower molars that do not form a straight, continuous, shearing ridge with the anterior cheek teeth. In contrast, desmodontines have laterally compressed mandibular cheek teeth that are incorporated into a continuous, straight (i.e., parallelling the long axis of the jaw) shearing ridge that includes the canines, premolars, and any additional molar teeth (present in *Diphylla*). Mormoopids and *Noctilio* have molars that do not form a straight, continuous, shearing ridge, suggesting that this is the primitive condition for phyllostomids.

This character has not been used in previous cladistic analyses, although many authors have described the morphology of the teeth in desmodontines (e.g., Miller, 1907; Slaughter 1970).

**Character 68:** *Paraconid always present on m1 (0); or sometimes absent (1); or always absent (2).* A paraconid is present on m1 in most phyllostomids (fig. 29B, E). In contrast, the paraconid is always absent from m1 in *Brachyphylla*, phyllonycterines, and most stenodermatines, including some species of *Sturnira* (e.g., *S. erythromos*; other *Sturnira* species, like *S. oporophilum*, have a distinct paraconid; fig. 29C–D, G–I). In some individuals of *Platyrrhinus helleri* (e.g., AMNH 263616; appears in six of 10 individuals examined for this character) a small paraconid is occasionally present but is absent, or appears less frequently, in other species (e.g., *P. dorsalis*, where it was absent in four of four specimens). This situation also occurs in *Vampyrodes* (e.g., AMNH 186381; appears in one of 10 individuals examined), and some species of *Dermanura* (e.g., *D. cinerea* AMNH 97075; appears in one of 10 individuals examined for this character). We scored *Dermanura* and *Platyrrhinus* with states 1 and 2 in the matrix. Due to difficulties in drawing homologies among the cusps of the lower molars in *Rhinophylla* and the desmodontines, we scored these taxa "?" in the matrix for this character and characters 69–70 (fig. 29A, F). The paraconid is present on m1 in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

Lim (1993; character 9) first introduced this character. However, Lim's (1993) original description did not draw any homologies
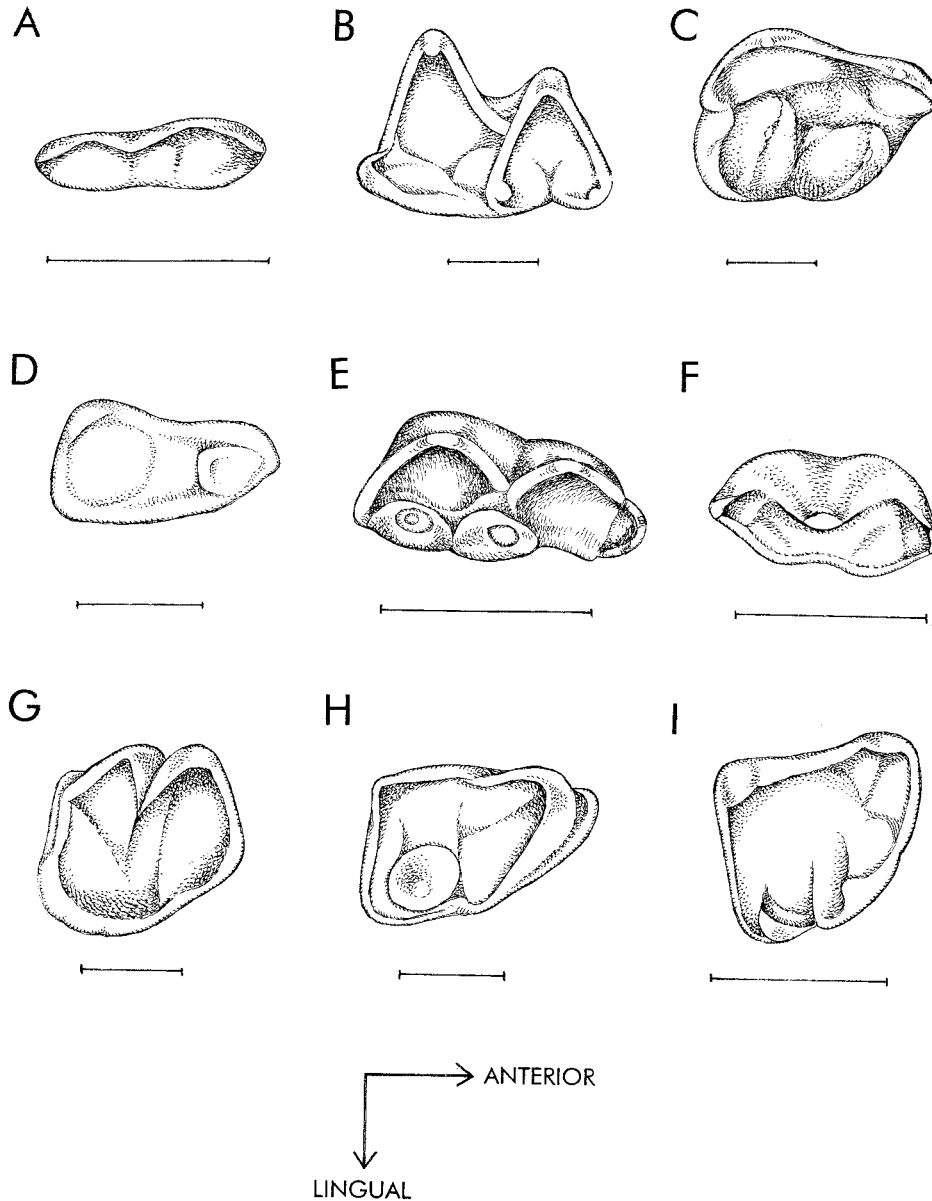
Fig. 29. Occlusal view of m1 in selected phyllostomids. **A.** *Desmodus rotundus* (AMNH 174303). **B.** *Phyllostomus hastatus* (AMNH 267905). **C.** *Brachyphylla cavernarum* (AMNH 208181). **D.** *Phyllonycteris poeyi* (AMNH 103542). **E.** *Glossophaga soricina* (AMNH 209354). **F.** *Rhinophylla pumilio* (AMNH 266192). **G.** *Chiroderma villosum* (AMNH 267191). **H.** *Ardops nicholsi* (AMNH 213954). **I.** *Sphaeronycteris toxophyllum* (AMNH 262637). Scale bar = 1 mm.

between cusps, describing the character states as four prominent cusps (0), or three prominent cusps (1). We find substantial disagreement between our observations and those reported by Lim (1993), who found the derived condition of this character (three prominent cusps) in only four taxa: *Chiroderma*, *Ectophylla*, *Mesophylla*, and *Vampyressa*. Our observations indicate that there are two prominent cusps in these taxa, an

enormous protoconid and a smaller hypoconid. In the remaining taxa Lim (1993) scored with the primitive condition (four prominent cusps), we observed from three to five distinct cusps. We prefer to divide observed variation in m1 cusp patterns into three separate characters (68–70), in order to account for this variation and putative cusp homologies.

Although Slaughter (1970) hypothesized that it is the lingual cusps that are lost in *Rhinophylla* and desmodontines, much of this argument rests on the relationships of these taxa to other phyllostomids. Therefore, we have chosen to score these taxa ''−'' until more detailed information is available concerning the homologies of the cusps in these taxa.

**Character 69:** *Metaconid present on m1 (0); or absent (1).* A metaconid is present on the lower m1 of most phyllostomids (fig. 29B–C, E, I). In contrast, the metaconid is absent from m1 in phyllonycterines and many stenodermatines (e.g., *Ardops*, *Uroderma*; fig. 29D, G–H). In some species of *Sturnira* (e.g., *S. lilium*) a metaconid is present, whereas in others this cusp is absent (e.g., *S. bidens*). A metaconid is present on m1 in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids. We scored desmodontines and *Rhinophylla* ''?'' for this character.

**Character 70:** *Entoconid present on m1 (0); or absent (1).* An entoconid is present on the lower m1 of most phyllostomids (fig. 29B–C, H–I). In contrast, the entoconid is absent from m1 in phyllonycterines and many stenodermatines (e.g., *Chiroderma*, *Mesophylla*; fig. 29D, G). In *Sturnira*, an entoconid is present in some species (e.g., *S. tildae*) and absent in others (e.g., *S. erythryomos*). An entoconid is present on m1 in mormoopids and *Noctilio*, suggesting that this is the primitive condition for phyllostomids. We scored desmodontines and *Rhinophylla* ''?'' for this character.

**Character 71:** *P3 and P4 in contact, no diastema present (0); or diastema sometimes or always present between P3 and P4 (1).* In most phyllostomids, the upper third and fourth premolars are in contact and there is no gap (diastema) present between these teeth. In contrast, in some phyllostomines (e.g., *Micronycteris hirsuta*, *Vampyrum*),

phyllonycterines, glossophagines, lonchophyllines, *Rhinophylla*, and many stenodermatines (e.g., *Chiroderma*, *Mesophylla*), a diastema is sometimes or always present between P3 and P4. In *Mormoops* a diastema separates these teeth, but in *Pteronotus* and *Noctilio* the upper third and fourth premolars are in contact, suggesting that this is the primitive condition for phyllostomids. We scored taxa in which P3 is absent (state 1 in character 56) ''−'' in the matrix.

Lim (1993: character 11) defined a single ordered ($0 \rightarrow 1 \rightarrow 2$) character based on diastemata in the lower jaw: ''No gaps between mandibular cheek teeth (0); space between mandibular premolars (1); additional space between mandibular premolar and molar (2).'' We apply this character to the maxillary, rather than mandibular, tooth row to avoid problems stemming from the loss of p3 in some phyllostomids (see character 58). We have chosen to split Lim's (1993) original character into two separate characters (and one new character we developed after including glossophagines in our analysis) to preserve our ideas about the homology of the various gaps. With few exceptions, our scoring of this character is identical to Lim's (1993). The only difference is the appearance of a diastema between the third and fourth upper premolars in *Platyrrhinus* and *Uroderma*, which does not occur in the lower tooth row.

**Character 72:** *P4 and M1 in contact, no diastema present (0); or diastema sometimes or always present between P4 and M1 (1).* In most phyllostomids, the upper fourth premolar and first molar are not separated by a diastema. In contrast, in phyllonycterines, lonchophyllines, most glossophagines (e.g., *Choeronycteris*, *Hylonycteris*), *Rhinophylla*, and some stenodermatines (e.g., *Chiroderma* and *Mesophylla*), a diastema is sometimes or always present between P4 and M1. In mormoopids and *Noctilio*, the upper fourth premolar and first molar are in contact, suggesting that this is the primitive condition for phyllostomids.

As noted above, we broke Lim's (1993: character 11) original character, which had been based on diastemata in the lower jaw, into two separate characters. Our observations differ little from Lim's (1993). The only

difference is the appearance of a P4–M1 diastema in all *Vampyressa* species included in our analysis. These gaps do not occur consistently in the lower tooth row. We also disagree with Phillips (1971) concerning this character in *Lonchophylla*. Phillips (1971) noted that a cingular style of P4 contacts the parastyle of M1 in *Lonchophylla*. However, we have found that there is no contact between these two teeth in at least some individuals of *Lonchophylla*.

**Character 73:** *M1 and M2 in contact, no diastema present (0); or diastema sometimes or always present between M1 and M2 (1).* In most phyllostomids, the upper first and second molars are in contact and there is no gap (diastema) present between these two teeth. However, many glossophagines (e.g., *Choeronycteris*, *Hylonycteris*), *Platalina*, *Rhinophylla*, *Ectophylla*, *Mesophylla*, and all *Vampyressa* species, a diastema is sometimes or always present between M1 and M2. In mormoopids and *Noctilio*, the upper first and second molars are in contact, suggesting that this is the primitive condition for phyllostomids. *Desmodus* lacks an M2 , consequently we scored this character ''−'' in this taxon.

This character has not been used in previous phylogenetic analyses of phyllostomids, but was described by other authors (e.g., Phillips, 1971).

## POSTCRANIUM

The following section includes characters of the postcranial musculoskeletal system excluding the hyoid region. Many of these characters are based on descriptions by Vaughan (1959), Vaughan and Bateman (1970), Strickler (1978), Altenbach (1979), and Straney (1980). Taxa examined in these studies are listed in table 4. We have revised many of the character descriptions given by Straney (1980: character numbers from appendix 1). Although we provide new data for some osteological characters, we did not collect new observational data for any of the myological characters drawn from prior studies.

**Character 74:** *Distal tip of clavicle attached by ligaments to coracoid process of scapula (0); or attached to both coracoid and acromion processes (1).* The distal tip of the clavicle is attached to the coracoid process of the scapula by ligaments in *Desmodus*, *Diphylla*, *Macrotus*, *Phyllostomus*, *Leptonycteris*, *Choeronycteris*, and *Carollia* (Vaughan, 1959; Strickler, 1978). There is no ligamentous connection to the acromion process in these taxa. In contrast, the distal tip of the clavicle is attached by ligaments to both the coracoid and acromion processes of the scapula in *Glossophaga* and *Centurio* (Strickler, 1978). The distal tip of the clavicle is attached to the coracoid only in mormoopids, but is attached to both the coracoid and acromion in *Noctilio* (Strickler, 1978). The primitive condition for phyllostomids cannot be assessed a priori.

This feature has not been used previously in a phylogenetic analysis.

**Character 75:** *M. occipitopollicalus with single cranial muscle belly (0); or with a cranial and a distal muscle belly (1).* M. occipitopollicalus is a complex muscle system that originates on the occiput of the skull and inserts into the metacarpal or first phalanx of the pollex (Strickler, 1978). In some species, a second tendon may insert onto the ventral metacarpal of digit one. This muscle complex includes a variable number of muscle bellies, segments of tendon, and segments of elastic tissue (Strickler, 1978). M. occipitopollicalus has a single cranial muscle belly in phyllostomines, *Brachyphylla*, *Choeronycteris*, *Glossophaga*, *Leptonycteris*, *Carollia*, *Centurio*, *Sturnira*, and *Uroderma* (Vaughan, 1959; Strickler, 1978; Straney, 1980; fig. 30A–B). This cranial muscle belly is also present in *Desmodus*, *Diphylla*, *Artibeus*, and *Chiroderma*; however, in these taxa an additional muscle belly is present distal to the first (Strickler, 1978; Straney, 1980; fig. 30C). In these taxa, the two muscle bellies are separated by a small proximal tendon and a distal stretch of elastic tissue (Straney, 1980; Strickler, 1978). Only the cranial belly is present in mormoopids; however, both cranial and distal muscle bellies are present in *Noctilio* (Strickler, 1978). Thus, the primitive state for phyllostomids cannot be assessed a priori.

Straney (1980: characters C1–2) developed two binary characters whose derived states are equivalent to our states 1 and 0,
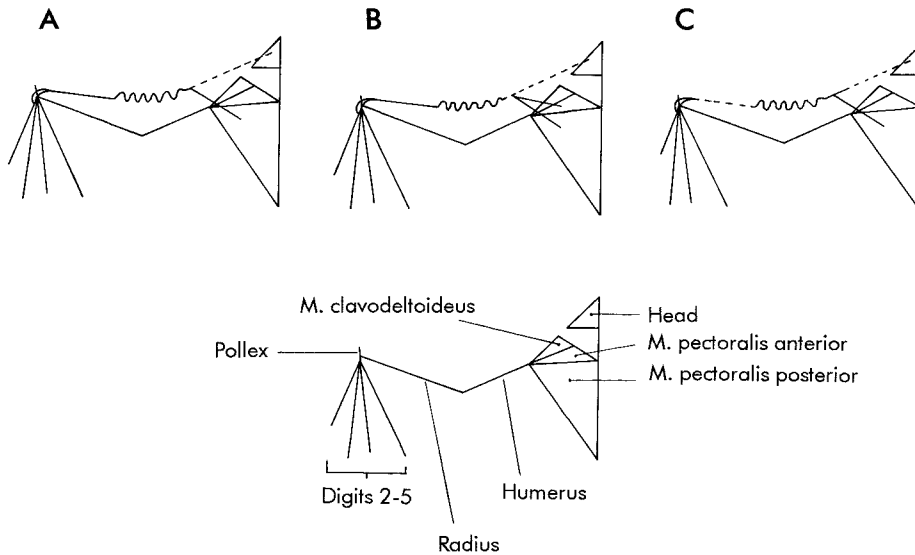
Fig. 30.    Diagramatic representation of the general conditions of the occipitopollicalus muscle complex with a key below (redrawn from Strickler, 1978: fig. 31). The solid line represents tendon, the dashed line is muscle, and the wavy line is elastic tissue. **A.** Condition in most phyllostomines, glossophagines, *Carollia*, and many stenodermatines. **B.** Condition in *Phyllostomus* and mormoopids. **C.** Condition in desmodontines, *Artibeus*, *Chiroderma*, and *Noctilio*.

respectively. Our scoring is identical to Straney's (1980).

**Character 76:** *M. occipitopollicalus has one connection to ventral flight musculature (0), or two attachments to ventral flight musculature (1).* In most phyllostomids, a single tendinous connection exists between the proximal tendon of m. occipitopollicalus and the ventral flight musculature (Vaughan, 1959; Strickler, 1978; Straney, 1980; fig. 30A, C). The single exception is *Phyllostomus*, which has two tendinous attachments to the ventral flight musculature (Strickler, 1978; Straney, 1980; fig. 30B). In mormoopids, there is a double tendinous attachment to the ventral flight musculature (Strickler, 1978; Straney, 1980). *Noctilio* has a single connection to the ventral flight musculature (Strickler, 1978; Straney, 1980). Due to this distribution of character states, the primitive state for phyllostomids cannot be assessed a priori.

Straney (1980: characters C3–4) developed two binary characters whose derived conditions are equivalent to our states 1 and 0, respectively. Our scoring is identical to Straney's (1980).

**Character 77:** *M. spinodeltoideus origi-* nates from vertebral border of scapula only (0); or from vertebral border of scapula and transverse scapular ligament (1).* In bats, m. deltoideus comprises three separate muscles: m. clavodeltoideus, m. acromiodeltoideus, and m. spinodeltoideus (Strickler, 1978). M. spinodeltoideus arises from the vertebral border of the scapula in *Choeronycteris*, *Glossophaga*, and *Leptonycteris* (Strickler, 1978). However, m. spinodeltoideus has an enlarged origin in *Desmodus*, *Diphylla*, *Macrotus*, *Phyllostomus*, *Carollia*, and *Centurio*, where it arises from the vertebral border of the scapula and part of the transverse scapular ligament (Vaughan, 1959; Strickler, 1978). In mormoopids, m. spinodeltoideus arises from the vertebral border of the scapula and the transverse scapular ligament (Strickler, 1978). In *Noctilio*, m. spinodeltoideus arises from the vertebral border of the scapula only (Strickler, 1978). Thus, the primitive condition for phyllostomids cannot be reconstructed a priori.

This feature has not been previously used in a phylogenetic analysis.

**Character 78:** *Caput mediale of m. triceps brachii inserts on both elbow sesamoid and caput laterale tendon (0); or on caput*

*laterale tendon only (1); or on elbow sesamoid only (2).* In bats, as in most mammals, the m. triceps brachii is composed of three heads: caput longum, caput laterale, and caput mediale (Strickler, 1978). In *Diphylla*, *Phyllostomus*, and *Carollia* the caput mediale of m. triceps brachii inserts on the elbow sesamoid (Strickler, 1978). In contrast, the caput mediale of m. triceps brachii inserts on the ventral edge of the tendon of the caput laterale in *Desmodus*, *Choeronycteris*, *Glossophaga*, *Leptonycteris*, and *Centurio* (Strickler, 1978). In *Mormoops*, the caput mediale of m. triceps brachii is absent (Vaughan and Bateman, 1970, Strickler, 1978), and we scored *Mormoops* "−" for this character. In *Pteronotus* and *Noctilio*, the caput mediale inserts on both the elbow sesamoid and the ventral edge of the caput laterale tendon (Vaughan and Bateman, 1970; Strickler, 1978). This distribution of character states suggests that the primitive condition for phyllostomids is the insertion of the caput mediale of m. triceps brachii on the elbow sesamoid and the caput laterale tendon.

This character has not been used previously in a phylogenetic analysis. Vaughan (1959), who described the postcranial musculature of *Macrotus*, noted only that the caput mediale of the m. triceps brachii inserted on the olecranon process of the ulna. This description is not detailed enough for us to score *Macrotus* for this character. Vaughan and Bateman (1970) described the origin and insertion of this muscle after examining all mormoopid species and 18 phyllostomid species, but did not describe the different insertions noted by Strickler (1978).

**Character 79:** *M. palmaris longus inserts on digit II (0); or does not insert on digit II (1).* M. palmaris longus originates on the distal tip of the spinous process of the humerus, divides into several tendons at the wrist, and inserts on various digits and tendons in the manus (Vaughan and Bateman, 1970). This muscle inserts on digit II in *Desmodus*, *Erophylla*, *Glossophaga*, and *Artibeus* (Altenbach, 1979; Vaughan and Bateman, 1970). In contrast, m. palmaris longus has no insertion on digit II in *Macrotus*, *Phyllostomus*, *Carollia*, and *Sturnira* (Vaughan, 1959; Vaughan and Bateman, 1970). In *Mormoops* and *Pter-*

*onotus parnellii*, m. palmaris longus inserts on digit II. In *Pteronotus quadridens*, *P. davyi*, and *P. personatus* the distal tendons of this muscle are small and difficult to trace (Vaughan and Bateman, 1970); therefore, we have scored *Pteronotus* with the state Vaughan and Bateman (1970) described for *Pteronotus parnellii*. Based on the distribution of character states among outgroup taxa, presence of an insertion of m. palmaris longus on digit II appears to be the primitive condition for phyllostomids.

Straney (1980: characters C5–7) based three characters on his descriptions of the insertion of m. palmaris longus: "Palmaris longus with insertion on digits one and two;" "Palmaris longus with insertion on digits one and three;" and "Palmaris longus with insertion on digits one, three, four, and five." However, Straney (1980) appears to have been unaware of the earlier study by Vaughan and Bateman (1970), and did not discuss how his results compared to theirs. Although Straney (1980) described the distribution of this character in many more phyllostomids than those examined by Vaughan and Bateman (1970), his descriptions frequently conflict with theirs, particularly the description of the insertion of m. palmaris longus onto digit II. Straney (1980) found that m. palmaris longus inserts on digit II in stenodermatines, *Phyllostomus*, and *Macrotus*, in contrast to Vaughan's (1959) and Vaughan and Bateman's (1970) reports that these taxa (or representatives of them, e.g., *Sturnira*) do not have an insertion on digit II. Further, Straney (1980) found that *Glossophaga* and mormoopids lack an insertion on digit II, whereas Altenbach (1979) and Vaughan and Bateman (1970) reported that an insertion on digit II was present in these taxa. Because Straney's (1980) descriptions differ so greatly from the reports by Vaughan (1959), Vaughan and Bateman (1970), and Altenbach (1979), we did not use Straney's (1980) descriptions to score this character.

**Character 80:** *M. palmaris longus does not insert on digit III (0); or inserts on digit III (1).* M. palmaris longus inserts on digit III in *Desmodus*, most phyllostomines (e.g., *Macrotus*, *Trachops*), *Erophylla*, *Anoura*, *Glossophaga*, *Lonchophylla*, and *Carollia*

(Vaughan, 1959; Vaughan and Bateman, 1970; Altenbach, 1979; Straney, 1980). In contrast, there is no insertion on digit III in *Phyllostomus* and stenodermatines (Vaughan and Bateman, 1970; Straney, 1980). M. palmaris longus does not insert on digit III in *Mormoops*, but does insert on this digit in *Pteronotus parnellii* (Vaughan and Bateman, 1970). In *Noctilio* there is no insertion on digit III (Straney, 1980). This distribution of character states among the outgroup taxa suggests that the absence of an insertion on digit III is the primitive condition for phyllostomids.

Unlike Straney's (1980) descriptions of the insertion of m. palmaris longus onto digit II (see character 79), his descriptions of the insertion of m. palmaris longus onto digit III agree, for the most part, with those of previous authors. The only differences are found in descriptions of this insertion in *Macrotus* and mormoopids. In *Macrotus*, Straney (1980) found no insertion on digit III, whereas Vaughan (1959) reported that an insertion was present on this digit. Straney (1980) reported that m. palmaris longus inserted on digit III in all mormoopids, whereas Vaughan and Bateman (1970) found that it did not insert on this digit in *Mormoops*. Although these disagreements do exist, we decided to utilize Straney's (1980: 53) text descriptions to score this character in taxa that were not described by previous authors.

**Character 81:** *M. palmaris longus does not insert on digit IV (0); or inserts on digit IV (1).* There is no insertion of m. palmaris longus on digit IV in *Desmodus*, *Macrotus*, *Phyllostomus*, *Carollia*, *Artibeus*, and *Sturnira* (Vaughan, 1959; Vaughan and Bateman, 1970; Altenbach, 1979). In contrast, m. palmaris longus inserts on digit IV in *Erophylla* and *Glossophaga* (Vaughan and Bateman, 1970). Both *Mormoops* and *Pteronotus parnellii* lack an insertion of m. palmaris longus on digit IV (Vaughan and Bateman, 1970), suggesting that this is the primitive condition for phyllostomids.

This character has not been used previously in a phylogenetic analysis. Straney (1980) did not describe the insertion of m. palmaris longus on digit IV.

**Character 82:** *M. palmaris longus does not insert on digit V (1); or inserts on digit V (1).* M. palmaris longus does not insert on digit V in *Macrotus*, *Phyllostomus*, *Artibeus*, and *Sturnira* (Vaughan, 1959; Vaughan and Bateman, 1970). However, in *Desmodus*, *Erophylla*, *Glossophaga*, and *Carollia*, m. palmaris longus inserts on digit V (Vaughan and Bateman, 1970; Altenbach, 1979). M. palmaris longus does not insert on digit V in *Mormoops* and *Pteronotus parnellii* (Vaughan and Bateman, 1970), suggesting that this is the primitive condition for phyllostomids.

This character has not been used previously in a phylogenetic analysis. Straney (1980) did not describe the insertion of m. palmaris longus on digit V.

**Character 83:** *M. flexor digitorum profundus inserts on digit IV (0); or does not insert on digit IV (1).* M. flexor digitorum profundus, which originates on the distal tip of the spinous process of the humerus, divides into multiple tendons at the carpus (Vaughan and Bateman, 1970). These tendons insert on digits I and III in all phyllostomids (Vaughan, 1959; Vaughan and Bateman, 1970; Altenbach, 1979). M. flexor digitorum profundus has an additional insertion on digit IV in *Phyllostomus* (Vaughan and Bateman, 1970). In other phyllostomids, there is no insertion on digit IV (Vaughan, 1959; Vaughan and Bateman, 1970; Altenbach, 1979). *Mormoops* and *Pteronotus* have an insertion on digit IV, in addition to the insertions on digits I, III, and V (Vaughan and Bateman, 1970). Presence of an insertion on digit IV appears to be the primitive condition for phyllostomids.

This is the first use of this character in a phylogenetic analysis, although Straney (1980: characters C8–9) based two characters on the insertion of this muscle into digits I, II, and III. Straney (1980), unlike other previous authors, did not find that all phyllostomids had insertions on digits I and III. Instead, Straney (1980: 53) reported that four taxa, *Lonchorhina*, *Macrophyllum*, *Macrotus*, and the outgroup taxon *Noctilio*, had insertions on digits I and II. Because Straney's (1980) descriptions differ so greatly from the reports by Vaughan (1959), Vaughan and Bateman (1970), and Altenbach (1979), we did not use Straney's (1980) descriptions to score this character.

**Character 84:** *Third metacarpal longer than fourth or fifth (0); or third and fourth metacarpals subequal in length, both longer than fifth (1); or fourth metacarpal longest (2); or fourth and fifth metacarpals subequal in length, both longer than third (3); or fifth metacarpal longest (4); or third and fifth metacarpals subequal in length, both longer than fourth (5); or third, fourth, and fifth metacarpals all subequal in length (6).* In *Lonchorhina*, *Micronycteris nicefori*, *Phyllostomus*, glossophagines, lonchophyllines, *Ametrida*, and *Centurio*, the third metacarpal is the longest of metacarpals three, four, and five. In *Macrophyllum*, *Mimon crenulatum*, *Brachyphylla*, phyllonycterines, *Carollia*, and many stenodermatines (e.g., *Ariteus*, *Uroderma*) the third and fifth metacarpals are subequal in length and both are always longer than the fourth metacarpal. In contrast, the third and fourth metacarpals are subequal in length and both are always longer than the fifth metacarpal in desmodontines and *Micronycteris brachyotis*. Finally, in most phyllostomines, *Rhinophylla*, and several stenodermatines (e.g., *Sturnira*, *Phyllops*) the fifth metacarpal is the longest. In only one taxon, *Enchisthenes*, did we observe the third, fourth, and fifth to all be subequal in length. In mormoopids, the third metacarpal is longer than the fourth and fifth, while in *Noctilio*, the fourth metacarpal is the longest. Thus, the primitive condition for phyllostomids cannot be determined a priori.

Simmons (1996: character 8) scored the metacarpal formula of species of *Micronycteris*. We had originally attempted to code this character in a similar fashion to that developed by Simmons (1996; the complete metacarpal formula, e.g., 3 > 4 > 5); however, due to the number of unique metacarpal formulas we discovered (more than nine), we found it more useful to express this diversity by creating a character for the longest metacarpal(s). We cannot create an additional character for the shortest metacarpal because these characters would not be independent in taxa like *Brachyphylla*, which has two metacarpals that are equal in length and longer than a third.

**Character 85:** *First phalanx of digit III of wing shorter than second phalanx (0); or first and second subequal (1).* In most phyllostomids, the first (proximal) phalanx of digit III is noticeably shorter than the second phalanx. In contrast, the first and second phalanges are subequal in *Micronycteris hirsuta*, *M. megalotis*, *M. minuta*, *Tonatia*, and phyllonycterines. In mormoopids and *Noctilio*, the first phalanx is shorter than the second, suggesting that this is the primitive condition for phyllostomids.

Simmons (1996: character 9) used this character in her study of relationships among species of *Micronycteris*; our character states and scoring are identical to hers.

**Character 86:** *First phalanx of digit IV of wing shorter than second phalanx (0); or subequal to second phalanx (1); or longer than second phalanx (2).* In most phyllostomids, the first (proximal) phalanx of digit IV is noticeably shorter than the second phalanx. In contrast, the first and second phalanges are subequal in many phyllostomines (e.g., *Chrotopterus*, *Mimon bennettii*), carolliines, *Ectophylla*, *Mesophylla*, and *Vampyressa pusilla*. The first phalanx is distinctly longer than the second in some phyllostomines (e.g., *Micronycteris hirsuta*, *Macrotus*), *Erophylla*, *Phyllops*, and *Centurio*. Taxonomic polymorphism occurs in three genera. In *Tonatia*, some species (e.g., *T. schulzi*) have the first and second phalanges subequal, whereas others (e.g., *T. saurophila*) have a first phalanx that is longer than the second. We scored *Tonatia* with states 1 and 2 in the matrix. In *Chiroderma* and *Platyrrhinus*, some species have a first phalanx shorter than the second (e.g., *C. salvini*, *P. helleri*), whereas others have the first and second phalanges subequal (e.g., *C. villosum*, *P. infuscus*). We scored *Chiroderma* and *Platyrrhinus* with states 0 and 1 in the matrix. In *Mormoops*, the first and second phalanges are subequal in length. In *Pteronotus* and *Noctilio*, the first phalanx is shorter than the second. This distribution of character states suggests that a first phalanx that is shorter than the second is the primitive condition for phyllostomids.

Simmons (1996: character 10) used this character in her study of relationships among species of *Micronycteris*. Although our character states and scoring are identical to hers, we have not ordered the character as she did (0 ↔ 1 ↔ 2).

**Character 87:** *Calcar present, equal to or longer than foot (0); or shorter than foot (1); or vestigial or absent (2).* The length of the calcar is equal to or greater than the length of the foot (including claws) in most phyllostomines. In contrast, the calcar is noticeably shorter than the foot in *Diphylla*, several phyllostomines (e.g., *Micronycteris nicefori*, *Phylloderma*), *Erophylla*, glossophagines, lonchophyllines, carolliines, and most stenodermatines (e.g., *Artibeus*, *Uroderma*). The calcar is either vestigial or entirely absent in *Desmodus*, *Diaemus*, *Brachyphylla*, *Phyllonycteris*, and *Sturnira*. In mormoopids and *Noctilio*, the calcar is equal to or longer than the foot, suggesting that this is the primitive state for phyllostomids.

Straney (1980: G6–8) developed three binary characters based on the length of the calcar: ''Calcar longer than foot,'' ''Calcar subequal to foot,'' and ''Calcar shorter than foot.'' We found that Straney's (1980) second character (G7) included what we consider to be two distinct conditions. Straney (1980) described the calcar as subequal to the foot in *Chrotopterus*, *Macrotus*, some species of *Micronycteris*, *Phylloderma*, some species of *Phyllostomus*, some species of *Tonatia*, *Trachops*, *Vampyrum*, *Choeronycteris*, *Platalina*, and unidentified stenodermatines. Although it may be reasonable to describe the calcar as subequal to the foot in *Choeronycteris* and *Platalina*, in all glossophagines that we examined, the calcar was consistently shorter than the foot (the same is true of the stenodermatines we examined). The calcar in many phyllostomines is apparently subequal to the foot; however, in several taxa the calcar is clearly longer than the foot (e.g., *Macrophyllum*), and in at least some species the calcar varies from equal to slightly longer than the foot (e.g., *Micronycteris brachyotis*; Simmons, 1996). As a result, we recognize ''calcar equal to or longer than foot'' as a single character state. Due to our revision of character states, our scoring of this character differs from Straney's (1980) for those taxa that he considered to have a calcar subequal to the foot. Our observations agree with those of Simmons (1996: 11) who used this character in an analysis of relationships among species of *Micronycteris*. We have added a new state ''calcar vestigial or ab-sent'' that was not used previously by Straney (1980) or Simmons (1996). We confirmed these observations with measurements on pickled specimens where necessary.

**Character 88:** *Posterior edge of plagiopatagium inserts onto lower leg or ankle region (0); or onto calcar (1); or onto lateral surface of first metatarsal (2); or onto dorsal surface of first metatarsal (3).* The posterior edge of the plagiopatagium inserts at, or proximal to, the ankle region in desmodontines, many phyllostomines (e.g., *Macrophyllum*, *Macrotus*), *Brachyphylla*, phyllonycterines, glossophagines, lonchophyllines, *Carollia*, and *Sturnira*. A unique condition among phyllostomids occurs in *Lonchorhina*, where the plagiopatagium is attached to the proximal part of the calcar creating a small ''pocket'' between the plagiopatagium and uropatagium. The posterior edge of the plagiopatagium inserts onto the lateral metatarsal in *Micronycteris hirsuta*, *Phylloderma*, *Phyllostomus*, *Rhinophylla*, and stenodermatines (except *Sturnira*). The plagiopatagium is attached to the dorsal surface of the first metatarsal in *Chrotopterus*, *Tonatia*, and *Vampyrum*. In mormoopids, the plagiopatagium is attached to the proximal part of the calcar creating a small ''pocket'' between the plagiopatagium and the uropatagium; however, the plagiopatagium is attached proximal to the ankle on the lower leg in *Noctilio*. Thus, the primitive condition for phyllostomids cannot be assessed a priori.

Straney (1980: characters G9–13) scored attachment site of the plagiopatagium in a series of binary characters. We have subsumed Straney's (1980) characters G9 (''wing attaches to lateral side of ankle'') and G13 (''wing attaches on lower leg'') into a single state (our state 0) because we were unable to divide the continuous range of variation of ankle/lower leg attachments that we observed into these discrete states. In addition to changing the character coding, we did not observe the attachment of the plagiopatagium to the calcar (scored as a vento-medial ankle attachment of the plagiopatagium in Straney's [1980] matrix) in *Macrotus* and *Mimon bennettii*, and found that *Tonatia* shares the same condition seen in *Chrotop-*

*terus* and *Vampyrum*, an attachment to the dorsal surface of the first metatarsal.

Owen (1987: character 6) also used this character, recognizing four states: attachment to the tibial region 0, attachment to the tarsal region 1, attachment to the metatarsal region 2, and attachment to the metatarsal-phalangeal joint 3 (ordered $0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3$). We have combined his first two states into our state 0, and the latter two conditions into our state 2, because of our finding that these conditions were variable within genera, or our inability to separate the variation we observed into these discrete states. However, our observations largely agree with his, with the exception of *Sturnira nana*. Owen (1987) observed that the plagiopatagium in *S. nana* is attached to the metatarsal region. However, we found that it inserts at the ankle, as in other *Sturnira* species. Owen (1987) also reported that in *Chiroderma doriae*, the attachment of the plagiopatagium is to the ankle region rather than the metatarsals as is the case in other *Chiroderma*. Unfortunately, we were unable to examine specimens of *C. doriae* and therefore score *Chiroderma* with state 2 in the matrix. Owen (1991: characters 14, 15, 16) used additive binary coding, but both his characters and scoring are equivalent to his earlier work.

Marques-Aguiar (1994: character 7) also used this character in her analysis of relationships among large-bodied *Artibeus* species. Marques-Aguiar (1994) recognized three states: plagiopatagium attaches at side of foot, attaches at ankle, or attaches at base of toes. We combined her state 0 (side of foot) with 1 (base of toes), because both states are often present within genera. Our observations agree with those of Marques-Aguiar (1994) with one exception. Marques-Aguiar (1994) reported that the plagiopatagium attaches to ankle in *Enchisthenes hartii*, whereas we observed (as did Owen, 1987) that in this species the attachment is to the metatarsals.

**Character 89:** *Tail of medium length, extends into uropatagium but is shorter than hind legs (0); or tail long, approximately equal to length of hind legs (1); or tail effectively absent, caudal vertebrae do not extend into uropatagium (2).* In most phyllostomines, phyllonycterines, most glossophagines, lonchophyllines, and *Carollia*, the tail is of moderate length and is shorter than the hind legs. A very long tail, approximately equal in length to the hind legs, is present in *Lonchorhina*, *Macrophyllum*, and *Macrotus*. The tail is effectively absent in desmodontines, *Vampyrum*, *Brachyphylla*, *Leptonycteris*, *Rhinophylla*, and stenodermatines. Taxonomic polymorphism occurs in *Anoura* where some species have a medium length tail (e.g., *A. caudifera*), whereas others lack a tail (e.g., *A. geoffroyi*). We scored *Anoura* with states 0 and 2 in the matrix. Examination of caudal vertebrae reveals that one or two small vertebrae may extend beyond the ischia in some individuals of these taxa. For example, some specimens of *Anoura geoffroyi* (e.g., USNM 49356) lack postischial vertebrae, whereas others have two vestigial postischial vertebrae (e.g., USNM 385799). As originally noted by Miller (1907), all specimens of *Brachyphylla* that we examined had three long, cylindrical postischial vertebrae similar to those found in all taxa with external tails; however, these vertebrae do not extend into the uropatagium. Because the condition in *Brachyphylla* externally appears identical to the condition in other taxa lacking tails, we scored this genus with state 2 in the matrix. In mormoopids and *Noctilio*, the tail is of moderate length, suggesting that this is the primitive condition for phyllostomids.

Straney (1980: G1–3) developed three binary characters devoted to tail morphology: ''Tail present,'' ''Tail short,'' and ''Tail to edge of uropatagium,'' whose derived conditions correspond to our character states. Our scoring agrees with that of Straney (1980) with the exception of *Rhinophylla*. Straney (1980) scored all carolliines as possessing a medium-length tail; however, an externally visible tail is absent in *Rhinophylla*. We have chosen to define tail length in relation to the hind legs rather than the uropatagium (as Straney [1980] did) because the uropatagium is more variable in length.

## HYOID APPARATUS

The following characters are based on descriptions by Sprague (1943) and Griffiths (1982, 1983b) for taxa appearing in table 4.

Because Griffiths (1982) repeats earlier (Griffiths, 1978) observations for *Macrotus*, *Glossophaga*, *Monophyllus*, *Artibeus*, and *Phyllops*, we cite only the later paper. We have revised many of Griffiths' (1982) character descriptions, but have not collected new observational data. We follow Griffiths' (1982, 1983b) terminology for osteological and myological features, which is identical to that used by Sprague (1943) with three exceptions: (1) Griffiths (1982, 1983b) identified the element termed the hypohyal by Sprague (1943) as the ceratohyal; (2) Griffiths (1982, 1983b) identified the element termed the ceratohyal by Sprague (1943) as the epihyal; and (3) Griffiths (1982, 1983b) identified the muscle termed m. constrictor pharyngeus inferior by Sprague (1943) as m. cricopharyngeus. Character numbers from Straney (1980) are from appendix 1; those from Griffiths (1982) are from table 1; and those from Gimenez et al. (1996) are from table 4. Straney (1980) based his descriptions on the work of Sprague (1943).

**Character 90:** *M. mylohyoideus undivided (0); or partly divided into anterior and posterior parts by a fleshy aponeurosis (1); or with a pronounced break, clearly divided into distinct anterior and posterior parts (2).* M. mylohyoideus consists of a single, undivided sheet of muscle in *Desmodus*, glossophagines, lonchophyllines, and *Carollia* (Wille, 1954; Griffiths, 1982; fig. 31A). *Sturnira* also has a single muscle belly (Sprague, 1943). In *Brachyphylla* and phyllonycterines, m. mylohyoideus is partly divided into anterior and posterior parts by a fleshy aponeurosis (Griffiths, 1982). In contrast, m. mylohyoideus exhibits a pronounced break and is clearly divided into distinct anterior and posterior parts in phyllostomines and most stenodermatines (Wille, 1954; Griffiths, 1982; fig. 31C). M. mylohyoideus is undivided in *Pteronotus* and *Noctilio* (Sprague, 1943), suggesting that this is the primitive condition for phyllostomids.

Straney (1980: characters E9–11) used three binary characters to describe variation in the morphology of m. mylohyoideus. Our character states 0 and 2 correspond to the derived conditions of Straney's (1980) characters E9 and E11, respectively. We did not include the information contained in Straney's (1980) character E10, which was based on Sprague's (1943) description of the entire anterior portion of the m. mylohyoideus as aponeurotic in *Phyllonycteris* and *Glossophaga* (a condition that is not equivalent to having two muscle masses separated by a fleshy aponeurosis). Griffiths (1982) observed that the mylohyoid was sometimes thin enough to reveal the geniohyoid deep to it, but that this condition was variable within glossophagine species. Morphology of m. mylohyoideus was not included in Griffiths' (1982) character analysis, or in that of Gimenez et al. (1996).

**Character 91:** *Medial fibers of m. sternohyoideus originate from medial manubrium (0); or from mesosternum (1); or from xiphoid process of sternum (2).* The medial fibers of m. sternohyoideus originate from the medial manubrium in phyllostomines, *Carollia*, and stenodermatines (including *Sturnira*; Sprague, 1943; Griffiths, 1982). The origin is shifted posteriorly to the mesosternum in *Desmodus*, *Brachyphylla*, and phyllonycterines (Griffiths, 1982). In glossophagines and lonchophyllines, the medial fibers of m. sternohyoideus originate entirely from the xiphoid process (Griffiths, 1982). Among the outgroups, the manubrium is the origin of the medial fibers of m. sternohyoideus in *Pteronotus* (Sprague, 1943). In *Noctilio*, m. sternohyoideus is not clearly differentiated into groups of medial and lateral muscle fibers. Instead, the single origin of all fibers in this taxon is the manubrium (Sprague, 1943). Nevertheless, the homologs of the medial and lateral fibers found in other phyllostomids are presumably present in *Noctilio*, thus we have scored *Noctilio* for this character and character 92. The distribution of character states in the outgroups suggests that a manubrial origin is the primitive condition for phyllostomids.

Griffiths (1982: characters 1–2) scored variation in the origin of m. sternohyoideus as two binary characters: "posterior shift of sternohyoid origin," and "xiphoid origin of sternohyoid." Gimenez et al. (1996) recently used this character and apparently followed Smith and Hood (1984) in regarding Griffiths' (1982) characters 1 and 2 as states of the same character. Gimenez et al.'s (1996: character 17) single multistate character is
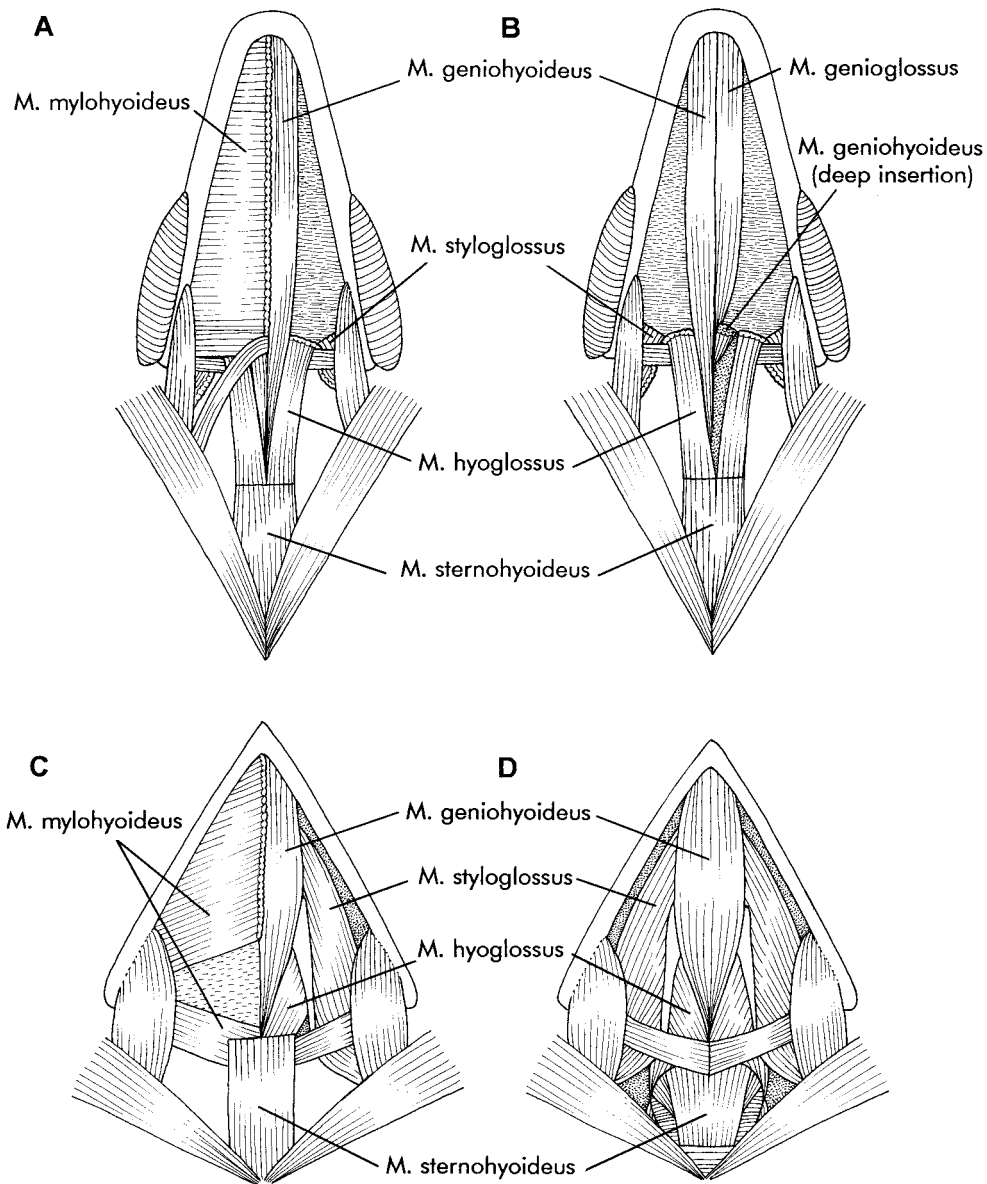
Fig. 31.   **A.** Superficial and **B.** deep views of the hyoid musculature of *Glossophaga soricina.* **C.** Superficial and **D.** deep views of the hyoid musculature of *Vampyressa pusilla* (redrawn from Griffiths, 1982: figs. 3, 4, 18, 19).

identical to ours in construction and coding. Griffiths' (1982) characters (which are subsumed under states 1 and 2 above) did not account for differences in the origins of medial versus lateral fibers of m. sternohyoideus. Accordingly, we chose to score variation in the origin of m. sternohyoideus as two multistate characters (our characters 91 and 92) which separately describe the origin of the two sets of fibers.

**Character 92:** *Lateral fibers of m. sternohyoideus originate from manubrium (0); or originate from manubrium and clavicle (1); or originate from clavicle and first rib (2); or originate from xiphoid process (3).* The lateral fibers of m. sternohyoideus orig-

inate from the manubrium in *Sturnira* (Sprague, 1943). These fibers originate from the lateral manubrium and clavicle in phyllostomines, *Erophylla*, *Carollia*, and stenodermatines (except *Sturnira*; Griffiths, 1982). The lateral fibers of m. sternohyoideus originate from the clavicle and the proximal head of the first rib in *Desmodus*, *Brachyphylla*, and *Phyllonycteris* (Griffiths, 1982). In glossophagines and lonchophyllines, the lateral fibers of m. sternohyoideus originate from the xiphoid process (Griffiths, 1982). Sprague (1943) noted that the lateral fibers of m. sternohyoideus originate from the manubrium in *Pteronotus* and *Noctilio*; thus, a manubrial origin appears to be primitive for phyllostomids.

**Character 93:** *M. sternohyoideus inserts via tendon on basihyal (0); or via raphe into the fibers of m. hyoglossus and m. genioglossus (1).* M. sternohyoideus inserts via tendon to the basihyal in *Desmodus*, phyllostomines, *Brachyphylla*, phyllonycterines, *Carollia*, and stenodermatines (Griffiths, 1982). In contrast, this muscle inserts via a raphe into the fibers of m. hyoglossus and m. genioglossus in glossophagines and lonchophyllines (Griffiths, 1982). Typically, there is no muscular connection to the hyoid apparatus in these taxa. A remnant of a basihyal tendon was found by Griffiths (1982) in one individual each of *Lionycteris spurelli* and *Lonchophylla robusta*, but the principal insertion was identical to that of other lonchophyllines. Accordingly, we scored these taxa with state 1 in the matrix. Although Sprague (1943) reported the insertion of m. sternohyoideus in *Pteronotus*, *Noctilio*, and *Sturnira*, these three taxa are scored ''?'' in the matrix (see discussion below). Thus, the primitive condition for phyllostomids cannot be reconstructed a priori.

Straney (1980), Griffiths (1982), and Gimenez et al. (1996) previously used this character. Our character states are equivalent to those recognized by these authors, although Griffiths (1982) and Gimenez et al. (1996) described what they believed to be the derived condition (our state 1) differently. Griffiths (1982: character 3) described the derived condition as ''loss of sternohyoid's connection to hyoid bone,'' whereas Gimenez et al. (1996: character 18) described the derived condition of their character (''connection of sternohyoideus muscle to hyoid bone'') as ''dissociated.'' Straney (1980: characters E19–20) erected two binary characters whose derived conditions are equivalent to our character states: ''Sternohyoid insertion on basihyal,'' and ''Sternohyoid insertion on raphe ventral [to] basihyal.''

Although our scoring of this character agrees with the work of Griffiths (1982) and Giminez et al. (1996), Straney (1980) scored *Desmodus* and glossophagines as possessing an insertion on the basihyal element, while he scored all other taxa for which data was available as possessing an insertion on the basihyal raphe. In the text, however, Straney (1980: 32) noted that *Desmodus* was unique among noctilionoid bats in possessing the insertion on the basihyal. Straney's (1980) description agrees with Sprague's (1943) discussion of this character. Sprague (1943) described an insertion on the basihyal raphe for *Phyllostomus*, *Phyllonycteris*, *Glossophaga*, *Carollia*, *Artibeus*, *Sturnira*, *Pteronotus*, and *Noctilio*. *Desmodus* possessed an insertion on the basihyal by means of a tendon (Sprague, 1943). Although Griffiths' (1982) examination of the hyoid apparatus demonstrated that Sprague's (1943) description of an insertion in the basihyal raphe is inaccurate for most taxa, no additional data are available for *Pteronotus*, *Noctilio*, or *Sturnira*. Because it seems unlikely that Sprague's (1943) description of this character is correct, we have chosen to score these taxa ''?'' in the matrix.

Wille (1954) reported that this muscle originates on the xiphoid process of the sternum and inserts into the tongue in glossophagines and lonchophyllines. As Griffiths (1978) noted, Wille (1954) seemed unaware that m. hyoglossus is greatly elongated in glossophagines and lonchophyllines. The muscle segment that Wille (1954) considered part of the sternohyoideus is actually part of m. hyoglossus (Griffiths, 1978).

**Character 94:** *Part of m. ceratohyoideus inserts on ceratohyal (0); or m. ceratohyoideus does not insert on ceratohyal (1).* Part of m. ceratohyoideus inserts on the ceratohyal element in *Micronycteris nicefori*, *Brachyphylla*, phyllonycterines, glossophagines, lonchophyllines, *Carollia*, and stenoderma-

tines (including *Sturnira*; Sprague, 1943; Griffiths, 1982). In contrast, this muscle does not insert on the ceratohyal in *Desmodus*, *Macrotus*, and *Phyllostomus* (Griffiths, 1982). Part of m. ceratohyoideus inserts on the ceratohyal element in *Pteronotus* (Sprague, 1943; Griffiths, 1983b) and *Noctilio* (Sprague, 1943), suggesting that this condition is primitive for phyllostomids.

Straney (1980), Griffiths (1982), and Gimenez et al. (1996) did not include any characters based on m. ceratohyoideus in their analyses, although Griffiths (1982) clearly described the variation that we have scored in our characters 94 and 95. Although Sprague (1943) described the attachment of m. ceratohyoideus to the ceratohyal in both *Pteronotus* and *Noctilio*, he referred to this connection as an origin, and noted that the insertion of this muscle in these taxa was on the thyrohyal.

**Character 95:** *M. ceratohyoideus does not insert on stylohyal (0); or part of m. ceratohyoideus inserts on stylohyal (1).* M. ceratohyoideus does not insert on the stylohyal element in *Brachyphylla*, phyllonycterines, many glossophagines (e.g., *Choeroniscus*, *Choeronycteris*), lonchophyllines, *Carollia*, and some stenodermatines (e.g., *Artibeus*, *Uroderma*; Griffiths, 1982; *Sturnira*; Sprague, 1943). In contrast, part of m. ceratohyoideus inserts on the stylohyal in *Desmodus*, phyllostomines, some glossophagines (e.g., *Glossophaga*, *Leptonycteris*), *Platyrrhinus*, and *Vampyressa pusilla* (Griffiths, 1982). M. ceratohyoideus does not insert on the stylohyal element in *Pteronotus* (Griffiths, 1983b) and *Noctilio* (Sprague, 1943), suggesting that this is the primitive condition for phyllostomids.

**Character 96:** *M. hyoglossus originates via tendon from basihyal bone (0); or from raphe which forms insertion of m. sternohyoideus (1).* M. hyoglossus originates via tendon from the basihyal bone in *Desmodus*, phyllostomines, *Brachyphylla*, phyllonycterines, *Carollia*, and stenodermatines (Griffiths, 1982). In contrast, m. hyoglossus originates from the raphe, which forms the insertion of m. sternohyoideus (the former basihyal raphe, now disconnected from the basihyal bone) in glossophagines and lonchophyllines (Griffiths, 1982). There is no direct connection of m. hyoglossus to the bones of the hyoid apparatus in these taxa. Although Sprague (1943) reported the origin of m. hyoglossus in *Pteronotus*, *Noctilio*, and *Sturnira*, these three taxa are scored "?" in the matrix (see discussion below). The primitive condition for phyllostomids cannot be reconstructed a priori.

Straney (1980: characters E21–22) used origin of m. hyoglossus as two binary characters, whose derived conditions are identical to our character states. However, Straney (1980) scored the raphe origin (our character state 1) as occurring in phyllostomines, brachyphyllines, carolliines, stenodermatines, *Pteronotus*, and *Noctilio*. Straney (1980) reported an origin from the basihyal (our state 0) in glossophagines and desmodontines. Based on Sprague's (1943) descriptions, only Straney's coding of *Noctilio*, which Sprague described as having an origin from the basihyal and thyrohyal, was inaccurate. Although Griffiths' (1982) examination of the hyoid apparatus demonstrated that Sprague's (1943) description of the origin of m. hyoglossus from the basihyal raphe was inaccurate for most taxa, no additional data are available for *Pteronotus*, *Noctilio*, or *Sturnira*. Because it seems unlikely that Sprague's (1943) description of this character is correct, we have chosen to score these taxa "?" in the matrix. Our scoring of this character was identical to that of Griffiths (1982: character 4), although he described the derived condition (our state 1) as "hyoglossus elongated and loses connection to hyoid bone." Our character states are also equivalent to those used by Gimenez et al. (1996: character 19), who described the derived condition in terms similar to those used by Griffiths (1982). Wille (1954: 317) reported that this muscle extends "from basihyal to basihyal raphe in geniohyoideus" in glossophagines and lonchophyllines. Given the observations of Griffiths (1982), this description appears to be incorrect.

**Character 97:** *M. geniohyoideus has single insertion via tendon to basihyal or basihyal raphe (0); or muscle splits near insertion, deep fibers insert directly on anterior surface of basihyal, superficial fibers insert in association with m. hyoglossus and m. sternohyoideus (1).* M. geniohyoideus has a

single insertion via tendon to the basihyal bone in *Desmodus*, phyllostomines, *Brachyphylla*, phyllonycterines, *Carollia*, and stenodermatines (Griffiths, 1982). In contrast, m. geniohyoideus splits as it passes posteriorly in lonchophyllines and glossophagines (Griffiths, 1982). The deep fibers of m. geniohyoideus insert directly on the anterior surface of the basihyal bone, while the superficial fibers form an insertion in association with m. hyoglossus and m. sternohyoideus (Griffiths, 1982). Although Sprague (1943) reported the origin of m. geniohyoideus in *Pteronotus*, *Noctilio*, and *Sturnira*, these three taxa are scored "?" in the matrix (see discussion below). The primitive condition for phyllostomids cannot be reconstructed a priori.

Straney (1980: characters E17–18) defined two binary characters to describe the insertion of m. geniohyoideus: "Geniohyoid insertion on basihyal" and "Geniohyoid insertion on raphe ventral to basihyal." The derived conditions of these characters are essentially equivalent to our character states, although Straney (1980), and Sprague (1943), who was his source, were apparently unaware that deep fibers of m. geniohyoideus retain their attachment to the basihyal in forms with the "raphe" insertion of the superficial fibers. Additionally, Straney (1980) scored all noctilionoids, except *Phyllostomus* and *Noctilio*, as having the insertion on the basihyal, which conflicts with Sprague's (1943) description. Sprague (1943) found that in *Phyllostomus*, *Phyllonycteris*, *Carollia*, *Artibeus*, *Sturnira*, *Pteronotus*, and *Noctilio*, the insertion of m. geniohyoideus was on the basihyal raphe, whereas in *Desmodus* and *Glossophaga* the insertion was on the entoglossal process of the basihyal. Sprague (1943) found no evidence of split insertions in these taxa. Although Griffiths' (1982) examination of the hyoid apparatus demonstrated that Sprague's (1943) description of the insertion of m. geniohyoideus was inaccurate for most taxa, no additional data are available for *Pteronotus*, *Noctilio*, or *Sturnira*. Because it seems unlikely that Sprague's (1943) description of this character is correct, we have chosen to score these taxa "?" in the matrix.

Our scoring of this feature was identical to that of Griffiths (1982: character 5) and Giminez et al. (1996: character 20), although both described the derived condition (our state 1) as "double insertion of geniohyoid." Wille (1954) also discussed the morphology of m. geniohyoideus in glossophagine and lonchophylline bats, describing an anterior and posterior part to this muscle. For the anterior part of the muscle, Wille (1954) only noted an insertion into the basihyal raphe; he was apparently unaware that there was a deep insertion of this muscle to the basihyal bone.

**Character 98:** *Superficial fibers of m. geniohyoideus pass ventral to basihyal and insert into fibers of m. hyoglossus and m. sternohyoideus via raphe (0); or superficial fibers insert in well-developed loop around ventral and dorsal surfaces of the intersection of m. hyoglossus and m. sternohyoideus (1).* For taxa with a split insertion of m. geniohyoideus, two conditions are possible for the insertion of the superficial fibers of this muscle. In some glossophagines (e.g., *Glossophaga*, *Lichonycteris*) and lonchophyllines, the superficial fibers pass ventral to the basihyal to form a weak insertion into fibers of m. hyoglossus and m. sternohyoideus via the former basihyal raphe (Griffiths, 1982). In the remaining glossophagines (e.g., *Choeronycteris*, *Hylonycteris*), the superficial fibers of m. geniohyoideus insert in a well-developed loop around ventral and dorsal surfaces of the intersection of m. hyoglossus and m. sternohyoideus. This "tunnel insertion" is unique among mammals (Griffiths, 1982). The primitive state for phyllostomids cannot be determined a priori because we scored *Pteronotus* and *Noctilio* "?" for character 97. We scored all taxa lacking a split insertion of m. geniohyoideus (state 0 of character 97), "−" for this character.

Griffiths (1982: character 6) scored this feature as "tunnel insertion of geniohyoid" (present/absent). Griffiths (1982) scored taxa lacking a split insertion and those with a split insertion but lacking a "tunnel" insertion as "absent." Gimenez et al. (1996: character 21) scored this character similarly; their character states correspond to ours. Sprague (1943) did not describe the tunnel insertion, consequently this character was not used by Straney (1980).

Wille (1954) described the posterior part

of m. geniohyoideus as forming a muscular tube that surrounds the sternohyoideus (= m. hyoglossus; Griffiths, 1978). Wille (1954) reported that this tube was present in all taxa he examined except *Glossophaga* and *Monophyllus*, where the posterior part of m. geniohyoideus formed a median belly between the two bellies of the sternohyoideus (= m. hyoglossus; Griffiths, 1982). Wille (1954) therefore does not agree with Griffiths (1982) on the taxonomic distribution of this character, because Griffiths (1982) reported that the tunnel insertion does not occur in *Lonchophylla*, whereas Wille (1954) reported the presence of the tunnel insertion in this taxon. We have chosen to follow Griffiths (1982) in this instance.

**Character 99:** *Right and left m. geniohyoideus muscles partly or completely fused across midline (0); or muscles not fused (1).* M. geniohyoideus is partly or completely fused with its counterpart across the midline in *Desmodus* and *Glossophaga* (Sprague, 1943). In contrast, the right and left m. geniohyoideus are not fused in *Phyllostomus*, *Phyllonycteris*, *Carollia*, *Sturnira*, and *Artibeus* (Sprague, 1943). These muscles are fused in *Pteronotus* and *Noctilio* (Sprague, 1943), suggesting that this condition is primitive for phyllostomids.

Straney (1980: characters E12–14) described fusion of m. geniohyoideus with three binary characters. We combined two of his characters, "Geniohyoids fused into single muscle" and "Geniohyoids unfused anteriorly," into a single character state because Sprague (1943) found that these muscles are never fused near their origins. Sprague's (1943) taxonomic descriptions disagree with the distributional account of this character appearing in his discussion section. We have used the description given in the discussion section (Sprague, 1943: 463) to score this character. Griffiths (1982) did not mention fusion of m. geniohyoideus with its counterpart and consequently this character was not used by Gimenez et al. (1996).

**Character 100:** *M. styloglossus inserts on lateral surface of tongue along much of its length (0); or inserts on posterolateral "corner" of tongue (1).* M. styloglossus inserts on the lateral surface of the tongue along much of its length in *Desmodus*, phyllostom-

ines, *Brachyphylla*, phyllonycterines, lonchophyllines, *Carollia*, and stenodermatines (Griffiths, 1982; including *Sturnira*; Sprague, 1943; fig. 31C–D). In contrast, m. styloglossus inserts on the posterolateral "corner" of the tongue in glossophagines (Griffiths, 1982; fig. 31A–B). M. styloglossus inserts on the lateral surface of the tongue along much of its length in *Pteronotus* and *Noctilio* (Sprague, 1943), suggesting that this is the primitive condition for phyllostomids.

Our scoring of this character is identical to that of Griffiths (1982: character 7) and Gimenez et al. (1996: character 22), although Griffiths (1982) described the derived condition (our state 1) as "posterior shift of styloglossus insertion."

**Character 101:** *M. genioglossus inserts into ventral surface of tongue along more than half of its length (0); or inserts into posterior half to third of ventral surface of tongue (1); or inserts into posterior quarter of ventral surface of tongue (2).* M. genioglossus inserts into the ventral surface of the tongue along much of its length in *Desmodus*, phyllostomines, *Brachyphylla*, phyllonycterines, *Carollia*, and stenodermatines (Griffiths, 1982). In contrast, this muscle inserts into the posterior half to third of the ventral surface of tongue in lonchophyllines (Griffiths, 1982). In glossophagines, this muscle inserts into the posterior quarter of the ventral surface of tongue (Griffiths, 1982). Although Sprague (1943) provided a description of the insertion of m. genioglossus in the bats he surveyed, the description is not detailed enough to permit us to score *Pteronotus*, *Noctilio*, and *Sturnira*. Because we cannot score our outgroups, the primitive state for phyllostomids cannot be reconstructed a priori.

In Griffiths' (1982: character 8) matrix the derived condition of this feature was "posterior shift of genioglossus insertion" (present/absent). Griffiths' (1982) descriptions, however, suggest that multiple conditions exist. Therefore, we followed Gimenez et al. (1996: character 23) in recognizing the three character states defined above.

**Character 102:** *M. stylohyoideus absent (0); or present (1); or sometimes present; polymorphic within species (2).* M. stylohyoideus is consistently absent in *Desmodus*,

phyllostomines, *Brachyphylla*, most glosso-phagines (e.g., *Anoura*, *Choeronycteris*), lon-chophyllines, and stenodermatines (including *Sturnira*; Sprague, 1943; Wille, 1954; Griffiths, 1982). In contrast, m. stylohyoideus is present in phyllonycterines, some glosso-phagines (e.g., *Glossophaga*, *Lichonycteris*), and *Carollia* (Griffiths, 1982). This muscle is variably present within species of *Leptonycteris* (Griffiths, 1982). M. stylohyoideus is present, but reduced and fused to m. sty-lopharyngeus, in *Pteronotus parnellii* (Griffiths, 1983b). This muscle is absent in *Noctilio* (Sprague, 1943). Thus, the primitive condition for phyllostomids cannot be established a priori.

Although our character states 0 and 1 are identical to those used by Griffiths (1982: character 9) and Gimenez et al. (1996: character 24), we have erected a separate character state to deal with the variation found within the species of *Leptonycteris* that Griffiths (1982) examined. Both Griffiths (1982) and Gimenez et al. (1996) scored *Leptonycteris* as 0/1, which is not an appropriate coding for situations of within-species variation (see Simmons, 1993).

**Character 103:** *Anterolateral slip of m. sphincter colli profundus present (0); or absent (1).* In bats, m. sphincter colli profundus originates from the fascia of the mylohyoid region, forms a variable number of slips, and inserts on the inner surface of the skin of the cervical region (Sprague, 1943; Griffiths, 1982). An anterolateral slip is present in *Desmodus*, phyllostomines, *Brachyphylla*, lon-chophyllines, *Carollia*, and stenodermatines (Griffiths, 1982; including *Sturnira*; Sprague, 1943). In contrast, this slip is absent in phyl-lonycterines and glossophagines (Griffiths, 1982). Among the outgroups, an anterolateral slip is absent in *Pteronotus*, but present in *Noctilio* (Sprague, 1943), so the primitive condition for phyllostomids cannot be determined a priori.

Griffiths (1982: character 10) treated the condition of m. sphincter colli profundus as one character, "reduction of m. sphincter colli profundus" (present/absent). However, this arrangement did not accommodate the variation Griffiths (1982) described in this muscle (see discussion in Smith and Hood, 1984). Gimenez et al. (1996: character 25)

attempted to score the variation described by Griffiths (1982) using four character states: "(0) well-developed, with two (or three) slips; (1) reduced to a few fibers (originated from the fascia of posterior milohyoid [sic] region); (2) almost complete reduction (eventually vestigial); (3) completely absent." We have chosen to divide the character some-what differently and treat presence or ab-sence of anterolateral and lateral slips in m. sphincter colli profundus as two characters (characters 103 and 104).

**Character 104:** *Lateral slip of m. sphincter colli profundus present (0); or absent (1).* The lateral slip of m. sphincter colli profundus is present in phyllostomines, *Brachyphylla*, many glossophagines (e.g., *Glossophaga*, *Leptonycteris*), lonchophyllines *Carollia*, and stenodermatines (Griffiths, 1982), except *Sturnira* where this slip is absent (Sprague, 1943). This slip is also absent in *Desmodus*, phyllonycterines, *Choeroniscus*, and *Choeronycteris* (Griffiths, 1982). These slips are absent in *Pteronotus* and *Noctilio* (Sprague, 1943), suggesting that this condi-tion is primitive for phyllostomids.

**Character 105:** *Lateral slip of m. sphincter colli profundus passes laterally (0); or passes anterolaterally to insert on skin of cervical region (1).* The lateral slip of m. sphincter colli profundus passes laterally from its origin in the fascia of the mylohyoid region to insert on the inner surface of the skin of the cervical region in phyllostomines, *Brachyphylla*, glossophagines that have this slip, lonchophyllines, and *Carollia* (Griffiths, 1982). In contrast, the lateral slip of m. sphincter colli profundus passes anteriorly and laterally in stenodermatines that have this slip (Griffiths, 1982). The primitive con-dition of this character for phyllostomids could not be established a priori because both *Pteronotus* and *Noctilio* lack the lateral slip of this muscle (Sprague, 1943). We scored taxa lacking the lateral slip of m. sphincter colli profundus (state 1 of character 104) "−" for this character.

This feature was not treated in Griffiths' (1982) or Gimenez et al.'s (1996) character analyses because stenodermatines, the only taxa with state 1, were not the focus of their studies.

**Character 106:** *M. cricopharyngeus con-*

sists of a single large slip (0), or two slips (1), or three slips (2), or more than three slips (3). M. cricopharyngeus consists of a single large slip in *Desmodus*. In *Brachyphylla*, phyllonycterines, and lonchophyllines, this muscle is composed of two distinct slips or bellies (Griffiths, 1982). M. cricopharyngeus consists of three slips in phyllostomines, *Carollia*, and stenodermatines (including *Sturnira*; Sprague, 1943; Griffiths, 1982). In glossophagines, the muscle consists of ''several slips'' (although Griffiths [1982: 18] is not clear, we interpret this as more than three slips). A single undivided slip is present in *Pteronotus* (Griffiths, 1983b) and *Noctilio* (Sprague, 1943), suggesting that this condition is primitive for phyllostomids.

Griffiths (1982: character 11) scored the morphology of m. cricopharyngeus as ''cricopharyngeus reduced to two bellies'' (present/absent), apparently assuming three slips was the primitive condition. Gimenez et al. (1996: character 26) recognized three states of this character that are equivalent to our states 1, 2, and 3. Although Griffiths (1982: 18) noted that this muscle consists of ''several slips'' in glossophagines (s.s.), he did not give the number of slips present. The single-slip condition seen in *Desmodus* and the outgroups was not included in Griffiths' (1982) or Gimenez et al.'s (1996) character analysis.

## TONGUE

Characters described in this section are based largely on features originally noted by Griffiths (1982; character numbers from his table 1), Gimenez (1993), and Gimenez et al. (1996; character numbers from their table 1). Taxa examined in these studies are listed in table 4. We have introduced several new characters, modified previous descriptions, and scored tongue morphology for all taxa included in this study except *Scleronycteris* and *Musonycteris*, for which specimens were unavailable. Nomenclature for papillae and other tongue structures follows Sonntag (1920), except where noted.

**Character 107:** *Medial circumvallate papillae present (0); or absent (1).* In most phyllostomids, two medial circumvallate papillae (MVPs) are present proximally on the dorsum of the tongue, one on either side of the midline (figs. 33A, 34A–C). In contrast, the MVPs are absent in desmodontines and some glossophagines (e.g., *Anoura*, *Choeroniscus*; fig. 32C). Mormoopids and *Noctilio* have two MVPs on the dorsum of the tongue (fig. 32A–B), suggesting that this is the primitive condition for phyllostomids.

Griffiths (1982: character 15) first used this character in a cladistic analysis, erecting states equivalent to ours. However, Griffiths (1982) did not score lonchophyllines with any state for this character (''see text'' appeared in his matrix instead of ''+'' or 0) to indicate that lonchophyllines lack both medial and lateral circumvallate papillae (see below). Gimenez (1993: characters 3.3.2.1, 3.3.5.1) and Gimenez et al. (1996: character 4) also used this character. Gimenez (1993) described the derived condition (absence of MVPs, her state 1) as MVPs vestigial or absent, whereas Gimenez et al. (1996) erected states identical to ours.

Griffiths (1982) reported the absence of MVPs not only in the taxa noted above, but also in *Lionycteris*, *Lonchophylla*, and *Platalina*. Griffiths and Criley (1989) also noted that *Lonchophylla* lacks all vallate papillae. In contrast, we observed MVPs in every specimen of *Lionycteris*, *Lonchophylla*, and *Platalina* that we examined (see appendix 1 for species and specimen numbers). Our results agree with the findings of Smith and Hood (1984), who reported the presence of these structures in *Lionycteris spurelli* and *Lonchophylla robusta*, and with those of Gimenez (1993) and Gimenez et al. (1996), who observed MVPs in *Lionycteris spurelli*, *Lonchophylla bokermanni*, *L. dekeyseri*, and *L. mordax*, although Gimenez (1993) had scored these papillae as ''vestigial or absent'' in *L. bokermanni*.

Griffiths (1982) reported that *Lichonycteris* has MVPs, whereas Gimenez (1993) and Gimenez et al. (1996) did not find MVPs in the specimens that they examined. Giminez (1993) coded *Lichonycteris* 0/1 to account for her observations and those of Griffiths (1982). We agree with Gimenez (1993) and Gimenez et al. (1996) that *Lichonycteris* lacks MVPs. Although Smith and Hood (1984) noted that *Centurio* lacks MVPs, the specimens that we examined all possess very small MVPs that are located at the proximal
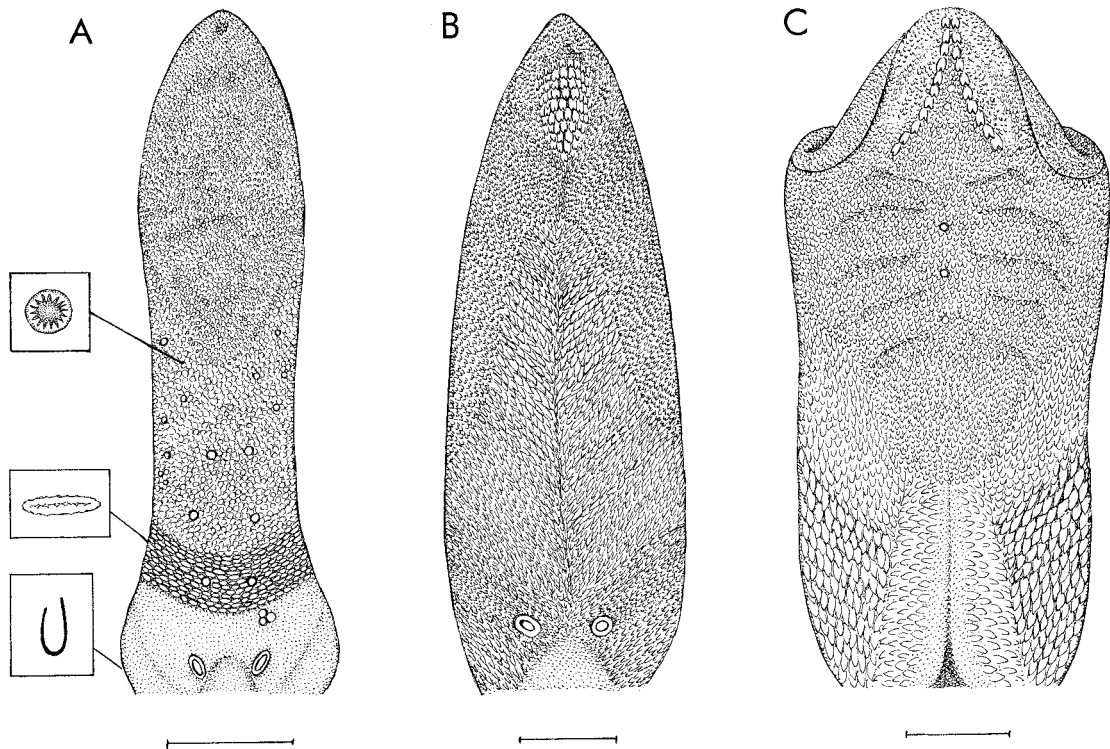
Fig. 32. Dorsal surface of the tongue in selected noctilionoids. **A.** *Pteronotus davyi* (AMNH 175276). Insets from top to bottom: basketlike papilla, basin-shaped medial posterior mechanical papilla, lateral circumvallate papilla. **B.** *Noctilio leporinus* (AMNH 175534) **C.** *Desmodus rotundus* (AMNH 210962). Scale bar = 2 mm.

extreme of the tongue. In addition, the papillary bodies of the MVPs are partly fused to the valla (see character 108), which makes observation very difficult and may account for the report of Smith and Hood (1984).

Gimenez (1993) and Gimenez et al. (1996) reported that MVPs were variably present in the specimens of *Lonchophylla thomasi* they examined (present in only three of the six specimens; Gimenez et al., 1996). We examined six specimens of *L. thomasi* and found MVPs present in all. Griffiths (1982: table 1) scored *Leptonycteris* as "variable" for this character, though in the text he noted that only one specimen of five *L. sanborni* (= *L. curasoae*) lacked one MVP. Our observations of *Leptonycteris curasoae* and *L. nivalis* agree with those of Park and Hall (1951), Greenbaum and Phillips (1974), Smith and Hood (1984), Gimenez (1993) and Gimenez et al. (1996), who reported that the MVPs were always present in *Leptonycteris*.

Based on our observations, we have chosen to score both *Leptonycteris* and *Lonchophylla* as having MVPs (state 0).

**Character 108:** *Papillary bodies of medial circumvallate papilla separate from valla, fossae complete (0); or papillary bodies fused anterolaterally and posteromedially to valla, fossae incomplete (1).* In most phyllostomids, the fossa of each MVP is complete and the papillary body is not fused to the vallum (fig. 35A). In contrast, in *Centurio* and *Sphaeronycteris* each MVP papillary body is fused with the vallum anterolaterally and posteromedially (fig. 35B). Consequently, the fossae are not circular furrows, but appear as paired slits on each side of the papillary body. In mormoopids and *Noctilio*, the MVP bodies are not fused to the valla and the fossae are complete, suggesting that this condition is primitive for phyllostomids. We scored the eight taxa lacking medial vallate
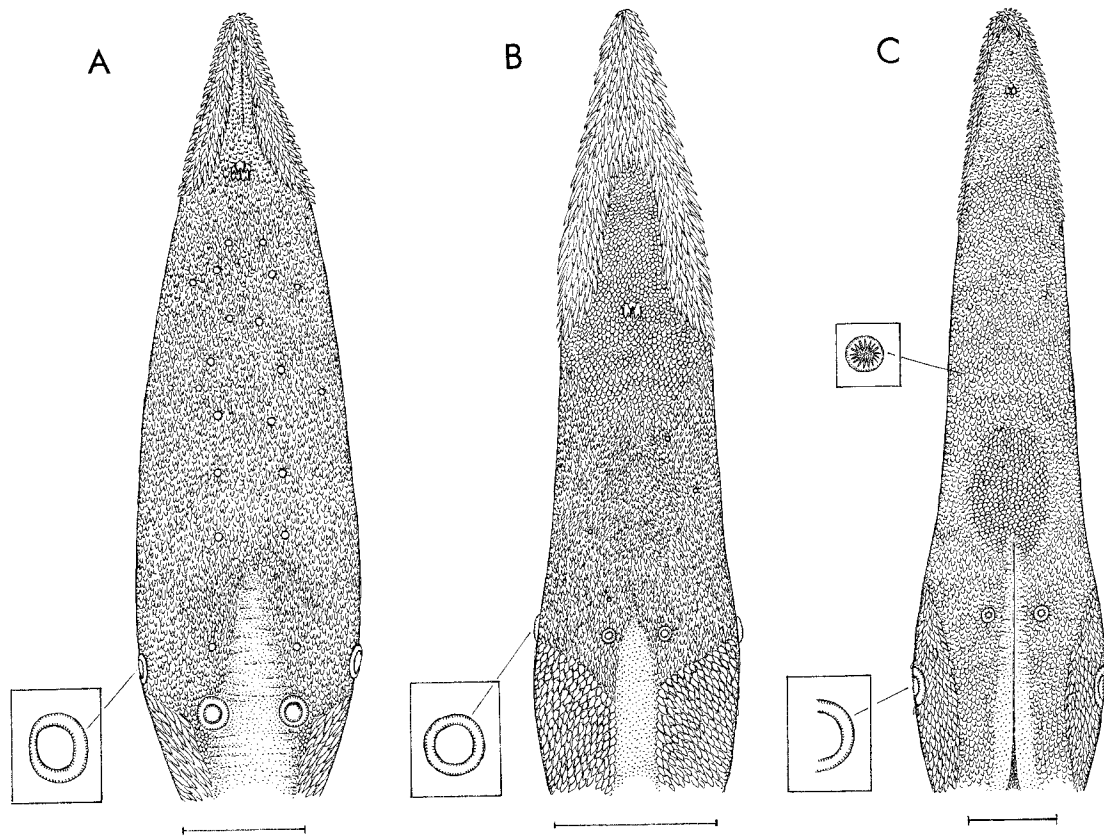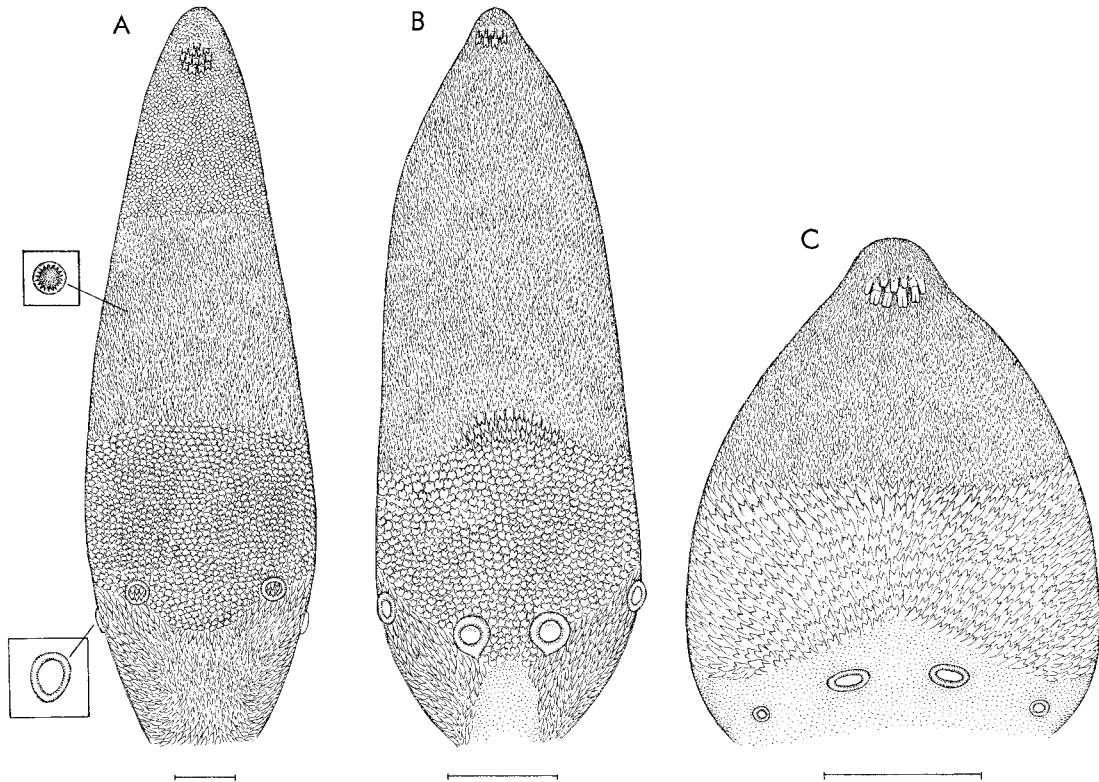
Fig. 33. Dorsal surface of the tongue in selected phyllostomids. Lowest inset is of a lateral circumvallate papilla. **A.** *Phyllonycteris poeyi* (AMNH 23762). **B.** *Glossophaga soricina* (AMNH 237911). *Lonchophylla thomasi* (AMNH 266107). Upper inset: basketlike papilla. Scale bar = 2 mm.

papillae (state 1 of character 107) ''−'' for this character.

Smith and Hood (1984) examined *Centurio*, but incorrectly reported that the MVPs were absent in this genus (see character 107). No previous study of tongue morphology has included *Sphaeronycteris*. Consequently, this character has not been used in previous cladistic analyses.

**Character 109:** *Lateral circumvallate papillae present (0); or absent (1).* Most phyllostomids have a pair of circumvallate papillae on the proximal part of the lateral surfaces of the tongue (figs. 33A–C, 34A–C). Desmodontines, *Brachyphylla*, and *Centurio* lack these lateral circumvallate papillae (LVPs; fig. 32C). LVPs are present in mormoopids, but absent in *Noctilio* (fig. 32A–B). Thus, the primitive condition for phyllostomids cannot be reconstructed a priori.

Griffiths (1982) did not use presence of LVPs as a character, but did note the loss of all circumvallate papillae in lonchophyllines in his matrix (see discussion under character 108). Gimenez (1993: characters 3.3.2.2, 3.3.5.3) and Gimenez et al. (1996: character 6) used presence of LVPs as a character and defined states identical to ours.

Griffiths (1982) indicated that lonchophyllines, *Brachyphylla*, and desmodontines lacked LVPs, and Griffiths and Criley (1989) noted that *Lonchophylla* lacks all vallate papillae. However, our observations agree with those of Smith and Hood (1984), Gimenez (1993), and Gimenez et al. (1996) who found that LVPs are present in all *Lionycteris* and *Lonchophylla* specimens they examined. Because specimens of *Lonchophylla robusta* and *Platalina* were not available for study, Giminez (1993) accepted Griffiths' (1982)

Fig. 34.    Dorsal surface of the tongue in selected phyllostomids. Lowest inset is of a lateral circumvallate papilla. **A.** Phyllostomus hastatus (AMNH 233176). Upper inset: basketlike papilla. **B.** Uroderma bilobatum (AMNH 171294). **C.** Ametrida centurio (AMNH 247645). Scale bar = 2 mm.

conclusion that these papillae appeared to be absent in these taxa. Our observations of LVPs in all specimens of *Lionycteris*, *Lonchophylla*, and *Platalina* that we examined (see appendix 1 for species and specimen numbers) confirm that these papillae are present in lonchophyllines. Unlike Greenbaum and Phillips (1974), who reported the absence of one of the two LVPs in one specimen each of *Leptonycteris curasoae* and *L. nivalis*, we did not find missing LVPs in any representative of *Leptonycteris* we examined.
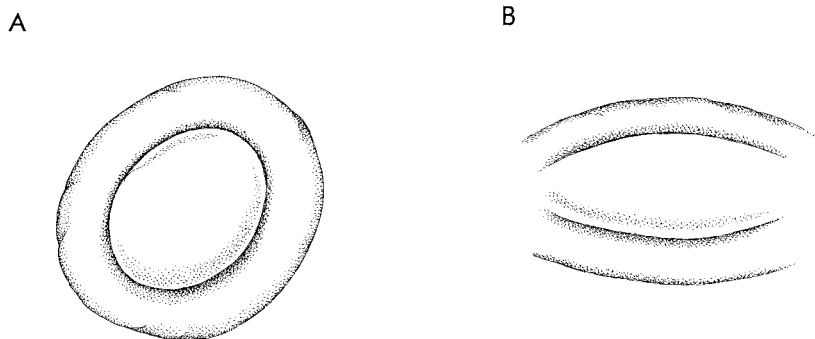


Fig. 35.    Close-up dorsal views of a medial circumvallate papilla in **A.** *Noctilio leporinus* (AMNH 243905) and **B.** *Centurio senex* (AMNH 99645).

Park and Hall (1951) reported the presence of only two vallate papillae in most taxa they examined (including *Leptonycteris*); however, as Greenbaum and Phillips (1974) noted, it appears these authors simply overlooked the lateral vallate papillae, reporting only on the presence of medial vallate papillae. Finally, Gimenez et al. (1996) indicated that all stenodermatines possess lateral vallate papillae. This study, however, did not include *Centurio*, which lacks these papillae (Smith and Hood, 1984; this study).

**Character 110:** *Lateral circumvallate papillae located on lateral surface of tongue (0); or in dorsolateral position, at border between lateral and dorsal surfaces of tongue (1); or on dorsal surface of tongue (2).* In most phyllostomids, LVPs are located on the lateral surface of the tongue (figs. 33A–C, 34A). However, in some stenodermatines (e.g., *Uroderma*, *Vampyrodes*), the LVPs are located at the steeply curved ''border'' between the dorsal and lateral surfaces of the tongue (fig. 34B). In other stenodermatines (e.g., *Ametrida*, *Artibeus*), the LVPs are located on the dorsal surface of the tongue (fig. 34C). In some of these taxa (e.g., *Pygoderma*), the LVPs are almost directly adjacent to the MVPs. Whereas mormoopids have LVPs that are located on the lateral surface of the tongue (fig. 32A), LVPs are absent in *Noctilio*; therefore, the primitive condition for phyllostomids appears to be a lateral position for the LVPs. We scored taxa lacking LVPs (state 1 of character 109) ''−'' for this character.

Gimenez (1993: character 3.3.4.2) first used the position of the LVPs as a character in cladistic analysis, and we follow her state definitions. Smith and Hood (1984: 450) characterized the LVPs as ''dorsal'' in all stenodermatines after examining *Ametrida*, *Artibeus*, *Centurio* (which lacks LVPs), and *Sturnira*. Smith and Hood's (1984) assessment of LVP position in *Ametrida* and *Artibeus* appears to be supported by our observations; however, we agree with Gimenez (1993) that *Sturnira* has dorsolateral LVPs.

Gimenez (1993) characterized the LVPs as being located laterally in *Vampyressa bidens* and *V. pusilla*. Our observations of LVPs in these species and *V. nymphaea* indicate that only *V. pusilla* has laterally located LVPs. In

the other *Vampyressa* species that we examined, these papillae are located in a dorsolateral position. In *Artibeus*, *Dermanura*, and *Koopmania*, Gimenez (1993) described the LVPs as being dorsolateral. In contrast, we found that the LVPs were located on the dorsum of the tongue all representatives of these taxa that we examined (see appendix 1 for specimens examined).

**Character 111:** *Pharyngeal region of tongue completely covered with papillae (0); or covered laterally with papillae and medially bare (1); or wholly unpapillated (2).* The pharyngeal region of the tongue lies proximal to the circumvallate papillae (Sonntag, 1925). In taxa lacking circumvallate papillae (e.g., desmodontines), this region apparently lacks fungiform papillae (Sonntag, 1925), providing a means of identification. Most phyllostomids have fleshy mechanical papillae covering the lateral sections of the pharyngeal region of the tongue (figs. 32C, 33A–C, 34B). In these taxa, a smooth, unpapillated bare patch is present medially, often extending distally between the MVPs. In some phyllostomines (e.g., *Chrotopterus*, *Phyllostomus*) and some stenodermatines (e.g., *Mesophylla*, *Vampyrodes*) the tongue lacks this medial bare patch and has a carpet of mechanical papillae over the entire pharyngeal region (fig. 34A). In contrast, many stenodermatines (e.g., *Ametrida*) have an entirely bare pharyngeal region (fig. 34C). One individual of *Pygoderma* (AMNH 248334) has a single medial line of papillae bisecting the otherwise bare pharyngeal region, whereas all other specimens we examined have a completely bare pharyngeal region. One individual of *Phyllops* (AMNH 176190) has approximately 14 papillae present laterally on both sides in the pharyngeal region, whereas all other specimens that we examined do not have any papillae present in the pharyngeal region. Similarly, a single specimen (USNM 522707) of *Stenoderma* has several papillae present laterally on both sides of the pharyngeal region, whereas all other specimens do not. We interpret these conditions as anomalies and score these genera with state 2 in the matrix. Mormoopids have a pharyngeal region that is bare (fig. 32A), whereas *Noctilio* has fleshy mechanical papillae surrounding a central bare patch

(fig. 32B). The primitive state for phyllostomids cannot be reconstructed a priori.

Gimenez (1993: characters 3.3.2.3; 3.3.3.3; 3.3.4.7–8) first used the location of papillae in the pharyngeal region in a cladistic analysis. One character (Gimenez, 1993: character 3.3.4.7) accounted for presence or absence of the pharyngeal papillae, and appeared only in the analysis of Stenodermatini genera (see Historical Background for details of Gimenez's [1993] analyses). The other character (Gimenez, 1993: character 3.3.2.3, 3.3.3.3, 3.3.4.8) described the two patterns of papillation (pharyngeal region completely covered or covered only laterally), and appeared in most analyses, except the analysis of Glossophagini genera. We have chosen to combine the two characters recognized by Gimenez (1993) to avoid the problems of missing data often associated with hierarchical characters.

In her analyses, Gimenez (1993) scored those Stenodermatini genera with bare pharyngeal regions (character 3.3.4.7: pharyngeal papillae absent) as having the laterally papillated state in the second character (character 3.3.4.8), rather than ''−'' as appropriate for a hierarchical character. In Gimenez's (1993) analysis of desmodontines, basal phyllostomines, and the tribes Phyllostomini, Glossophagini, and Stenodermatini, she scored Phyllostomini and Stenodermatini as having only the laterally papillated condition. In fact, these taxa are polymorphic, with both laterally papillated and totally papillated conditions occurring in Phyllostomini and Stenodermatini genera. Although mormoopids have a completely bare pharyngeal region, Gimenez's (1993) character did not include this condition as a state, and she scored mormoopids as having a medially bare pharyngeal region.

Gimenez (1993) described the pharyngeal region of *Phylloderma* as being fully papillated. We observed a smooth medial pharyngeal region laterally flanked by fleshy, filiform papillae in all specimens we examined (see appendix 1 for specimens examined). In *Mesophylla* and *Vampyrodes*, Gimenez (1993) described the pharyngeal region as being laterally papillated and medially bare. We observed a completely papillated pharyngeal region in both genera.

**Character 112:** *Lingual sulci absent (0); or lateral lingual sulci present (1); or ventral lingual sulci present (2).* Lingual sulci are present in *Desmodus*, *Diaemus*, and lonchophyllines, but are absent in all other phyllostomids. In *Desmodus* and *Diaemus*, the sulci are located on the ventral aspect of the tongue and run anteriorly from the frenulum (a median vertical fold present on the floor of the mouth) along the distal half of the tongue (fig. 36C). The sulci do not meet at the tongue tip. In lonchophyllines, sulci are found on the lateral surface of the tongue, beginning just distal to the LVPs and coursing to the tongue tip, where the right and left sulci meet (fig. 36D). The sulci in lonchophyllines appear to be relatively deeper than those of *Desmodus* and *Diaemus* and are bordered by a fringe of hairlike papillae (see character 113), which is absent in the desmodontine taxa. Mormoopids and *Noctilio* lack lingual sulci, suggesting that this is the primitive condition for phyllostomids.

Griffiths (1982: character 12) defined a character for presence or absence of a papilla-lined lingual sulcus. Our character states 0 and 1 are roughly equivalent to those of Griffiths (1982), although we have added an extra state to include the variation introduced by the desmodontines, which Griffiths (1982) described but did not consider in his analysis. Unlike Griffiths (1982), we consider the hairlike papillae lining the sulcus in lonchophyllines in the context of a different character (see character 113). Wille (1954) reported the presence of a groove along the lateral margins of half the length of the tongue in *Leptonycteris nivalis*. This groove does not appear to be present in *Leptonycteris*, as was previously noted by Park and Hall (1951), Winklemann (1971), and Greenbaum and Phillips (1974).

Griffiths and Criley (1989) found that the sulci of *Desmodus* and *Diaemus* are ventral to the lingual nerve and the transverse muscle mass (fig. 36A), but in lonchophyllines the sulci are dorsal to these structures (fig. 36B). On this basis, these authors suggested that the sulci in desmodontines and lonchophyllines are not homologous. Gimenez (1993: characters 3.3.2.8, 3.3.5.14) erected two different lingual sulcus characters, one for the presence of a ventral sulcus, the other
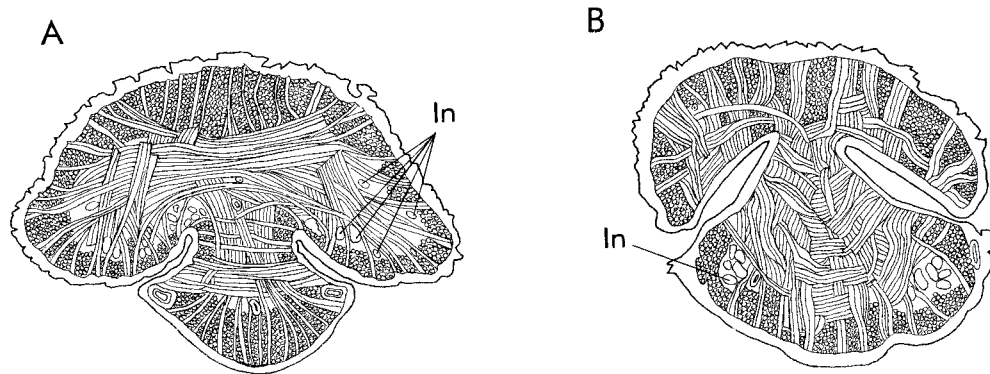
Fig. 36. Cross sections of the tongues of **A.** *Desmodus rotundus* and **B.** *Lonchophylla robusta* illustrating differences between the lingual sulci in these species (redrawn from Griffiths and Criley, 1989: fig. 2). Note that the sulci of *Desmodus* are ventral to the lingual nerve (ln), but in *Lonchophylla* the sulci are dorsal to this structure.

for the presence of a lateral sulcus. Her character 3.3.2.8 is equivalent to our state 2 as a binary (present/absent) character. Gimenez's (1993) second character (3.3.5.14), "presence of a lateral lingual sulcus bordered by filiform papillae," is equivalent to our character state 1. Gimenez et al. (1996: character 2) defined and scored a character for the presence of a lateral lingual sulcus, following Griffiths and Criley's (1989) and Gimenez's (1993) assessment that the lateral and ventral lingual sulci are not homologous. We prefer to make no such a priori assessments and included both types of sulci as states in a single character to allow all possible transformations.

**Character 113:** *Brush of hairlike papillae around the distal margin of tongue absent (0); or present (1).* Long, thin, filiform papillae, known as "hairlike" papillae (Park and Hall, 1951), are present laterally on the distal part of the tongue in phyllonycterines, glossophagines, and lonchophyllines (fig. 33A–C). The hairlike papillae form a brushlike tongue tip in these taxa. Hairlike papillae are absent in all other phyllostomids (figs. 32C, 34A–C). Hairlike papillae are also absent in mormoopids and *Noctilio* (fig. 32A–B), suggesting that absence of these papillae is the primitive condition for phyllostomids.

Griffiths (1982: characters 12, 14) defined two binary (present/absent) characters based on hairlike papilla morphology and distribution: "groove in tongue lined with hairlike

papillae," and "brush tip formed by hairlike papillae." He coded phyllonycterines and glossophagines "absent" for the former and "present" for the latter, whereas the reverse was true for lonchophyllines. Smith and Hood (1984: 448–449) objected to these characters, which appeared to score presence of "*Glossophaga*-type" and "lonchophylline-type" tongues, obscuring the potential homology of the hairlike papillae, which are not found on the tongues of other phyllostomids.

Gimenez (1993: character 3.3.5.11) used a single unordered multistate character with three states (absent, 0; present but short and few in number, 1; present and abundant, 2) to describe variation of hairlike papillae. Gimenez et al. (1996: character 14) retained states 0 and 1 (Gimenez, 1993), but added two new states: brushlike tip present, with abundant hairlike papillae 2, and brushlike tip extremely well developed, with abundant and very long hairlike papillae 3 (see character 115). Gimenez et al. (1996) ordered the transformations in this character (0 ↔ 1 ↔ 2 ↔ 3). In addition to this character, Gimenez et al. (1996: character 3) included a separate character describing the line of filiform papillae that runs along the lateral lingual sulcus in lonchophyllines.

We prefer to recognize the presence of hairlike papillae, derived relative to the outgroups, as a single state, with additional hierarchically dependent characters (characters
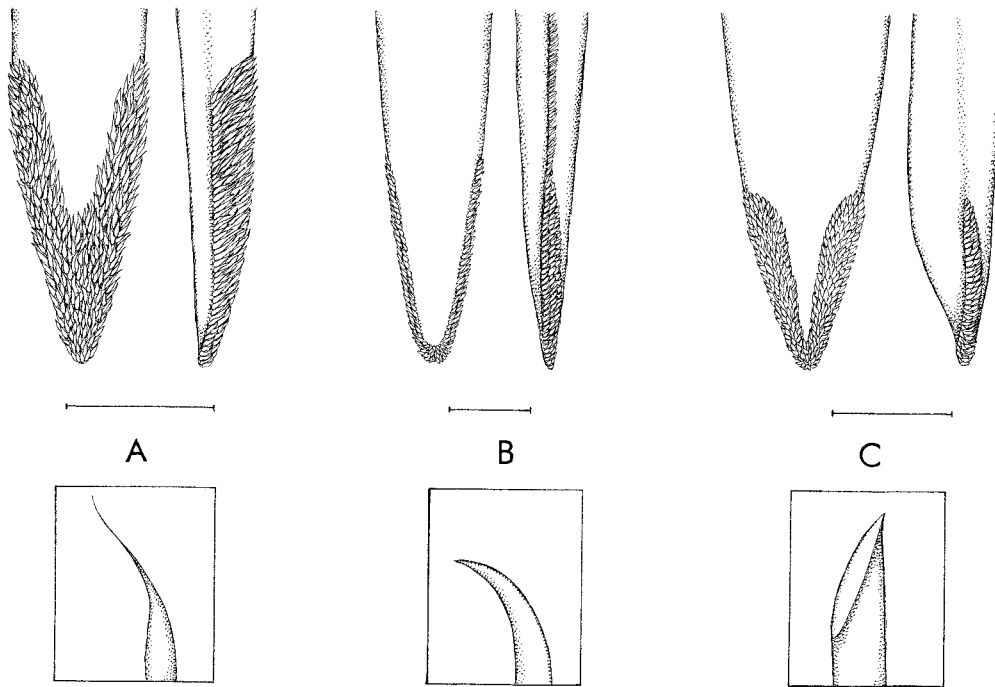
Fig. 37.   Dorsal (left) and lateral (right) views of the tongues of representative species with hairlike papillae. Insets feature close-ups of individual hairlike papillae. **A.** *Glossophaga soricina* (AMNH 237911). **B.** *Lonchophylla thomasi* (AMNH 267452). **C.** *Phyllonycteris poeyi* (AMNH 236698). Scale bar = 2 mm.

114 and 115) to accommodate variation in the distribution and shape of the papillae. This approach best reflects our views of potential homologies.

**Character 114:** *Hairlike papillae confined to lateral margin of distal third of tongue, with a single line of papillae that extends roughly to LVPs (0); or hairlike papillae distributed around lateral margin and dorsum of distal third of tongue, not arranged in a single line (1).* The distribution of hairlike papillae differs substantially among taxa in which they are present. In lonchophyllines, the papillae are restricted to the distal part of the lateral surface of the tongue, with a single line of hairlike papillae running just ventral to the lingual sulci, extending posteriorly roughly to the LVPs (fig. 37B). These single lines of papillae are not developed in phyllonycterines and glossophagines (fig. 37A, C). In these taxa, the papillae are found on the lateral and dorsal surfaces of the tongue, and a narrow channel (''median trough,'' or ''anterior groove'' of Park and Hall, 1951)

that lacks hairlike papillae runs down the midline of the dorsum of the tongue. Mormoopids and *Noctilio* lack hairlike papillae, so the primitive state for phyllostomids cannot be assessed a priori. We scored taxa that lack hairlike papillae (state 0 of character 113) ''−'' for this character.

As noted above, Griffiths (1982: characters 12, 14) was the first to define characters based on distribution of hairlike papillae. Gimenez's (1993: character 3.3.5.11) character states 1 (present but short and few in number) and 2 (present, long and abundant) are roughly equivalent to our states 0 and 1, respectively and our scoring is identical to hers. Gimenez et al.'s (1996: character 14) character incorporated aspects of both distribution pattern and shape of individual papilla, which we have chosen to treat as two separate characters (this character and character 115).

**Character 115:** *Hairlike papillae fleshy and conical (0); or fleshy and conical with filamentous tips (1); or cylindrical with el-*

*lipse-shaped distal end (2).* Phyllonycterines, glossaphagines, and lonchophyllines are each characterized by a different shape of hairlike papilla. The individual hairlike papillae of lonchophyllines are short, fleshy, and conical (fig. 37B, inset). In glossaphagines, the papillae are longer and thinner than in lonchophyllines, and have filamentous tips (see scanning electron micrographs in Vaughan, 1986; fig. 37A, inset). These papillae most closely resemble hairs. Phyllonycterines have cylindrical hairlike papillae (fig. 37C, inset). The distal ends of these papillae appear as though they have been sliced obliquely, producing ellipsoid ends. Mormoopids and *Noctilio* lack this papilla type; thus the primitive state for phyllostomids cannot be established a priori. We scored taxa without hairlike papillae (state 0 of character 113) ''−'' for this character.

Although previous workers have not used shape of the hairlike papillae as a separate character, Gimenez et al. (1996: character 14) incorporated papilla presence, morphology, and distribution into a single character. Gimenez et al. (1996) recognized three conditions, roughly corresponding to our character states (see character 113).

**Character 116:** *All or most medial-posterior mechanical papillae inclined toward the pharyngeal region of the tongue (0); or all oriented toward tongue tip (1); or all oriented toward midline of tongue (2); or papillae not inclined (3).* Gimenez (1993) defined the medial-posterior mechanical papillae as those mechanical papillae that lie between the MVPs and the anterior mechanical papilla. In taxa that lack MVPs (e.g., desmodontines), we define this region as roughly the middle third of the tongue. All or most of the medial-posterior mechanical papillae are inclined toward the pharyngeal region of the tongue in most phyllostomids (figs. 32C, 33A–C, 34A). In contrast, all of the medial-posterior mechanical papillae are inclined toward the tip of the tongue in all stenodermatines with the exception of *Sturnira* (fig. 34B–C). In *Mormoops* these papillae are directed pharyngeally. In *Pteronotus*, the medial-posterior mechanical papillae are unlike the fleshy, filiform papillae in other noctilionoids (fig. 32A). Instead, these papillae are basin-shaped and directed dorsally (i.e., they

are not inclined). In *Noctilio*, the posterior-most medial-posterior mechanical papillae are on ridges that curve anteriorly towards the lateral margins of the tongue (fig. 32B). The ridges disappear as the papillae on them become more sharply pointed (roughly one third of the area of the medial-posterior mechanical papillae is ridged). The individual medial-posterior mechanical papillae are directed toward the midline of the tongue. Thus, the primitive condition for phyllostomids cannot be reconstructed a priori.

Park and Hall (1951) noted that the medial-posterior mechanical papillae incline anteriorly in *Artibeus* among the phyllostomids they studied, but Gimenez (1993: character 3.3.4.11) was the first to use this information in a cladistic analysis. Our character states and scoring are equivalent to hers.

**Character 117:** *Small patch of anteriorly directed medial-posterior mechanical papillae always absent, all papillae oriented toward pharyngeal region (0); or medial patch present in some individuals; polymorphic within species (1); or medial patch always present (2).* Among those phyllostomids in which the medial-posterior mechanical papillae are principally directed toward the pharyngeal region (state 0 of character 116), a small patch of papillae near the midline of tongue may be oriented toward the tip of the tongue. This patch is always present in *Micronycteris sylvestris*, *Lionycteris*, and *Platalina*, and is sometimes present in *Lonchophylla* (e.g., *Lonchophylla thomasi* AMNH 266107; fig. 33C). In *Mormoops*, the small patch of anteriorly directed papillae is not present. The medial-posterior mechanical papillae are not directed toward the pharyngeal region in *Noctilio* and *Pteronotus*, and we scored these genera ''−'' for this character. Thus the primitive state for phyllostomids appears to be the absence of the anteriorly directed patch of papillae. We scored taxa in which the medial-posterior mechanical papillae are not principally directed toward the pharyngeal region (states ''1,'' ''2,'' or ''3'' for character 116) ''−'' for this character.

Gimenez (1993: characters 3.3.5.9) first used this feature in a cladistic analysis, and our character states are equivalent to hers. Gimenez (1993) left *Lonchophylla* unscored because the medial-posterior mechanical pa-

pillae were too small and rudimentary to permit confident observation. Gimenez et al. (1996: 49) indicated that a patch of distally directed papillae may be seen not only in *Lionycteris*, but in ''some of the best preserved tongues of *Lonchophylla* species.'' This description corroborates our observation of such a patch in *Lonchophylla thomasi*.

**Character 118:** *Long-tipped, bifid anterior mechanical papillae absent (0); or present at border between anterior mechanical papillae and medial-posterior mechanical papillae (1).* In most phyllostomids, the small, keratinized anterior mechanical papillae and the larger, fleshy medial-posterior mechanical papillae meet near the middle of the tongue (figs. 32C, 33A–C, 34A, C). No other papilla type is present at this juncture. In contrast, this juncture is covered by a narrow, transverse band of keratinized bifid papillae in many stenodermatines (e.g., *Artibeus*, *Uroderma*; fig. 34B). The individual papillae are erect and directed toward the pharyngeal region. Each papilla tip has a long, thin, cornified filament. These papillae seem to be uniformly present in the species that possess them, although they may be absent in one poorly preserved specimen of *Koopmania* (AMNH 80340) of the five we examined. We interpret this possible condition as an aberration, and therefore score *Koopmania* as having long-tipped, bifid anterior mechanical papillae. Long-tipped, bifid anterior mechanical papillae are absent in mormoopids and *Noctilio* (fig. 32A–B), suggesting that this is the primitive condition for phyllostomids.

Gimenez (1993: character 3.3.4.10) first used presence of long-tipped, bifid anterior mechanical papillae as a character. Gimenez (1993) noted that in most taxa, these papillae are not well differentiated, and the junction between these papillae and the fleshy medial-posterior mechanical papillae is more or less transverse. In contrast, Gimenez (1993) indicated that *Mesophylla macconelli*, *Vampyressa bidens*, and *V. pusilla* have well differentiated long-tipped, bifid anterior mechanical papillae, and that the junction between the anterior and medial-posterior mechanical papillae is V-shaped with the medial-posterior papillae penetrating into the

anterior region medially. We found that the shape of the juncture between the anterior and medial-posterior mechanical papillae shows continuous variation from transverse or slightly V-shaped to strongly V-shaped. Accordingly, we have scored only the presence of these papillae, not the shape of the zone in which they occur. We also found well-differentiated, long-tipped, bifid anterior mechanical papillae in several additional taxa (see above).

**Character 119:** *Basketlike medial-posterior mechanical papillae absent (0); or present (1).* In most phyllostomids, the medial-posterior mechanical papillae are thick, fleshy, and have one or more rounded points. However, some of the medial-posterior mechanical papillae are what Park and Hall (1951) termed ''basketlike.'' Basketlike papillae occur in phyllostomines, *Brachyphylla*, some glossophagines (e.g., *Hylonycteris*, *Lichonycteris*), *Lionycteris*, *Lonchophylla*, carolliines, and *Sturnira* (figs. 33C, 34A). These papillae have central concavities and fleshy, cylindrical bases. The rim of each basketlike papilla is usually uneven, with the posterior part of the rim higher than the anterior. The entire rim, or just the posterior part, may be adorned with from one to more than 10 pointed projections, which appear to form a fringe along the edge of the rim. Basketlike papillae are present in *Pteronotus* and *Mormoops* (fig. 32A), but are absent in *Noctilio* (fig. 32B), making the state primitive for phyllostomids impossible to reconstruct a priori.

Gimenez (1993: characters 3.3.2.5, 3.3.3.5, 3.3.4.9, 3.3.5.7) erected four separate characters to describe morphology of the medial-posterior mechanical papillae in her analyses of various subsets of taxa. Gimenez et al. (1996: character 10) scored presence/absence of basketlike papillae, which they called ''posteromedian conical papillae,'' in a separate binary character. The multiple characters used by Gimenez (1993) included eight states describing the basketlike papillae and other papilla types, many of which are apparently autapomorphic. For example, Gimenez (1993: character 3.3.2.5) erected a state for the ''craterlike'' papillae of *Pteronotus*, which she considered to be autapomorphic, describing them as ''circular and

differentiated in the form of a crater . . . with a depression and fringed border.'' However, Gimenez (1993: character 3.3.3.5) reported similar papillae, which she described as ''circular, in the form of a crater . . . with a reduced fringe,'' in *Lonchorhina*, *Mimon crenulatum*, and unspecified species of *Tonatia*. Gimenez (1993) scored the ''craterlike'' papillae of *Lonchorhina* and *Tonatia* with a separate state from those of *Mimon crenulatum*, in which she called the ''craterlike'' papillae ''huge and irregular.'' We treat all ''basketlike'' papillae as potentially homologous, including Gimenez's (1993) ''craterlike'' papillae, because they are very similar in appearance (e.g., presence of fringe, and central concavity), and position on the tongue, despite some differences in relative size (e.g., as in *Mimon crenulatum*). Furthermore, because each tongue includes a variety of different basketlike types ranging from smooth to fringed, we chose to subsume all of the varieties in a single state rather than attempting to subdivide what appears to be a range of variation in the number of points in the fringe.

Despite the differences in scoring we noted above, we agree with virtually all of Gimenez's (1993) assessments, except her finding that basketlike papillae are present in *Glossophaga* and are present but reduced in size in *Platalina* (data apparently taken from Griffiths, 1982). We find that these papillae are absent in both genera. Gimenez et al. (1996) also scored basketlike papillae as present in *Glossophaga*, as well as *Monophyllus*, which was not mentioned in their text or list of specimens examined. Our observations indicate that *Monophyllus* lacks basketlike papillae. Giminez et al. (1996: 49) scored *Lichonycteris* ''1/v,'' indicating that this character is polymorphic in this taxon. The reason for this scoring given in their text was that *Lichonycteris* has other kinds of papillae in this region in addition to basketlike papillae, a factor that does not come into consideration in our version of this character. Gimenez et al. (1996) scored *Lonchophylla* as ''0/–,'' indicating that basketlike papillae are present in some species, but that the character is not applicable in others because these papillae are so reduced (e.g., *L. dekeyseri*). Unfortunately, we were unable to examine

*Lonchophylla dekeyseri*, but our observations of *L. robusta* and *L. thomasi* agree with Gimenez et al.'s (1996) reports of tiny basketlike papillae in *L. mordax* and *L. bokermanni*; thus, we decided to score *Lonchophylla* with state 1. In addition, we found that *Sturnira* has proximally fringed basketlike papillae similar to those of phyllostomines, rather than the anteriorly fringed, posteriorly smooth papillae described for this taxon by Gimenez (1993). Park and Hall (1951) first described the presence of basketlike papillae in *Carollia*, but did not observe these papillae in any other phyllostomid they examined (including *Macrotus*, *Leptonycteris*, *Glossophaga*, *Choeronycteris*, *Artibeus*, and *Desmodus*), whereas we found these papillae to be present in many of these taxa.

**Character 120:** *Cluster of horny papillae located near tip of tongue (0); or located significantly proximal to tongue tip (1).* In most phyllostomids, the horny papillae (sensu Park and Hall, 1951) are located near the tip of the tongue; less than 20% of tongue length is distal to the horny papillae (figs. 32C, 33A, C, 34 A–C). In contrast, the horny papillae are located in a more proximal position on the tongue in glossophagines (fig. 33B). In these taxa, more than 25% of the tongue length is distal to the horny papillae. In mormoopids and *Noctilio* the horny papillae are located near the tip of the tongue (fig. 32A–B), suggesting that this condition is primitive for phyllostomids.

Griffiths (1982) indicated that lonchophyllines lack horny papillae, but Smith and Hood (1984), Gimenez (1993), and Gimenez et al. (1996) noted the presence of distinct apical horny papillae in *Lionycteris* and *Lonchophylla*; our results confirm that they are indeed present in all lonchophyllines. Gimenez (1993: character 3.3.5.12) was the first to use this character, and our states are equivalent to hers. However, Gimenez (1993) considered the horny papillae of phyllonycterines to be located in a relatively proximal position from the lingual apex, and scored them with the same state as glossophagines. Gimenez et al. (1996: character 13) defined and scored the character the same way. In contrast, we found that the horny papillae are located near the tongue tip in phyllonycterines, whereas only glossophagines have the

more proximally located horny papillae. Rough quantification supports this scoring, as the largest gap in the distribution of values for percentage of tongue length distal to the horny papillae falls between the phyllonycterines and the glossophagines (data available on request).

**Character 121:** *Horny papillae arranged in lines or elliptical cluster (0); or large* V-*shaped cluster (1).* In most phyllostomids, the horny papillae form an elliptical cluster (which may be reduced to a few rows of horny papillae) near the tip of the tongue (figs. 33A–C, 34A–C). In contrast, desmodontines have a large V-shaped arrangement of horny papillae which follows the general outline of the tongue tip, spreading laterally and proximally from the near apical position to cover the tongue's width near the tip (31C). In mormoopids and *Noctilio*, the patch of horny papillae forms an elliptical cluster (fig. 32A–B), suggesting that this is the primitive condition for phyllostomids.

Gimenez (1993: character 3.3.2.7) first used the V-shaped distribution of horny papillae as a binary character. Griffiths (1982) and Gimenez et al. (1996) did not use this character, because desmodontines were not the focus of their studies. Although Park and Hall (1951), who described an elliptical rather than V-shaped cluster of horny papillae in desmodontines, and Vierhaus (1983) included desmodontine papillae under the description "horny papillae," Smith and Hood (1984) suggested that the keratinized papillae in desmodontines are not comparable to the horny papillae of other phyllostomids. Based on our observations, the only difference between these papillae in desmodontines and those in other phyllostomids is the pattern of distribution, not the actual structure of the individual papillae.

**Character 122:** *All horny papillae present in elliptical cluster equal in size (0); or some papillae markedly larger than others (1).* In most phyllostomids, there are one or two horny papillae that are larger than the others (fig. 38C–G). In contrast, *Lonchorhina*, *Macrophyllum*, *Vampyrum*, and *Rhinophylla* do not have one or two horny papillae that are larger than others; rather, all the horny papillae are roughly equal in size (fig. 38A–B). In mormoopids and *Noctilio*, the horny pa-

pillae are all equal in size, suggesting that this is the primitive condition for phyllostomids. We scored taxa that have a V-shaped cluster of papillae (state 1 of character 121) "−" for this character.

This character has no direct counterpart in previous phylogenetic analyses (see discussion under character 124).

**Character 123:** *Horny papillae all large (0); or all small (1).* Among taxa with horny papillae that are all roughly equal in size, *Vampyrum* and *Rhinophylla* have more than 15 very large papillae in the center of the cluster, which are surrounded by additional smaller horny papillae (fig. 38A). In contrast, *Lonchorhina* and *Macrophyllum* have an elliptical cluster composed of equally sized horny papillae, all of which are very small (fig. 38B). Mormoopids have very small horny papillae. In *Noctilio*, the papillae in the center of the cluster, more than 15 in number, are all equally large. Because of this distribution of character states, the primitive condition for phyllostomids cannot be assessed a priori. We scored taxa that have a V-shaped cluster of horny papillae (state 1 of character 121) or those with papillae of different sizes in the cluster (state 1 of character 122) "−" for this character.

This character has no direct counterpart in previous phylogenetic analyses (see discussion in character 124). To assess the relative sizes of these papillae, we drew representative tongues to the same scale for comparison.

**Character 124:** *Single large horny papilla present in center of elliptical cluster (0); or two large horny papillae present in center of elliptical cluster (1).* A single large papilla is present in the elliptical cluster of horny papillae in most phyllostomines (e.g., *Phyllostomus*, *Tonatia*), *Brachyphylla*, phyllonycterines, *Anoura*, lonchophyllines, *Carollia*, and several stenodermatines (e.g., *Artibeus*, *Sturnira*; fig. 38C–E). This large papilla is located approximately on the midsagittal line of the tongue. In *Micronycteris minuta*, *Mimon crenulatum*, most glossophagines (fig. 38F), and some stenodermatines (e.g., *Ardops*, *Pygoderma*; fig. 38G), there are two large papillae in the cluster, one on either side of the midline of the tongue. In mormoopids and *Noctilio*, all horny pa-
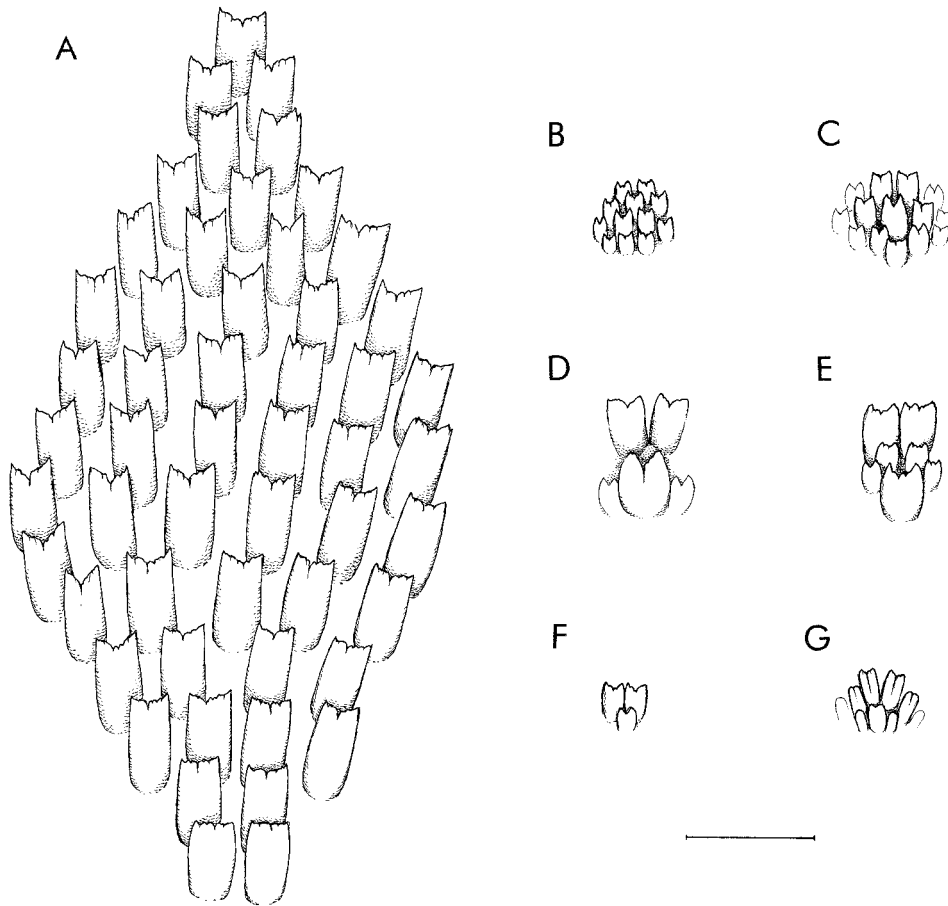
Fig. 38. Close-up dorsal views of the clusters of horny papillae, including central, anterior, flanking, and posterior, in selected phyllostomids. **A**. *Vampyrum spectrum* (AMNH 202292). **B**. *Lonchorhina aurita* (AMNH 149218). **C**. *Phyllostomus hastatus* (AMNH 233176). **D**. *Erophylla sezekorni* (AMNH 186977). **E**. *Platalina genovensium* (AMNH 257108). **F**. *Glossophaga soricina* (AMNH 214417). **G**. *Ametrida centurio* (AMNH 267375). Scale bar = 1 mm.

pillae are roughly equal in size. Consequently, these taxa are scored ''−'' for this character and the primitive state for phyllostomids cannot be determined a priori. We scored taxa that have a V-shaped cluster of horny papillae (state 1 of character 121) or those with papillae of uniform size in the cluster (state 0 of character 122) ''−'' for this character.

Griffiths (1982; character 16) was the first to use arrangement of the horny papillae in a cladistic analysis, although Smith and Hood (1984: 449) later dismissed this effort as a ''Rorschach analysis'' of horny papillae patterns. Our observations suggest that, as

Griffiths (1982) initially noted, these patterns are potentially phylogenetically informative. It is evident that the number and distribution of horny papillae are consistent within species/genera and vary among them. Other authors have also found consistent patterns in phyllostomid horny papillae. For example, Greenbaum and Phillips (1974) noted that all specimens of *Leptonycteris* they examined had two large central horny papillae. Park and Hall (1951: 65) reported that there were ''Generally . . . seven papillae in a group, two to four of which are always larger than the others and horny instead of fleshy.'' Although, we found that there was no differ-

ence in keratinization for the large and small horny papillae, Park and Hall's (1951) comments demonstrate that they also observed some consistent pattern. Even Smith and Hood (1984) indicated that a consistent pattern appeared to be present in *Lionycteris* and *Lonchophylla*. These authors observed a large anterior papilla with two large papillae posterior to it.

Our definitions of characters and character states dealing with these papillae differ substantially from Griffiths' (1982) treatment. Griffiths (1982: character 16) identified a single pattern of interest, the "3/4 pattern" (one row of 3 large papillae and a second row of 4 large papillae), which he scored as a binary character. Thus, Griffiths (1982) grouped several unique patterns (see characters 122 to 127) into a single, plesiomorphic state defined by absence of a recognizable 3/4 pattern (Smith and Hood, 1984). We found that many of the taxa in which Griffiths (1982: 31) recognized a "less orderly" patch of horny papillae (e.g., *Macrotus*, many stenodermatines) are characterized by distinctive patterns. Griffiths (1982) observed two large papillae in *Carollia*, whereas we found one. Gimenez (1993: character 3.3.5.13) followed Griffiths (1982) in recognizing only the 3/4 pattern, again scoring this as a binary character. She scored only *Choeroniscus*, *Choeronycteris*, and *Hylonycteris* with the derived condition (the presence of the 3/4 pattern). In all other taxa, she reported that this pattern was absent—clearly at odds with our description of horny papillae patterns, and the previous report by Griffiths (1982).

Gimenez et al. (1996: character 12) subdivided the patterns observed among nectar-feeding phyllostomids and their allies into four states. They described state 1 as a triangular arrangement of three papillae, one small papilla anterior to two larger ones (Gimenez, 1996). They scored *Glossophaga*, *Monophyllus*, *Leptonycteris*, and lonchophyllines as having this state. Based on Griffiths' (1982) descriptions, Gimenez et al. (1996) also scored *Erophylla* and *Phyllonycteris* with this state, although these taxa have one large papilla anterior to two smaller ones. Gimenez et al. (1996) erected a separate state for *Anoura* (state 3), which they described as having an autapomorphic pattern of three to four papillae in a transverse row with smaller papillae anterior to this row. However, the *Anoura* that we examined have a single large central papilla surrounded by smaller papillae. Gimenez et al. (1996) scored *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Lichonycteris* as having the 3/4 pattern (state 2), three small papillae anterior to four larger papillae, the central two of which are largest. Finally, they described all other phyllostomids as having a poorly defined state (0): "8–15 main papillae arranged in a circular to nearly square cluster" (Gimenez et al., 1996: character 12).

We divided the horny papillae pattern into several characters (124 to 127) in such a way as to allow scoring of the consistent variation that we observed. The first of these (this character) describes the number of large papillae (what we term the "main papillae"), which provide a landmark for descriptions of the remaining horny papillae (anterior, posterior, or lateral to the main papillae). We believe, based on position and overall similarity, that each of the character states defined here describes a potentially homologous pattern.

**Character 125:** *Three small papillae present anterior to main papilla(e) (0); or one papilla present (1); or no papillae present (2).* Among phyllostomids with an elliptical cluster of horny papillae, many have one or more papillae located anterior to the main papilla(e). Three small papillae are present anterior to the main papilla(e) in phyllostomines (fig. 38C), *Brachyphylla* (except AMNH 213731 in which the anterior-most appears to be missing), some glossophagines (e.g., *Choeroniscus*, *Lichonycteris*), *Carollia*, and all stenodermatines (fig. 38G). The middle of the three papillae is usually slightly anterior to the other two and is centered roughly on the midline of the tongue. We considered *Brachyphylla* AMNH 213731 aberrant, and scored this taxon with state 0 in the matrix. In contrast, in some glossophagines (e.g, *Glossophaga*, *Leptonycteris*) there is only a single papilla anterior to the main papilla (fig. 38F). No papillae are present anterior to the main papilla(e) in phyllonycterines and lonchophyllines (fig 38D–E). Mormoopids and *Noctilio* have horny papillae of uniform size, so the primitive state

for phyllostomids cannot be determined a priori. We scored taxa that have a V-shaped cluster of horny papillae (state 1 of character 121) or those with papillae of uniform size in the cluster (state 0 of character 122) ''−'' for this character.

The ''3/4'' pattern used by Griffiths (1982: character 16) and Gimenez (1993; character 3.3.5.13) included the presence of three small anterior papillae. Gimenez et al. (1996: table 2) scored *Erophylla* and *Phyllonycteris* as having one anterior papilla. However, the ''anterior'' papilla in phyllonycterines is much larger than other surrounding horny papillae, so we interpret it as the main papilla of the cluster (see character 124). Consequently, we score phyllonycterines as lacking small anterior papillae. Gimenez et al.'s (1996; character 12) state ''8–15 main papillae arranged in a circular to nearly square cluster,'' scored as present in phyllostomines, *Brachyphylla*, and stenodermatines, apparently included three papillae that we observed anterior to the central largest papilla(e) in these taxa. If this is the case, our observations are largely in agreement with those of Gimenez et al.(1996).

**Character 126:** *Two or more small horny papillae present posterior to main papilla(e) (0); or absent (1).* Two or more small horny papillae are present posterior to the main papilla(e) in most phyllostomids (fig. 38C–E). These are typically aligned on either side of the midline of the tongue. In contrast, there are no horny papillae posterior to the main papilla(e) in all glossophagines (fig. 38F), except *Anoura*, and many stenodermatines (e.g., *Uroderma*, *Sphaeronycteris*; fig. 38G). Mormoopids and *Noctilio* have horny papillae of uniform size, so the primitive state for phyllostomids cannot be determined a priori. We scored taxa that have a V-shaped cluster of horny papillae (state 1 of character 121) or those with papillae of uniform size in the cluster (state 0 of character 122) ''−'' for this character.

**Character 127:** *Main horny papilla(e) flanked by a pair of smaller horny papillae, one on each side (0); or no papillae present lateral to main papilla(e) (1).* Most phyllostomids have one small horny papillae located on each side of the main papilla(e) (fig. 38C–D, G). In contrast, these are absent in *Glos-*

*sophaga*, *Leptonycteris*, *Monophyllus*, and lonchophyllines (fig. 38E–F). In some specimens of *Phyllonycteris* (e.g., AMNH 23762) these papillae are occasionally absent. Mormoopids and *Noctilio* have horny papillae of uniform size; thus, the primitive state for phyllostomids cannot be determined a priori. We scored taxa that have a V-shaped cluster of horny papillae (state 1 of character 121) or those with papillae of different sizes in the cluster (state 1 of character 122) ''−'' for this character.

Griffiths' (1982: character 16) 3/4 character included the presence of four papillae in the posterior row: two central large papillae and two smaller flanking papillae. Similarly, the state described by Gimenez et al. (1996: character 12) as ''8–15 main papillae arranged in a circular to nearly square cluster,'' apparently included a flanking pair. Our observations agree with those of previous authors.

**Character 128:** *Paired lingual arteries present, lingual veins not enlarged (0); or single, midline lingual artery present, lingual veins enlarged (1).* A pair of lingual arteries is present in the tongue of *Desmodus*, phyllostomines, *Brachyphylla*, lonchophyllines, *Carollia*, and stenodermatines (Griffiths, 1982). The lingual veins are not enlarged in these taxa (Griffiths, 1982). A single, midline lingual artery and a pair of enlarged lingual veins are present in phyllonycterines and glossophagines (Griffith, 1982). The condition of the lingual vascular system has not been reported for mormoopids or noctilionids, but most mammals have paired lingual arteries (Griffiths, 1982), suggesting that this condition may be primitive for phyllostomids.

Griffiths (1982: characters 17–18) treated the lingual vascular system in two characters: ''single midline lingual artery'' (present/absent) and ''enlarged lingual veins'' (present/absent). However, these features may be functionally correlated, and they have identical taxonomic distributions. Accordingly, we chose to treat the lingual arteries and veins as part of a single character.

## DIGESTIVE TRACT

Forman (1971, 1973) and Forman et al. (1979) described the morphology of the di-

gestive tract in phyllostomids; taxa included in these studies are listed in table 4. Straney (1980: character numbers are taken from his appendix 1) used these data to construct a character for use in a phylogenetic analysis (see discussion below). We did not collect any new data observational data for this character.

**Character 129:** *Brunner's glands present at gastroduodenal juncture (0); or absent (1).* Brunner's glands, which secrete mucus, are present at the gastroduodenal juncture in phyllostomines, glossophagines, and *Sturnira* (Forman, 1973; Forman et al., 1979). Brunner's glands are absent in this region of the stomach in *Brachyphylla* and the remaining stenodermatines (Forman, 1973; Forman et al., 1979). In some species of *Artibeus*, *Dermanura*, and *Platyrrhinus*, Brunner's glands are present, whereas in other species in these genera these glands are absent. We score these genera with both states 0 and 1 in the matrix. Mormoopids and *Noctilio* have "unusually" abundant Brunner's glands at the gastroduodenal juncture (Forman, 1971), suggesting that presence of Brunner's glands in this region may be the primitive state for phyllostomids.

Straney (1980: character A1) defined a single binary character based on the number of Brunner's glands distributed in the proximal part of the duodenum, describing the derived state as "Brunner's glands present but not numerous." Straney (1980) scored the taxon "Phyllostomatinae" with the primitive condition of this character (i.e., Brunner's glands present and numerous). Straney (1980) scored all glossophagines, stenodermatines, carolliines, and brachyphyllines as having Brunner's glands that were less numerous than those in the phyllostomines. However, it is not easy to determine how abundance of these glands should be treated. Forman (1971: 274) described Brunner's glands in mormoopids and noctilionids as "unusually abundant," whereas glands in four phyllostomines were described by Forman et al. (1979: 225) as "relatively numerous." *Anoura* and *Glossophaga* have "relatively more abundant" glands than *Choeroniscus* and *Lichonycteris* do (Forman, 1971: 277), whereas some *Artibeus* species have "sparse" Brunner's glands and some *Der-*

*manura* species have "numerous" Brunner's glands at the gastroduodenal juncture (Forman et al., 1979: 225). Because it is difficult to determine exactly which states should be considered homologous, and it seems likely to us that such descriptions may actually describe states on a continuum, we have chosen to disregard such information until such data can be more readily quantified.

## REPRODUCTIVE TRACT

The following characters are based on Hood and Smith's (1982, 1983) descriptions and analysis of variation in the female reproductive tract, and Straney's (1980: character numbers from appendix 1) descriptions of the male reproductive tract (see table 4). We have made only minor changes in the character descriptions presented by these authors and did not collect any additional data.

**Character 130:** *Male accessory gland includes compact white body situated anteromedially (0); or compact white body absent (1).* All phyllostomids have an accessory gland (seminal vesicles and prostate) composed of two parts: a pink, vesiculate, anterior portion, and a white, compact, posterior portion (Straney, 1980). However, in some phyllostomines (e.g., *Phyllostomus*, *Trachops*), *Glossophaga*, *Carollia*, and *Sturnira*, the accessory gland includes a third part: a compact white body situated anteromedially (this body may be the seminal vesicles; Straney, 1980). In mormoopids, the accessory gland is also tripartite with a pink, vesiculate, anterior part; a compact, white, posterior part; and a compact, white anteromedial part. The accessory bulb in *Noctilio* is not tripartite and is primarily pink and vesiculate. However, a compact white body is present and it is situated anteromedially (Straney, 1980). This distribution of character states suggests that presence of a compact white anteromedial body is the primitive condition for phyllostomids.

Straney (1980: characters B1–3, and 239) developed three binary characters based on the morphology of the male accessory gland: "(1) Prostate of two parts; caudal part dark, vesiculate; cranial part small, white, compact; (2) Prostate three parted; as in (1) but caudal part with a large, compact white re-

gion; (3) Prostate of two parts; caudal part white, compact; cranial part dark vesiculate.'' We did not use information pertaining to other parts of the male accessory gland because they do not appear to be informative at this taxonomic level (i.e., within phyllostomids). We followed Straney's (1980: 23–28) text descriptions to score taxa rather than his data matrix, because he seems to have scored mormoopids incorrectly in the matrix (indicating they have only a bipartite, not a tripartite accessory gland). Although Straney (1980) scored *Macrophyllum* in his matrix for this character, he did not describe or list specimen numbers for this taxon; therefore, we did not score *Macrophyllum* for this character.

**Character 131:** *Uterine horns approximately one half length of common uterine body (0); or one quarter length of common uterine body (1), or uterus fully simplex, uterine horns not distinct from common body (2).* The length of the uterine horns is approximately one half the length of common uterine body in *Desmodus* (Hood and Smith, 1982, 1983; fig. 39A). External uterine fusion is somewhat greater in some phyllostomines (e.g., *Macrotus*, *Trachops*), which have uterine horns that are one quarter the length of the common uterine body (Hood and Smith, 1982, 1983; fig. 39B). In contrast, the uterus is simplex (the uterine horns are not distinct from common body of the uterus) in other phyllostomines (e.g., *Phylloderma*, *Phyllostomus*), *Brachyphylla*, *Phyllonycteris*, *Lonchophylla*, glossophagines, carolliines, and stenodermatines (Hood and Smith, 1982, 1983; fig. 39C–D). The length of the uterine horns is approximately one half the length of common uterine body in mormoopids and *Noctilio* (Hood and Smith, 1982, 1983; fig. 39A), suggesting that this condition is primitive for phyllostomids.

Our scoring of this character follows that proposed by Hood and Smith (1982: character 1); however, we have eliminated their character state 0 (''uterine horns 3/4 length of body''), because this state does not appear in any of the taxa in our study. Hood and Smith (1982) had ordered transformations in this character.

**Character 132:** *Cornual lumina distinct, join within the common uterine body (0); or reduced to tubular intramural cornua (1); or completely fused to form a single common lumen, no remnant of cornual lumina (2).* The cornual lumina are distinct and join the common uterine lumen within the common uterine body in *Desmodus* and some phyllostomines (e.g., *Macrotus*, *Trachops*; Hood and Smith, 1982, 1983; fig. 39A–B). In contrast, the cornual lumina are reduced to tubular intramural uterine cornua (IUC) in other phyllostomines (e.g., *Phyllostomus*, *Phylloderma*), *Brachyphylla*, *Phyllonycteris*, *Lonchophylla*, glossophagines, and carolliines (Hood and Smith, 1982, 1983; fig. 39C). There is a single common uterine lumen and no remnants of the cornual lumina in stenodermatines (Hood and Smith, 1982, 1983; fig. 39D). The cornual lumina are distinct and join the common uterine lumen within the common uterine body in mormoopids and *Noctilio* (Hood and Smith, 1982, 1983), suggesting that this condition is primitive for phyllostomids.

Our scoring of this character generally follows that proposed by Hood and Smith (1982: character 3), although we combined two character states defined by those authors (state 0: ''short common uterine lumen, cornual lamina join within the common uterine body'' and state 1: ''large common uterine lumen, cornual lumina join immediately within the common uterine body'') because the former condition is found only in one outgroup taxon (*Noctilio*). Our state 0 includes these two conditions. Hood and Smith (1982) ordered transformations in this character.

**Character 133:** *Oviducts enter lateral border of uterine horns or body (0); or enter fundic border of uterine body (1); or enter fundic border of uterine body near the midsagittal line (2).* The oviducts enter the lateral border of the uterine horns or body in *Desmodus* and phyllostomines (Hood and Smith, 1982, 1983; fig. 39A–B). The location of this intersection is shifted anteromedially so that the oviducts enter the fundic border of the uterine body in *Brachyphylla*, *Phyllonycteris*, glossophagines, *Lonchophylla*, and carolliines (Hood and Smith, 1982, 1983; fig. 39C). In stenodermatines, the oviducts enter the uterus more medially, near the midsagittal line on the fundic border (Hood
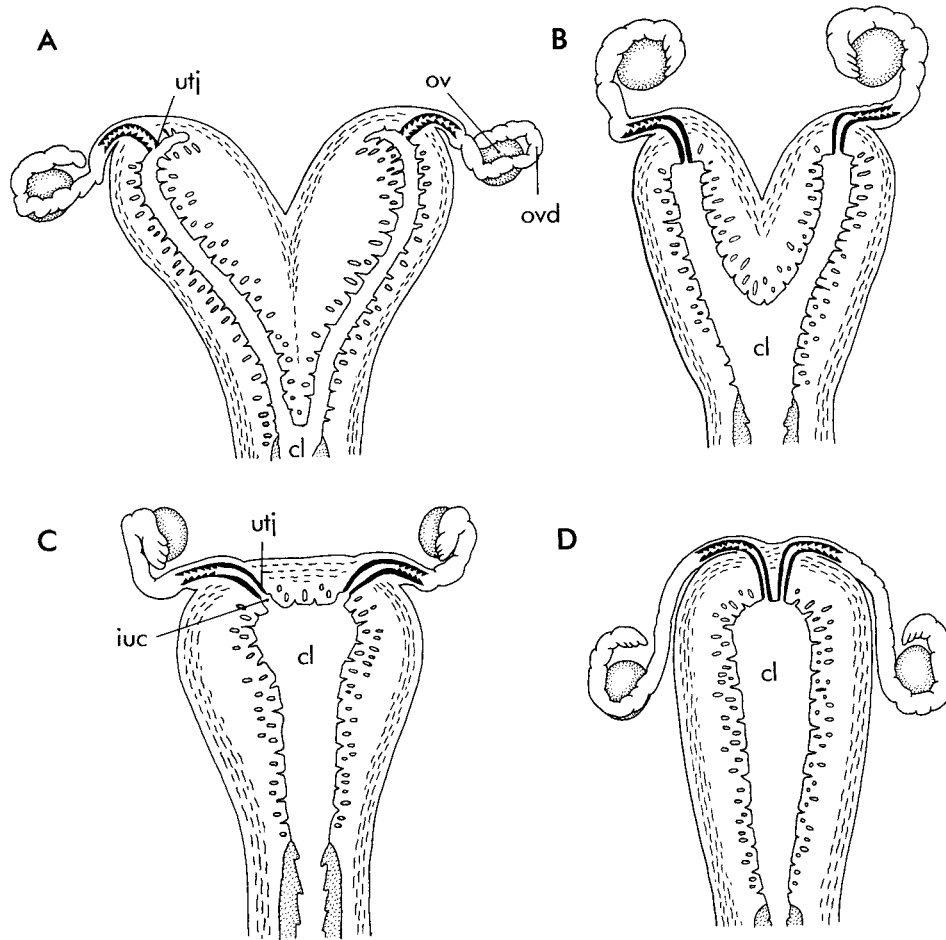
Fig. 39. Semidiagrammatic, frontal sections of the female reproductive tract in three phyllostomids and one outgroup taxon representing the range of variation among noctilionoids (redrawn from Hood and Smith, 1983: figs. 3, 4, 6). **A.** *Noctilio albiventris*. **B.** *Macrotus californicus*. **C.** *Leptonycteris curasoae*. **D.** *Artibeus jamaicensis*. Abbreviations: cl: common uterine lumen; iuc: intramural uterine cornua; ov: ovary; ovd: oviduct; utj: uterotubal junction. Abbreviations follow those used by Hood and Smith (1982, 1983).

and Smith, 1982, 1983; fig. 39D). The oviducts enter the lateral border of the uterine horns or body in mormoopids and *Noctilio* (Hood and Smith, 1982, 1983; fig. 39A), suggesting that this is the primitive condition for phyllostomids.

This character was previously used in a phylogenetic analysis by Hood and Smith (1982: character 5); our character is identical to theirs, except we have not ordered transformations.

**Character 134:** *Ovarian ligament extends from ovary to external entry of oviduct (0);*

*or extends from ovary to lateral border of uterus (1).* The ovarian ligament extends from the ovary to the external entry of the oviduct into the uterus in *Desmodus*, phyllostomines, *Brachyphylla*, *Phyllonycteris*, glossophagines, and *Lonchophylla* (Hood and Smith, 1982, 1983; fig. 40A). In contrast, the ovarian ligament extends from the ovary to the lateral border of uterus in carolliines and stenodermatines (Hood and Smith, 1982, 1983; fig. 40B). The ovarian ligament extends from the ovary to the external entry of the oviduct into the uterus in mormoopids
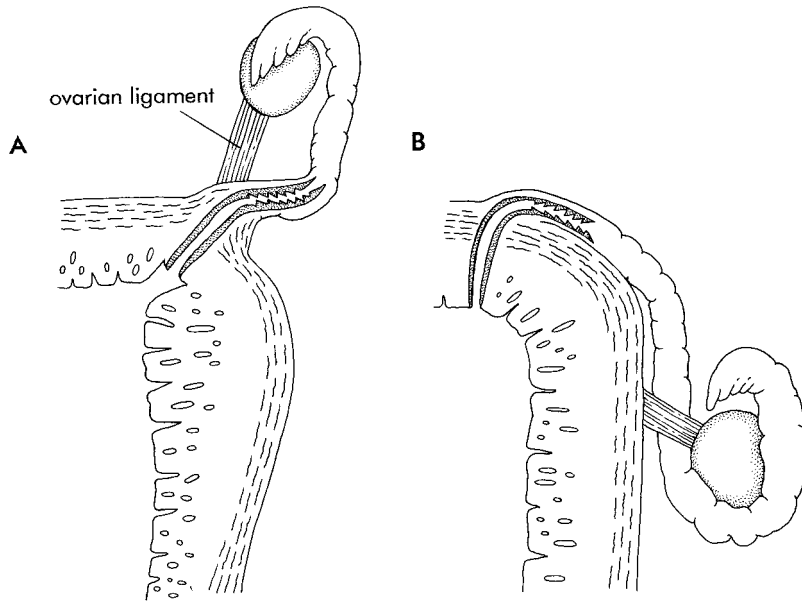
Fig. 40. Diagram illustrating the two different types of attachment of the ovary to the uterus via the ovarian ligament: **A.** to the external oviductal entry, or **B.** to the lateral uterine wall (redrawn from Hood and Smith, 1983: fig. 15).

and *Noctilio* (Hood and Smith, 1982, 1983; fig. 40A), suggesting that this is the primitive condition for phyllostomids.

This character is identical to that used by Hood and Smith (1982: character 6) in their phylogenetic analysis.

## BRAIN

The following characters are based on descriptions of brain morphology provided by McDaniel (1976), Bhatnager (1988), Baron et al. (1996a, 1996b), and Wible and Bhatnagar (1996; see table 4). Straney (1980: character numbers from his appendix 1) used features of the brain in an analysis of phyllostomine relationships, but did not present new observational data.

**Character 135:** *Accessory olfactory bulb absent (0); or present (1).* In most phyllostomids, the accessory olfactory bulb, the part of the forebrain receiving sensory information from the vomeronasal organ, is well developed (Wible and Bhatnagar, 1996). In contrast, the accessory olfactory bulb is absent in *Brachyphylla* (Wible and Bhatnagar, 1996), *Choeroniscus*, and *Rhinophylla* (Baron et al., 1996). The accessory olfactory bulb

is also absent in *Mormoops*, *Pteronotus personatus*, and *P. gymnotus*, and *Noctilio* (Wible and Bhatnagar, 1996). The accessory olfactory bulb is present in *Pteronotus parnellii* (Wible and Bhatnagar, 1996). Therefore, the primitive state for phyllostomids appears to be absence of the accessory olfactory bulb.

Wible and Bhatnagar (1996) first defined and mapped this character onto preexisting phylogenies of bats; however, they expressed some reservations concerning its use because the absence of the accessory olfactory bulb is perfectly correlated with a reduced or absent vomeronasal epithelial tube (VET) in mammals (i.e., a VET that lacks neuroepithelium; see character 39). However, because reduced VET have structures that indicate a sensory function (e.g., vomeronasal nerves, paravomeronasal ganglia, and receptorlike cells), Wible and Bhatnagar (1996) considered this character separately from the VET character. We do the same here, adding that the accessory olfactory bulb has been described in many more taxa than has the vomeronasal organ. Because we are not certain of the state of the VET in these taxa (i.e., the

VET could be well developed in one of these taxa while the accessory olfactory bulb is absent), we felt it unwise to combine these two characters. Our scoring and character construction are equivalent to those used by Wible and Bhatnagar (1996), although due to choice of outgroups, their primitive and derived states differ from ours.

**Character 136:** *Cerebellar vermis does not cover medial longitudinal fissure or inferior colliculi (0); or cerebellar vermis completely covers longitudinal fissure between inferior colliculi, inferior colliculi exposed dorsally only along lateral edges of cerebellar vermis (1); or inferior colliculi completely covered by cerebellar vermis and cerebral hemispheres, colliculi not visible in dorsal view (2).* The inferior colliculi are fully to mostly exposed dorsally in many phyllostomines (e.g., *Mimon crenulatum*, *Trachops*; fig. 41A; McDaniel, 1976; Baron et al., 1996a, 1996b). The medial longitudinal fissure is visible between the inferior colliculi in these taxa, and the right and left colliculi appear to be located directly adjacent to one another. In contrast, a rostral extension of the cerebellar vermis covers the medial longitudinal fissure between the inferior colliculi in *Diphylla*, some phyllostomines (e.g., species of *Micronycteris*), phyllonycterines, and many stenodermatines (e.g., *Centurio*, *Mesophylla*; McDaniel, 1976; Bhatnager, 1988; Baron et al., 1996a, 1996b; fig. 41B). The inferior colliculi are partly covered medially in these genera, and lateral portions of the inferior colliculi are visible along the edges of the cerebellar vermis. As a result, the right and left colliculi appear to be separated from one another when viewed dorsally. Finally, the inferior colliculi are completely covered by the cerebellar vermis and cerebral hemispheres in *Desmodus*, *Diaemus*, some phyllostomines (e.g., *Phylloderma*), *Brachyphylla*, *Lonchophylla*, glossophagines, carolliines, and many stenodermatines (e.g., *Enchisthenes*, *Uroderma*; McDaniel, 1976; Bhatnager, 1988; Baron et al., 1996a, 1996b; fig. 41C). No portion of the inferior colliculi is visible in these taxa. Taxonomic polymorphism occurs in some genera. In *Phyllostomus*, only *P. elongatus* has dorsally exposed inferior colliculi whereas all other species have complete coverage (McDaniel, 1976).
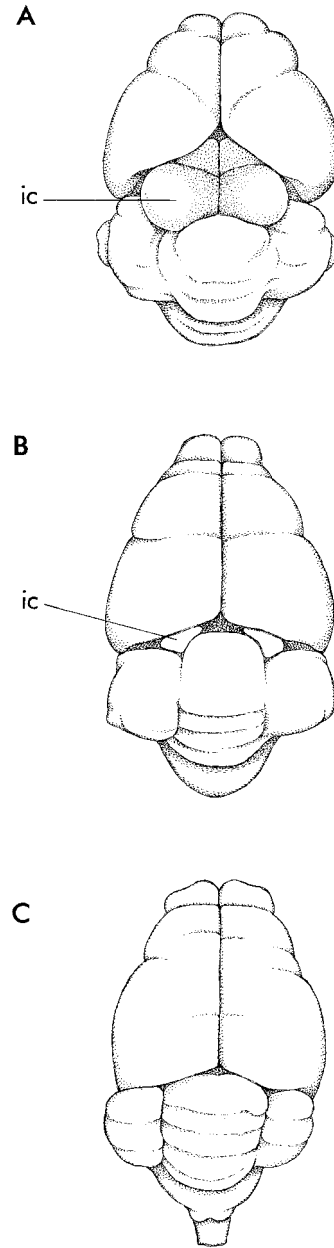


Fig. 41. Semidiagrammatic illustrations of the dorsal brain in three phyllostomids illustrating the range of variation in coverage of the inferior colliculi (ic) by the cerebellar vermis. **A.** *Mimon crenulatum*. **B.** *Mesophylla macconnelli*. **C.** *Lichonycteris obscura* (drawn from McDaniel, 1976: figs. 2, 20, 42).
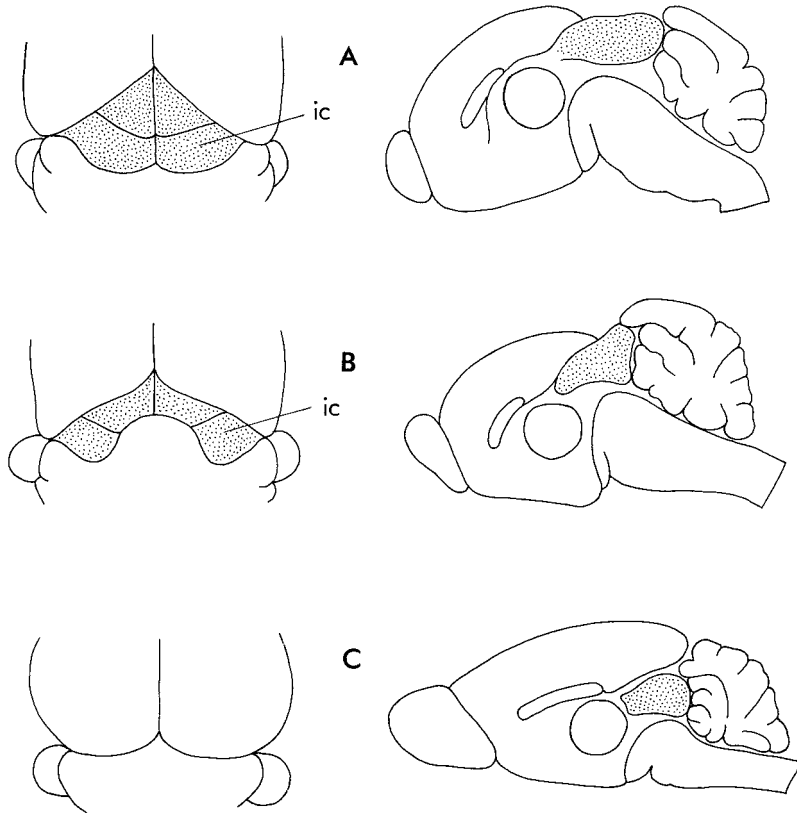
Fig. 42.   Diagramatic dorsal view (left) and longitudinal section of one hemisphere (right) of the chiropteran brain illustrating the progressive coverage of the median longitudinal fissure and inferior colliculi (ic). **A.** Complete exposure of the median longitudinal fissure and inferior colliculi. **B.** Partial coverage of both the fissure and inferior colliculi. **C.** Complete coverage of the fissure and colliculi. Note that the cerebellar vermis covers the inferior colliculi, but the relationship of the inferior colliculi to each other does not change (redrawn from Schober and Brauer, 1974: fig. 99)

Accordingly, we score *Phyllostomus* with states 0 and 2 in the matrix. In *Artibeus*, *Dermanura*, *Platyrrhinus*, and *Sturnira* some species in each genus have partly exposed inferior colliculi, whereas their congeners have completely covered inferior colliculi (McDaniel, 1976); we score these taxa with states 1 and 2 in the matrix. The inferior colliculi are only partly exposed in *Mormoops*, *Pteronotus*, and *Noctilio albiventris*, but are fully exposed dorsally in *Noctilio leporinus* (Baron et al., 1996a, 1996b). This distribution of character states suggests that partial exposure of the inferior colliculi is the primitive condition for phyllostomids.

Straney (1980: characters D1–2) treated dorsal exposure of the inferior colliculi in two binary characters: "Inferior colliculi contiguous at midline" and "Inferior colliculi separate at midline." Although the latter is misleading (the inferior colliculi are not actually separated, just covered medially; fig. 42), the derived conditions of these characters correspond to our states 0 and 1. Straney (1980) did not score complete coverage of the inferior colliculi by cerebral and cerebellar tissues. However, Straney (1980) left blank spaces in his matrix to indicate that the condition of the inferior colliculi was unknown in glossophagines and carolliines because they were completely covered by the cerebellar vermis. In his matrix, Straney (1980) appears to have mistakenly scored desmodontines, brachyphyllines, and stenodermatines for the derived conditions of both of his characters even though he cor-

rectly notes in his text (Straney, 1980: 39) that the inferior colliculi, when they can be viewed in these taxa, are separated.

Our scoring of this character agrees with McDaniel's (1976) descriptions, with the exception of *Artibeus jamaicensis*, which we have scored as state 1, and McDaniel described as having state 2. We scored *Artibeus jamaicensis*, and several other taxa, based on figures (e.g., McDaniel, 1976; Bhatnager, 1988) when text descriptions were not clear about the exposure and contiguity of the inferior colliculi. Our scoring of *Artibeus jamaicensis* agrees with the description of this taxon by Schober and Brauer (1974).

## SEX CHROMOSOMES

The following character is based on descriptions of chromosome morphology provided by Baker (1967, 1970, 1973, 1979), Forman et al. (1968), Hsu et al.(1968), Baker and Lopez (1970), Baker and Bleier (1971), Patton and Gardner (1971), Stock (1975), Cadena and Baker (1976), Gardner (1977a), Bass (1978), Patton and Baker, (1978), Baker and Bass (1979), Baker et al. (1979, 1981b, 1982), Johnson (1979), Myers (1981) (for a complete list of taxa covered by karyological studies see Baker et al., 1982). We have not collected any additional observational data for this character.

**Character 137:** *Sex-determining system XX/XY; X chromosomes never translocated to autosomes (0); or sex determining system* $XX/XY_1Y_2$; *X chromosomes translocated to autosomes (1); or X chromosomes sometimes translocated to autosomes; polymorphic within species (2).* Most phyllostomids, like most other mammals, have an XX/XY sex-determining system (Baker, 1967, 1970, 1973, 1979; Hsu et al., 1968; Forman et al., 1968; Baker and Hsu, 1970; Baker and Lopez, 1970; Baker and Bleier, 1971; Baker et al. 1973; Nagorsen and Peterson, 1975; Cadena and Baker, 1976; Gardner, 1977a; Bass, 1978; Patton and Baker, 1978; Baker and Bass, 1979; Baker et al., 1979; Johnson, 1979; Honeycutt et al., 1980; Baker et al., 1981a, 1981b, 1982). In species with this system, males and females have an equivalent number of chromosomes. However, some species of *Choeroniscus*, some species

of *Carollia*, and many stenodermatines (e.g., *Artibeus*, *Ametrida*) have an $XX/XY_1Y_2$ sex system (Baker, 1967, 1970, 1973, 1979; Hsu et al., 1968; Baker and Hsu, 1970; Baker and Lopez, 1970; Baker and Bleier, 1971; Greenbaum et al., 1975; Stock, 1975; Gardner, 1977a; Baker et al., 1979, 1981b, 1982; Johnson, 1979; Myers, 1981). In these taxa, the X chromosomes are translocated to autosomes. Thus males have an unpaired Y chromosome (because the X is translocated to an autosome), and the homolog of the autosome carrying the X is referred to as a second Y. Some individuals of *Carollia castanea*, and *C. brevicauda*, *C. perspicillata*, and *C. subrufa* have an $XX/XY_1Y_2$ system (Baker, 1967, 1979; Hsu et al., 1968; Baker and Bleier, 1971; Patton and Gardner, 1971; Stock, 1975; Baker et al., 1982). *Choeroniscus godmani* has an $XX/XY_1Y_2$ system, whereas *C. minor* (= *C. intermedius*) does not (Baker, 1967, 1970, 1979; Patton and Gardner, 1971; Stock, 1975; Baker et al., 1982). *Dermanura cinerea* has an $XX/XY_1Y_2$ system, whereas other species in this genus do not. Thus, we score *Carollia* with states 1 and 2 in the matrix, and score *Choeroniscus* and *Dermanura* with states 0 and 1. Mormoopids (Baker, 1967; Baker and Hsu, 1970; Baker and Lopez, 1970; Patton and Baker, 1978; Sites et al., 1981) and *Noctilio* (Patton and Baker, 1978) have XX/XY sex chromosomes, suggesting that this is the primitive condition for phyllostomids.

Although several authors have drawn conclusions about phylogenetic relationships using the sex chromosomes (e.g., Baker and Lopez, 1970; Greenbaum et al., 1975), this is the first use of this feature as a character in a cladistic analysis.

## RESTRICTION SITES

The following characters are based on a study of restriction sites present in the transcribed portion of the rDNA complex conducted by Van Den Bussche (1991, 1992; see table 4; see fig. 43 for all sites). We have not collected any additional data for these characters. Restriction site numbers are those established by Van Den Bussche (1991, 1992) and are used to facilitate discussion.

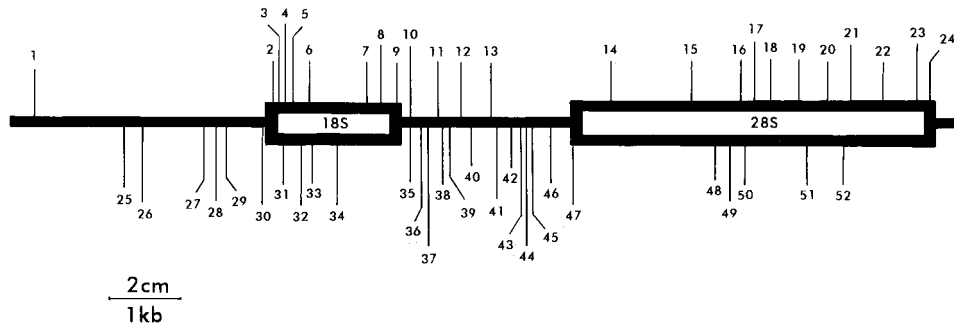**Character 138:** *Restriction site 28 present*

Fig. 43. Restriction site map of the transcribed portion of the rDNA complex, including all sites from Van Den Bussche's (1991) original study. Restriction sites variable within noctilionoids and *Homo* are below the line, invariant (those found in all taxa in the study) are above the line (redrawn from Van Den Bussche, 1991: fig. 2).

*(0); or absent (1).* In most phyllostomids, an *Xba* I restriction site (Van Den Bussche's character 28) is present in the external transcribed spacer (ETS; Van Den Bussche, 1991, 1992). However, in *Platyrrhinus*, *Uroderma*, and *Vampyrodes*, this restriction site is absent (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

Our scoring of this character and those that follow are identical to that of Van Den Bussche (1991, 1992: character 28); however, Van Den Bussche (1991, 1992) scored *Hylonycteris* ''9'' for this character and characters 139, 141, 142, 143, 146, and 148 below to indicate that there was missing data for this taxon, whereas we use ''?'' for this purpose.

**Character 139:** *Restriction site 32 present (0); or absent (1).* A *Hinc* II restriction site (character 32) is present in the ETS of most phyllostomids (Van Den Bussche, 1991, 1992). However, in *Chrotopterus*, *Mimon crenulatum*, *Artibeus*, *Chiroderma*, and *Sturnira* this restriction site is absent (Van Den Bussche, 1991, 1992). The *Hinc* II (character 32) restriction site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 140:** *Restriction site 36 present (0); or absent (1).* In most phyllostomids a *Xho* I restriction site (character 36) is present in the ETS (Van Den Bussche, 1991, 1992). However, in *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris*, this restriction site is absent (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 141:** *Restriction site 38 present (0); or absent (1).* An *Sst* I restriction site (character 38) is present within the 18S gene in most phyllostomids (Van Den Bussche, 1991, 1992). In contrast, this restriction site is absent in *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Pygoderma*, and *Stenoderma* (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 142:** *Restriction site 43 present (0); or absent (1).* In most phyllostomids, an *Nco* I restriction site (character 43) is present in the internal transcribed spacer (ITS; Van Den Bussche, 1991, 1992). However, in *Chrotopterus* and *Trachops*, this restriction site is absent (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 143:** *Restriction site 46 present (0); or absent (1).* Most phyllostomids have an *Nco* I restriction site (character 46) in the ITS (Van Den Bussche, 1991, 1992). In contrast, this restriction site is absent in *Ariteus*,

*Pygoderma*, and *Stenoderma* (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 144:** *Restriction site 47 present (0); or absent (1).* In most phyllostomines, a *Stu* I restriction site (character 47) is present in the ITS (Van Den Bussche, 1991, 1992). However, this restriction site is absent in *Macrophyllum*, *Brachyphylla*, *Phyllonycteris*, lonchophyllines, glossophagines, carollines, and stenodermatines (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 145:** *Restriction site 49 present (0); or absent (1).* In most phyllostomids, a *Pvu* II restriction site (character 49) is present in the ITS (Van Den Bussche, 1991, 1992). However, in *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris*, this restriction site is absent (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 146:** *Restriction site 50 present (0); or absent (1).* A *Bam*H I restriction site (character 50) is present in the ITS in most phyllostomids (Van Den Bussche, 1991, 1992). In contrast, in many phyllostomines (e.g., *Phyllostomus*, *Trachops*), *Leptonycteris*, *Monophyllus*, and lonchophyllines this restriction site is absent (Van Den Bussche, 1991, 1992). This restriction site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 147:** *Restriction site 52 present (0); or absent (1).* Most phyllostomids have a *Stu* I restriction site (character 52) present in the ITS (Van Den Bussche, 1991, 1992). However, this restriction site is absent in *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris* (Van Den Bussche, 1991, 1992). This site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992),

suggesting that this is the primitive condition for phyllostomids.

**Character 148:** *Restriction site 53 present (0); or absent (1).* In most phyllostomids, a *Bgl* II restriction site (character 53) is present in the ITS (Van Den Bussche, 1991, 1992). In contrast, this restriction site is absent in *Lonchophylla* and *Lionycteris* (Van Den Bussche, 1991, 1992). This restriction site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

**Character 149:** *Restriction site 54 present (0); or absent (1).* In glossophagines, lonchophyllines, and stenodermatines except *Sturnira*, a *Xho* I restriction site (character 54) is present in the ITS (Van Den Bussche, 1991, 1992). However, in desmodontines, phyllostomines, *Brachyphylla*, *Phyllonycteris*, and *Sturnira*, this restriction site is absent (Van Den Bussche, 1991, 1992). This restriction site is present in *Mormoops* and *Noctilio* (Van Den Bussche, 1991, 1992), suggesting that this is the primitive condition for phyllostomids.

## *Eco*RI-DEFINED DNA REPEAT

Van Den Bussche et al. (1993) described the structure of an *Eco*RI-defined nuclear satellite DNA repeat in phyllostomid bats; taxa included in this study are listed in table 4. We did not collect any new data for this character.

**Character 150:** *900 base pair* Eco*RI-defined nuclear satellite DNA repeat absent (0); or present (1).* An *Eco*RI-defined nuclear satellite DNA repeat is present in *Artibeus*, *Dermanura*, and *Koopmania* (Van Den Bussche et al., 1993). However, this repeat is absent in all other phyllostomids (Van Den Bussche et al., 1993). The repeat is absent in *Mormoops* and *Noctilio*, suggesting that this is the primitive condition for phyllostomids.

Van Den Bussche et al. (1993) discussed the phylogenetic implications of the taxonomic distribution of this feature, but did not formally define and score it as a character.

# RESULTS

## TAXONOMIC CONGRUENCE ANALYSIS

As described in the Materials and Methods section, we divided our data set into a series of partitions to facilitate comparisons with previous studies and to evaluate the utility of each partition for resolving relationships at different hierarchical levels and in different parts of the tree. Results of the separate analyses of the partitions are presented below, followed by a summary. The entire data matrix is presented in appendix 2; data on polymorphism and completeness is presented in table 5.

**Pelage and Integument:** A heuristic search using 38 unordered characters for all taxa resulted in more than 30,000 most parsimonious trees (183 steps each, CI = 0.503, RI = 0.789). A strict consensus of these trees is shown in figure 44. Desmodontinae appears as a monophyletic group in this tree; *Desmodus* and *Diaemus* form a clade. The desmodontines are the sister taxon of a polytomy including *Brachyphylla*, *Erophylla*, *Phyllonycteris*, and a clade of the remaining phyllostomids. Within this latter group the positions of many taxa are unresolved. However, four clades occur in all 30,000 trees: (1) a clade of glossophagines and lonchophyllines, (2) a group composed of two pairs of sister taxa, *Chrotopterus* and *Vampyrum*, and *Tonatia* and *Trachops*, (3) a clade in which *Micronycteris minuta*, *Macrotus*, and *M. brachyotis* are the successive sister taxa of *M. hirsuta* and *M. megalotis*, and (4) a clade of ''short-faced'' stenodermatines in which *Centurio* and *Sphaeronycteris* are sister taxa.

Glossophagines and lonchophyllines are each monophyletic. Within the glossophagine clade, *Glossophaga*, *Monophyllus*, and a clade of the remaining genera form a polytomy. This last group is largely unresolved, with the exception of two pairs of sister taxa: *Anoura* and *Leptonycteris*, and *Hylonycteris* and *Lichonycteris*. Within the lonchophylline clade, *Lionycteris* and *Lonchophylla* are sister taxa.

**Skull and Dentition:** A heuristic search using 35 unordered craniodental characters

for all taxa resulted in more than 30,000 most parsimonious trees (119 steps each, CI = 0.555, RI = 0.832). A strict consensus of these trees is shown in figure 45. In this tree, Phyllostominae is monophyletic and appears as the sister taxon of a clade comprising the remaining phyllostomids. The basal node of the latter clade is a polytomy of *Brachyphylla*, *Sturnira*, a clade that includes desmodontines and numerous stenodermatines, and another clade that includes phyllonycterines, glossophagines, lonchophyllines, carolliines, and the remaining stenodermatines.

The desmodontine-stenodermatine group includes three clades: (1) the desmodontines, with *Desmodus* and *Diaemus* as sister taxa, (2) *Platyrrhinus* and *Uroderma*, and (3) *Ametrida* and *Sphaeronycteris*. Relationships among these groups and the other genera in this clade are unresolved (see fig. 45).

*Carollia* occupies the first branch of the remaining large clade. The positions of several taxa within the larger group are unresolved: *Erophylla*, *Phyllonycteris*, *Platalina*, *Rhinophylla*, and *Chiroderma* are part of a polytomy that also includes a clade of *Ectophylla*, *Mesophylla*, and the three *Vampyressa* species (no resolution in this clade), and another clade including *Lonchophylla*, *Lionycteris*, and all glossophagines. *Lonchophylla* and *Lionycteris* are basally unresolved within this group. At the next node, *Glossophaga*, *Leptonycteris* and *Monophyllus* form a polytomy with a monophyletic group of the remaining glossophagines. Within this group, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* form a clade. *Lichonycteris* and *Scleronycteris* form a polytomy with the *Choeroniscus* group. *Hylonycteris* and *Anoura* are successive sister taxa to the *Lichonycteris-Choeroniscus* group.

**Postcranium:** A heuristic search using 16 unordered postcranial characters for all taxa resulted in more than 30,000 most parsimonious trees (68 steps each, CI = 0.441, RI = 0.764). The strict consensus of these trees (not shown) is completely unresolved.

**Hyoid Apparatus:** A heuristic search using 17 unordered hyoid characters for 27 taxa (see table 4) resulted in 24 most parsimoni-

TABLE 5
**Completeness and Taxonomic Polymorphism in Data Matrix**

| Terminal taxon | Characters scored with single state[a] | Characters scored with two or more states | Characters scored "–" | Characters scored "?" | Percent complete[b] |
|---|---|---|---|---|---|
| Brachyphyllinae | | | | | |
| *Brachyphylla* | 125 (83.3%) | 0 | 15 (10.0%) | 10 (6.6%) | 93.4% |
| Carolliinae | | | | | |
| *Carollia* | 133 (88.7%) | 2 (1.3%) | 14 (9.3%) | 1 (0.7%) | 99.3% |
| *Rhinophylla* | 96 (64.0%) | 2 (1.3%) | 15 (10.0%) | 37 (24.7%) | 75.3% |
| Desmodontinae | | | | | |
| *Desmodus* | 121 (80.7%) | 0 | 24 (16.0%) | 5 (3.3%) | 96.7% |
| *Diaemus* | 79 (52.7%) | 0 | 21 (14.0%) | 50 (33.3%) | 66.7% |
| *Diphylla* | 98 (65.3%) | 0 | 20 (13.3%) | 32 (21.3%) | 78.7% |
| Glossophaginae | | | | | |
| *Anoura* | 125 (83.3%) | 3 (2.0%) | 11 (7.3%) | 11 (7.3%) | 92.7% |
| *Choeroniscus* | 113 (75.3%) | 3 (2.0%) | 14 (9.3%) | 20 (13.3%) | 86.7% |
| *Choeronycteris* | 119 (79.3%) | 0 | 14 (9.3%) | 17 (11.3%) | 88.7% |
| *Glossophaga* | 140 (93.3%) | 0 | 9 (6.0%) | 1 (0.7%) | 99.4% |
| *Hylonycteris* | 108 (72.0%) | 0 | 12 (8.0%) | 30 (20.0%) | 80.0% |
| *Leptonycteris* | 132 (88.0%) | 0 | 10 (6.7%) | 8 (5.3%) | 94.7% |
| *Lichonycteris* | 104 (69.3%) | 0 | 13 (8.7%) | 33 (22.0%) | 78.0% |
| *Monophyllus* | 124 (82.7%) | 0 | 9 (6.0%) | 17 (11.3%) | 88.7% |
| *Musonycteris* | 69 (46.0%) | 0 | 11 (7.3%) | 70 (46.7%) | 53.3% |
| *Scleronycteris* | 52 (34.7%) | 0 | 11 (7.3%) | 87 (58.0%) | 42.0% |
| Lonchophyllinae | | | | | |
| *Lionycteris* | 120 (80.0%) | 0 | 8 (5.3%) | 22 (14.6%) | 84.7% |
| *Lonchophylla* | 125 (83.3%) | 1 (0.7%) | 9 (6.0%) | 15 (10.0%) | 90.0% |
| *Platalina* | 103 (68.7%) | 0 | 11 (7.3%) | 36 (24.0%) | 76.0% |
| Phyllonycterinae | | | | | |
| *Erophylla* | 108 (72.0%) | 0 | 13 (8.7%) | 29 (19.3%) | 80.7% |
| *Phyllonycteris* | 119 (79.3%) | 1 (0.7%) | 13 (8.7%) | 17 (11.3%) | 88.0% |
| Phyllostominae | | | | | |
| *Chrotopterus* | 105 (70.0%) | 0 | 9 (6.0%) | 36 (24.0%) | 76.0% |
| *Lonchorhina* | 101 (67.3%) | 3 (2.0%) | 11 (7.3%) | 35 (23.3%) | 76.7% |
| *Macrophyllum* | 103 (68.7%) | 0 | 12 (8.0%) | 35 (23.3%) | 76.7% |
| *Macrotus* | 137 (91.3%) | 0 | 9 (6.0%) | 4 (2.7%) | 97.3% |
| *Micronycteris* | | | | | |
| M. *brachyotis* | 84 (56.0%) | 0 | 10 (6.7%) | 56 (37.3%) | 62.7% |
| M. *hirsuta* | 99 (66.0%) | 0 | 8 (5.3%) | 43 (28.7%) | 71.3% |
| M. *megalotis* | 100 (66.7%) | 0 | 9 (6.0%) | 41 (27.3%) | 72.7% |
| M. *minuta* | 99 (66.0%) | 0 | 9 (6.0%) | 42 (28.0%) | 72.0% |
| M. *nicefori* | 105 (70.0%) | 0 | 12 (8.0%) | 33 (22.0%) | 78.0% |
| M. *sylvestris* | 82 (54.7%) | 0 | 11 (7.3%) | 57 (38.0%) | 62.0% |
| *Mimon bennettii* | 90 (60.0%) | 0 | 10 (6.7%) | 50 (33.3%) | 66.7% |
| *Mimon crenulatum* | 103 (68.7%) | 0 | 11 (7.3%) | 36 (24.0%) | 76.0% |
| *Phylloderma* | 92 (61.3%) | 0 | 12 (8.0%) | 46 (30.7%) | 69.3% |
| *Phyllostomus* | 132 (88.0%) | 3 (2.0%) | 12 (8.0%) | 3 (2.0%) | 98.0% |
| *Tonatia* | 101 (67.3%) | 5 (3.3%) | 12 (8.0%) | 32 (21.3%) | 78.7% |
| *Trachops* | 110 (73.3%) | 0 | 11 (7.3%) | 29 (19.3) | 80.7% |
| *Vampyrum* | 99 (66.0%) | 0 | 13 (8.7%) | 38 (25.3%) | 74.7% |

TABLE 5
*Continued*

| Terminal taxon | Characters scored with single state[a] | Characters scored with two or more states | Characters scored "–" | Characters scored "?" | Percent complete[b] |
|---|---|---|---|---|---|
| **Stenodermatinae** | | | | | |
| *Ametrida* | 102 (68.0%) | 0 | 13 (8.7%) | 35 (23.3%) | 76.7% |
| *Ardops* | 102 (68.0%) | 0 | 10 (6.7%) | 38 (25.3%) | 74.7% |
| *Ariteus* | 105 (70.0%) | 0 | 10 (6.7%) | 35 (23.3%) | 76.7% |
| *Artibeus* | 129 (86.0%) | 4 (2.7%) | 14 (9.3%) | 3 (2.0%) | 98.0% |
| *Centurio* | 100 (66.7%) | 0 | 22 (14.7%) | 28 (18.7%) | 81.3% |
| *Chiroderma* | 97 (64.7%) | 7 (4.7%) | 13 (8.7%) | 33 (22.0%) | 78.0% |
| *Dermanura* | 93 (62.0%) | 8 (5.3%) | 13 (8.7%) | 36 (24.0%) | 76.0% |
| *Ectophylla* | 86 (57.3%) | 0 | 16 (10.7%) | 48 (32.0%) | 68.0% |
| *Enchisthenes* | 103 (68.7%) | 0 | 14 (9.3%) | 33 (22.0%) | 78.0% |
| *Koopmania* | 83 (55.3%) | 0 | 13 (8.7%) | 54 (36.0%) | 64.0% |
| *Mesophylla* | 100 (66.7%) | 0 | 13 (8.7%) | 37 (24.7%) | 75.3% |
| *Phyllops* | 104 (69.3%) | 0 | 11 (7.3%) | 35 (23.3%) | 76.7% |
| *Platyrrhinus* | 115 (76.7%) | 6 (4.0%) | 14 (9.3%) | 15 (10.0%) | 90.0% |
| *Pygoderma* | 100 (66.7%) | 0 | 11 (7.3%) | 39 (26.0%) | 74.0% |
| *Sphaeronycteris* | 85 (56.7%) | 0 | 14 (9.3%) | 51 (34.0%) | 66.0% |
| *Stenoderma* | 102 (68.0%) | 0 | 10 (6.7%) | 38 (25.3%) | 74.7% |
| *Sturnira* | 120 (80.0%) | 8 (5.3%) | 15 (10.0%) | 7 (4.7%) | 95.3% |
| *Uroderma* | 123 (82.0%) | 0 | 14 (9.3%) | 13 (8.7%) | 91.3% |
| *Vampyressa bidens* | 84 (56.0%) | 0 | 13 (8.7%) | 53 (35.3%) | 64.7% |
| *Vampyressa nymphaea* | 96 (64.0%) | 0 | 13 (8.7%) | 41 (27.3%) | 72.7% |
| *Vampyressa pusilla* | 108 (72.0%) | 0 | 14 (9.3%) | 28 (18.7%) | 81.3% |
| *Vampyrodes* | 105 (70.0%) | 0 | 13 (8.7%) | 32 (21.3%) | 78.7% |
| **Mormoopidae** | | | | | |
| *Mormoops* | 106 (70.7%) | 1 (0.7%) | 26 (17.3%) | 18 (12.0%) | 88.0% |
| *Pteronotus* | 103 (68.7%) | 4 (2.6%) | 26 (17.3%) | 17 (11.3%) | 88.7% |
| **Noctilionidae** | | | | | |
| *Noctilio* | 113 (75.3%) | 1 (0.7%) | 28 (18.6%) | 8 (5.3%) | 94.7% |

[a] Includes only character states 0, 1, 2, etc.; inapplicable ("–") or missing data ("?") are excluded. Percentage calculated using the total number of characters (150).

[b] Percent complete (percentage of characters that can be scored based on available data) is calculated by subtracting the percentage of characters scored "?" from 100%.

ous trees (40 steps each, CI = 0.625, RI = 0.893); a strict consensus of these trees is shown in figure 46. In this tree, there are two large clades of phyllostomids, one composed of *Desmodus*, *Brachyphylla*, phyllonycterines, glossophagines, and lonchophyllines, and the other composed of phyllostomines, carolliines, and stenodermatines. In the former clade, *Desmodus* occupies the basal branch. *Brachyphylla*, the sister taxa *Erophylla* and *Phyllonycteris*, and a clade comprising glossophagines and lonchophyllines form a polytomy. *Lionycteris*, *Lonchophylla*,

*Platalina*, and a clade of glossophagines also form a polytomy. Within the glossophagine clade, there is a sister group relationship between *Monophyllus* and *Glossophaga*, which form a clade with *Lichonycteris*. A second clade contains the sister taxa *Anoura* and *Leptonycteris*, the sister taxa *Choeroniscus* and *Choeronycteris*, and *Hylonycteris*.

In the other large clade, *Carollia* and *Sturnira* are successive sister taxa to the group that includes phyllostomines and other stenodermatines. In the phyllostomine-stenodermatine clade, *Macrotus* and *Phyllostomus* are
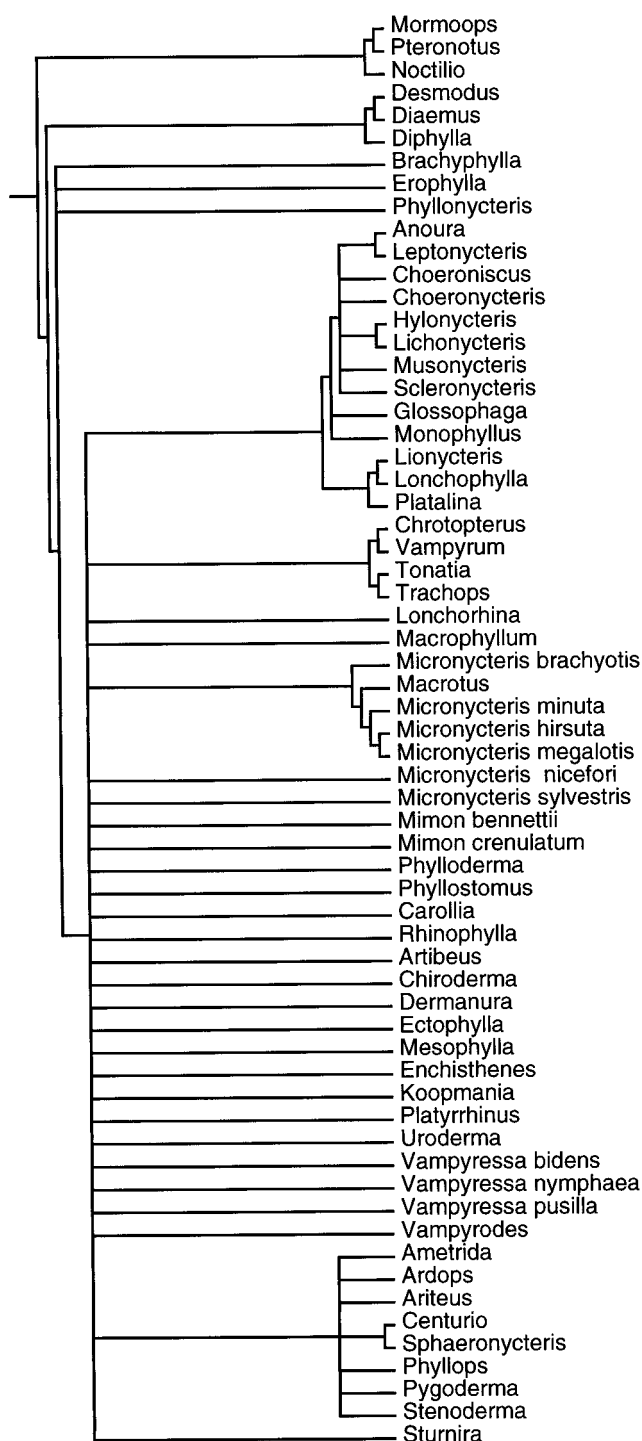
Fig. 44.    Results of a heuristic search of 38 pelage and integument characters for all 63 taxa. The tree shown here is a strict consensus of more than 30,000 most parsimonious trees, each of 183 steps (CI = 0.503, RI = 0.789).
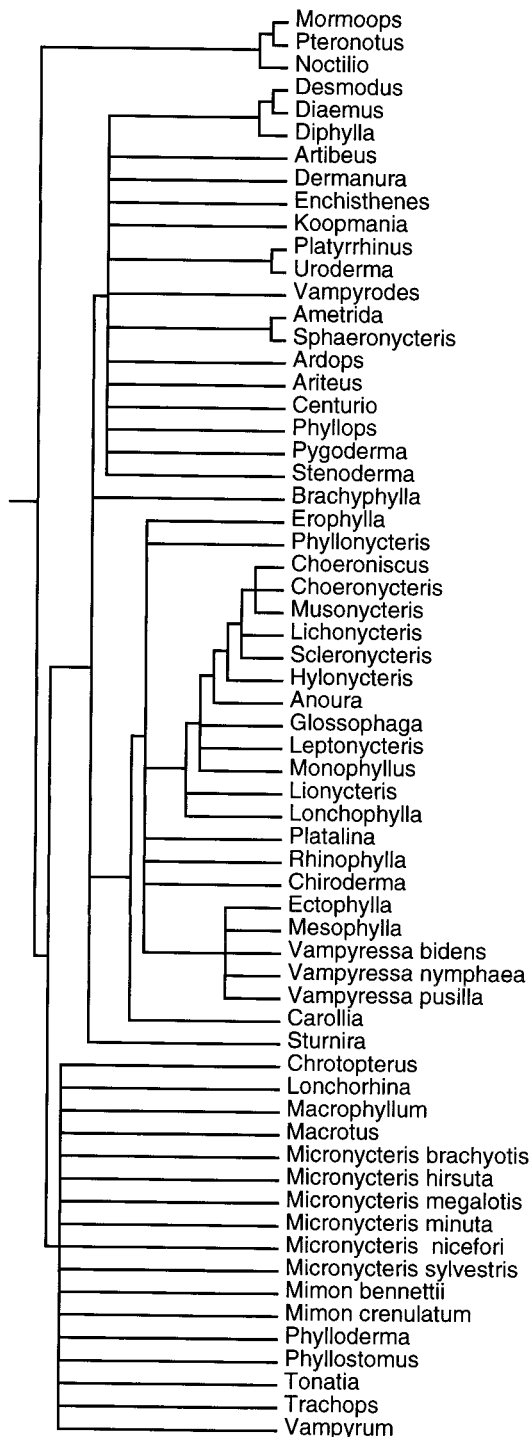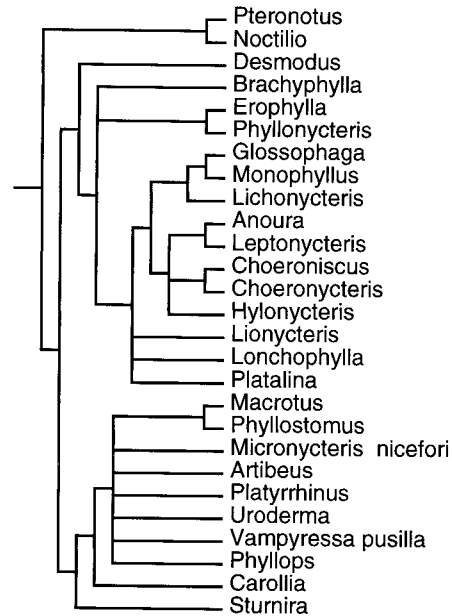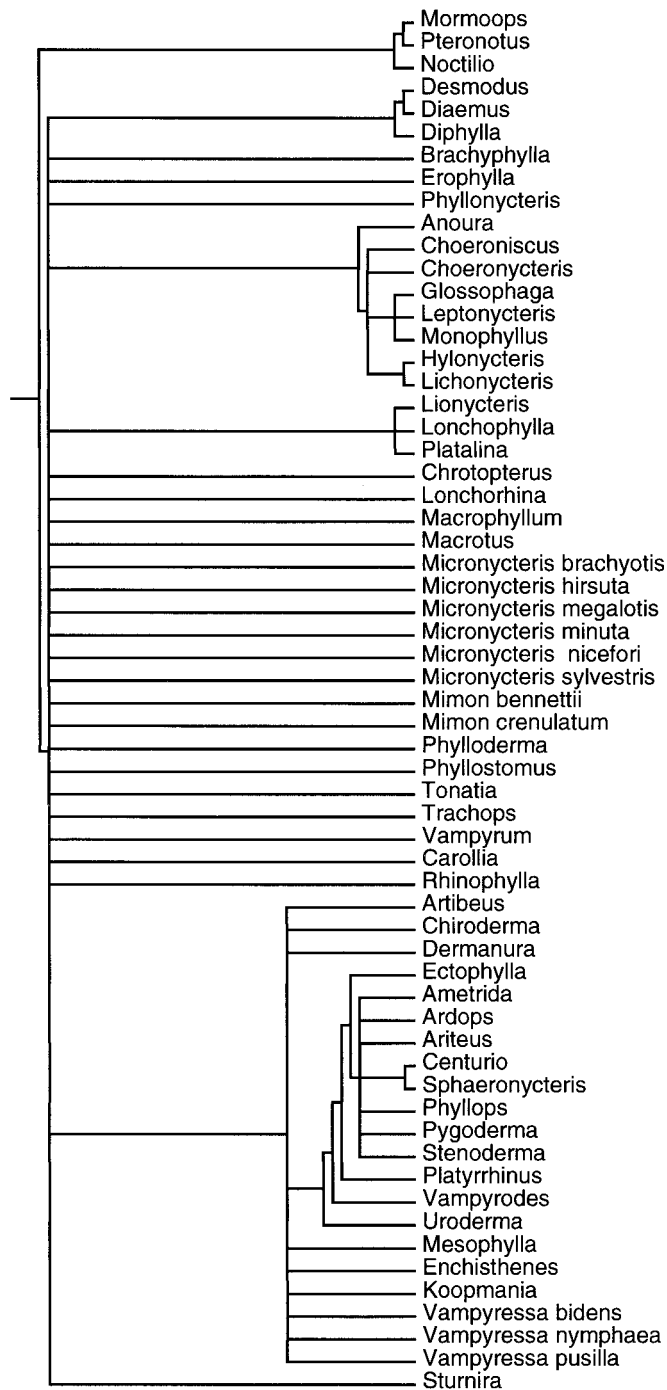
Fig. 45. Results of a heuristic search of 35 craniodental characters for all 63 taxa. The tree shown here is a strict consensus of more than 30,000 most parsimonious trees, each of 119 steps (CI = 0.555, RI = 0.832).
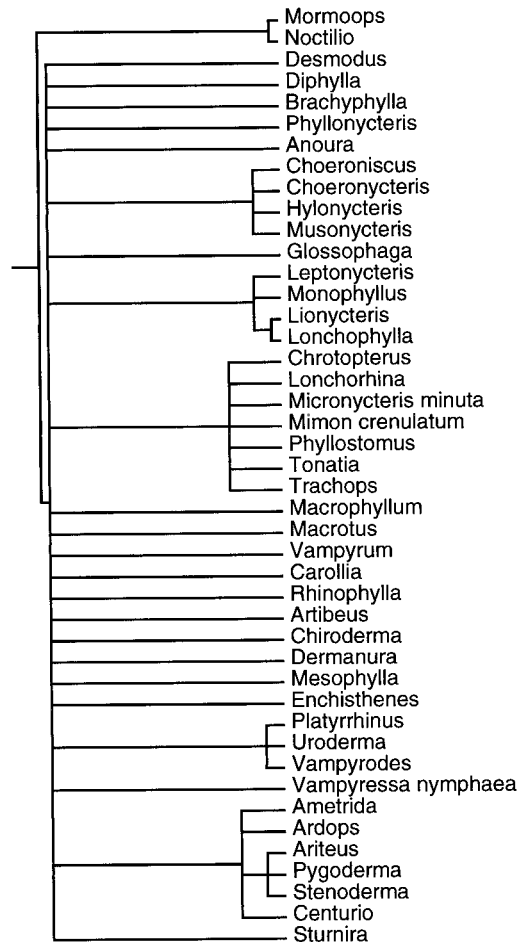


Fig. 46. Results of a heuristic search of 17 hyoid characters for 27 taxa. The tree shown here is a strict consensus of 24 most parsimonious trees, each of 40 steps (CI = 0.625, RI = 0.893).

sister taxa. Relationships among the remaining genera are unresolved.

**Tongue:** A heuristic search using 22 unordered tongue characters for 61 taxa (*Musonycteris* and *Scleronycteris* were excluded; see Character Descriptions: Tongue) resulted in more than 30,000 most parsimonious trees (55 steps each, CI = 0.564, RI = 0.876); a strict consensus of these trees is shown in figure 47. Although the positions of many taxa in this tree are unresolved, a few clades appear in all 30,000 trees. Desmodontinae, Glossophaginae, and Lonchophyllinae are each monophyletic. The relationships among these groups and the genera of phyllostomines, brachyphyllines, phyllonycterines, carolliines, *Sturnira*, and a clade consisting of the remaining stenodermatines could not be resolved using these data.

Within the monophyletic subfamilies, several additional relationships are apparent. Within Desmodontinae, *Desmodus* and *Diaemus* are sister taxa. *Anoura* appears as the sister taxon of the remaining glossophagines. Within this glossophagine clade, the relationships of *Choeroniscus* and *Choeronycteris*

Fig. 47.    Results of a heuristic search of 22 tongue characters for 61 taxa. The tree shown here is a strict consensus of more than 30,000 most parsimonious trees, each of 55 steps (CI = 0.564, RI = 0.876).

are unresolved. These two genera form a polytomy with (1) a clade comprising *Glossophaga*, *Leptonycteris*, and *Monophyllus*, and (2) the sister taxa *Hylonycteris* and *Lichonycteris*.

All stenodermatines, except *Sturnira*, form a clade. Within this large group, the relationships of most taxa remain unresolved. However, all ''short-faced'' stenodermatines form a clade and within this group *Centurio* and *Sphaeronycteris* are sister taxa. Successive sister taxa to the ''short-faced'' clade are *Ectophylla*, *Platyrrhinus*, *Uroderma*, and *Vampyrodes*.

**Digestive Tract:** A heuristic search using 1 unordered character for 24 taxa (see table 4) resulted in 51 most parsimonious trees (4 steps each, CI = 1.000, RI = 1.000). The strict consensus of these trees (not shown) is completely unresolved.

**Reproductive Tract:** A heuristic search using 5 unordered characters for 33 taxa (see table 4) resulted in more than 30,000 most parsimonious trees (10 steps each, CI = 0.800, RI = 0.966). The strict consensus of these trees (not shown) is completely unresolved.

**Brain:** A heuristic search using 2 unordered characters for 52 taxa (see table 4) resulted in more than 30,000 most parsimonious trees (11 steps each, CI = 0.909, RI = 0.960). The strict consensus of these trees (not shown) is completely unresolved.

**Sex Chromosomes:** A heuristic search using 1 unordered character for 56 taxa (see table 4) resulted in 51 most parsimonious trees (4 steps each, CI = 1.000, RI = 1.000). The strict consensus of these trees (not shown) is completely unresolved.

**Restriction Sites:** A heuristic search using 12 unordered characters for 44 taxa (see table 4) resulted in 120 most parsimonious trees (17 steps, CI = 0.706, RI = 0.917); a strict consensus of these trees is shown in figure 48. Although the relationships of many taxa could not be resolved using these data, several clades occur in all 120 most parsimonious trees. A clade of phyllostomines includes: *Chrotopterus*, *Lonchorhina*, *Micronycteris minuta*, *Mimon crenulatum*, *Phyllostomus*, *Tonatia*, and *Trachops*. In another clade, *Monophyllus* and *Leptonycteris* form a polytomy with the sister taxa *Lionycteris* and



Fig. 48. Results of a heuristic search of 12 restriction site characters for 44 taxa. The tree shown here is a strict consensus of 120 most parsimonious trees, each of 17 steps (CI = 0.706, RI = 0.917).

*Lonchophylla*. *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, and *Musonycteris* form a polytomy. *Uroderma*, *Platyrrhinus*, and *Vampyrodes* form a clade, as do all ''short-faced'' stenodermatines. Within the ''short-faced'' group, *Ariteus*, *Pygoderma*, and *Stenoderma* form a clade.

***Eco*RI-Defined DNA Repeat:** A heuristic search using 1 unordered character for 30 taxa (see table 4) resulted in 1 most parsimonious tree (1 step, CI = 1.000, RI = 1.000). The strict consensus of these trees (not shown) includes a single clade of *Artibeus*, *Dermanura*, and *Koopmania*.

**Summary:** In the strict consensus trees of four data partitions, Glossophaginae appears as monophyletic group (see table 6 for this and other clades). Glossophaginae is found in the strict consensus trees from the pelage and integument, craniodental, hyoid, and tongue analyses. Monophyly of Desmodontinae is supported by analyses of the pelage and integument, craniodental, and tongue partitions. Monophyly of Lonchophyllinae is supported by three data partitions (pelage and integument, tongue, restriction sites). Both Phyllonycterinae and Phyllostominae appear as monophyletic groups in the strict consensus trees of a single data partition (hyoid and craniodental, respectively). Surprisingly, Carolliinae and Stenodermatinae are not monophyletic in the strict consensus trees of any of these data partitions. However, "short-faced" stenodermatines appear as a monophyletic group in the strict consensus trees of three data partitions. A number of other higher-level clades appear in the strict consensus trees of single data partitions (see table 6).

There is some disagreement between the hyoid partition and the pelage and integument partition concerning relationships among the nectar-feeding taxa. The hyoid partition unites brachyphyllines, phyllonycterines, glossophagines, and lonchophyllines in a single clade, and unites this clade with desmodontines. In contrast, glossophagines and lonchophyllines form a clade with carolliines, phyllostomines, and stenodermatines in the pelage and integument tree (see fig. 44). Brachyphyllines and phyllonycterines are the sister taxa of this large clade. The pelage and integument partition and the craniodental partition also place different taxa as the most basal branch of the family (Desmodontinae and Phyllostominae, respectively). Most relationships at lower taxonomic levels (e.g., between genera) are supported by only a single partition, but are not contradicted by others (compare figs. 44, 45, 46, 47, and 48). However, both the pelage and integument and tongue partitions recover the clade comprising *Hylonycteris* and *Lichonycteris*, as well as the clade comprising *Centurio* and *Sphaeronycteris*.

## CHARACTER CONGRUENCE ANALYSIS

We used the entire data matrix in our character congruence analysis. The data matrix is presented in appendix 2; data on polymorphism and completeness is presented in table 5. A heuristic search using all 150 unordered characters resulted in 18 optimal trees (613 steps; CI = 0.462; RI = 0.765). The strict consensus of these trees is shown in figure 49. Monophyly of Desmodontinae (decay value: 8; bootstrap: 100) is strongly supported. Within Desmodontinae, *Desmodus* and *Diaemus* are sister taxa; this relationship is strongly supported with a decay value of 6 and a bootstrap value of 100.

Desmodontinae is the first (most basal) branch within Phyllostomidae. At the next node, there is a polytomy consisting of (1) *Brachyphylla*, (2) a clade comprising phyllonycterines, lonchophyllines, and glossophagines, and (3) a clade that includes phyllostomines, carollines, and stenodermatines. This large clade has a decay value of 2 and a bootstrap value of 36. In nine of the most parsimonious trees, *Brachyphylla* appears as the sister taxon of the phyllostomine, carolliine, and stenodermatine group. In the other nine trees, *Brachyphylla* is the sister taxon of a more inclusive clade that includes the phyllonycterines, lonchophyllines, glossophagines, phyllostomines, carollines, and stenodermatines.

Phyllonycterinae (decay: 7; bootstrap: 100), Lonchophyllinae (decay: 3; bootstrap: 92), and Glossophaginae (decay: 4; bootstrap: 95) are each monophyletic. Phyllonycterinae is the sister taxon of the very strongly supported lonchophylline-glossophagine clade (decay value: 7; bootstrap value: 96). Within Lonchophyllinae, *Lonchophylla* and *Lionycteris* are sister taxa, a relationship that is moderately supported with a decay value of 2 and a bootstrap value of 80. Within Glossophaginae, *Scleronycteris*, the sister taxa *Hylonycteris* and *Lichonycteris*, and an unresolved clade including *Choeroniscus*, *Choeronycteris*, and *Musonycteris* form a strongly supported polytomy (decay: 3; bootstrap: 93). Successive sister taxa to this group are *Anoura*, *Leptonycteris*, and the sister taxa *Glossophaga* and *Monophyllus*

TABLE 6
**Summary of Data Partition Results for Higher-Level Taxa**[a]

| Clade | Data partition supporting clade monophyly |
| --- | --- |
| Carolliinae[b] | None |
| Desmodontinae[c] | Pelage and integument, craniodental, tongue |
| Glossophaginae | Pelage and integument, craniodental, hyoid, tongue[d] |
| Lonchophyllinae | Pelage and integument, tongue, restriction sites[e] |
| Phyllonycterinae[f] | Hyoid |
| Phyllostominae | Craniodental |
| Stenodermatinae | None |
| "Short-faced" Stenodermatines | Pelage and integument, tongue, restriction sites |
| Brachyphyllinae + Carolliinae + Desmodontinae + Glossophaginae + Lonchophyllinae + Phyllonycterinae + Stenodermatinae | Craniodental |
| Brachyphyllinae + Desmodontinae + Lonchophyllinae + Glossophaginae + Phyllonycterinae | Hyoid |
| Brachyphyllinae + Glossophaginae + Lonchophyllinae + Phyllonycterinae | Hyoid |
| Brachyphyllinae + Carolliinae + Glossophaginae + Lonchophyllinae + Phyllonycterinae + Phyllostominae + Stenodermatinae | Pelage and integument |
| Carolliinae + Glossophaginae + Lonchophyllinae + Phyllostominae + Stenodermatinae | Pelage and integument |
| Carolliinae + Phyllostominae + Stenodermatinae | Hyoid |
| Glossophaginae + Lonchophyllinae | Pelage and integument, hyoid |

[a] For those data partitions that had at least one resolved clade of subfamilial rank or higher. Use of subfamilial names in higher-level clades is for convenience and does not indicate that these groups are monophyletic in these partitions.

[b] *Rhinophylla* does not appear in the hyoid analysis, so monophyly of Carolliinae cannot be evaluated using this data partition.

[c] Only *Desmodus* appears in the hyoid analysis, thus monophyly of Desmodontinae cannot be evaluated using this data partition.

[d] *Musonycteris* and *Scleronycteris* were not included in this parition due to missing data.

[e] Restiction sites are not available for *Platalina*, which does not appear in this analysis.

[f] Only *Phyllonycteris* appears in the restriction site analysis, thus monophyly of Phyllonycterinae cannot be evaluated using this data partition.

(see fig. 49 for additional decay and boot-strap values not mentioned in the text). In six of the most parsimonious trees, *Musonycteris* appears as the sister taxon of *Choeroniscus*. In another six trees, *Musonycteris* is the sister taxon of a clade containing *Choeroniscus* and *Choeronycteris*. In the remaining six trees, relationships within the clade containing *Musonycteris*, *Choeroniscus* and *Choeronycteris* are unresolved. *Scleronycteris* appears in three positions (six trees each): as the sister taxon of a clade including *Hylonycteris* and *Lichonycteris*; as the sister taxon of *Choeronycteris*, *Choeroniscus*, and *Musonycteris*; and as the sister taxon of a clade including the *Choeronycteris* group and *Hylonycteris* and *Lichonycteris*.

Phyllostominae is monophyletic, but is weakly supported (decay: 2; bootstrap: 40). Phyllostominae includes four clades: (1) *Phyllostomus* and *Phylloderma*, (2) two pairs of sister taxa: *Lonchorhina* and *Macrophyllum*, and *Mimon bennettii* and *M. crenulatum*, (3) *Trachops*, *Tonatia*, *Chrotopterus*, and *Vampyrum*, and (4) all *Micronycteris* species and *Macrotus* (see fig. 49 for additional decay and bootstrap values not mentioned in the text). The *Micronycteris* and *Trachops* groups form a weakly supported clade, and the *Lonchorhina* and *Phyllostomus* groups are successive sister taxa to this group. The subgenus *Micronycteris* is monophyletic, with *M. hirsuta* and *M. megalotis* as sister taxa; this sister group relationship is very strongly supported with a decay value of 3 and a bootstrap value of 85. Successive
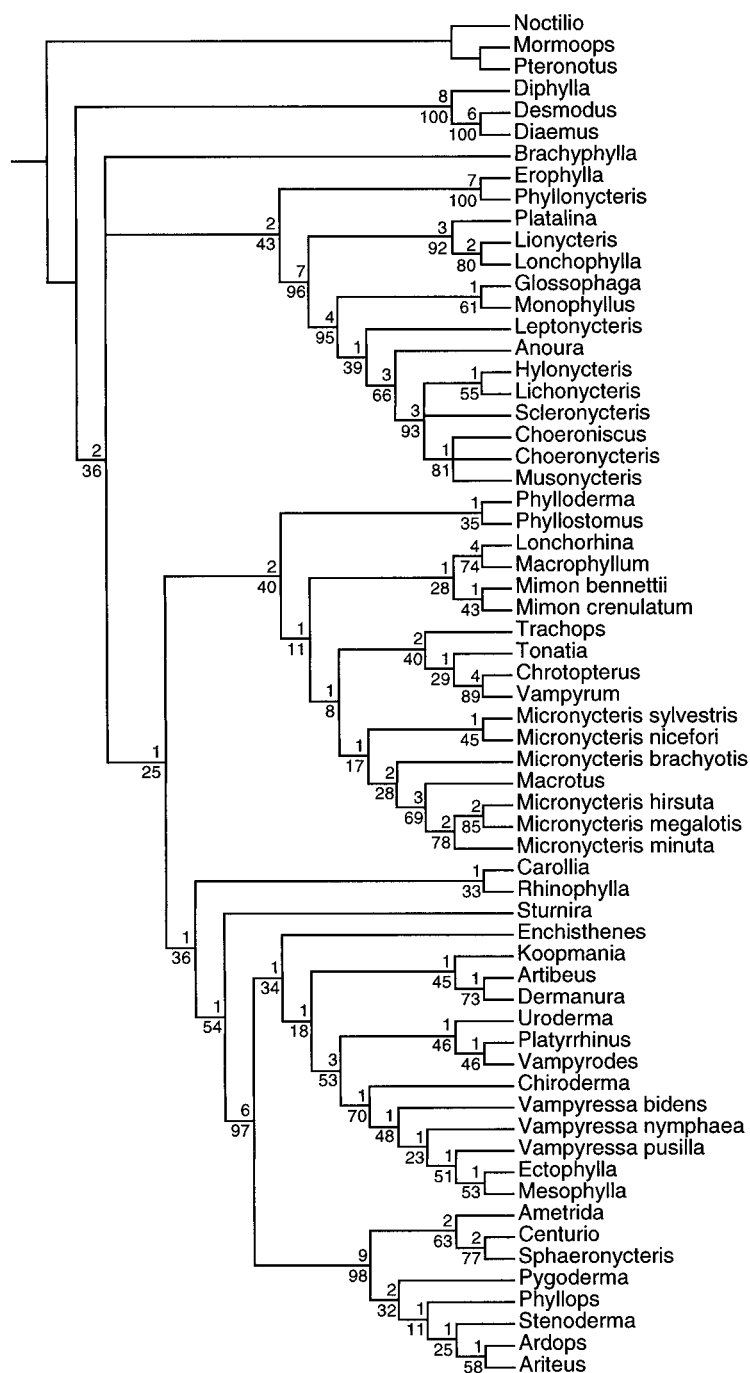
Fig. 49.   Results of a heuristic search using all 150 characters for all 63 taxa. The tree shown here is a strict consensus of 18 most parsimonious trees, each of 613 steps (CI = 0.463; RI = 0.765). Numbers appearing above the lines are decay values, below the lines are bootstrap values.

sister taxa to the subgenus *Micronycteris* are *Macrotus*, *Micronycteris brachyotis*, and the sister taxa *M. sylvestris* and *M. nicefori*. Within the *Trachops* group, *Tonatia* and *Trachops* are successive sister taxa to *Chrotopterus* and *Vampyrum*. The sister group relationship between *Chrotopterus* and *Vampyrum* is very strongly supported with a decay value of 4 and a bootstrap value of 89.

Carolliinae (decay value: 1; bootstrap: 33) and Stenodermatinae (decay value: 1; bootstrap: 54) are each monophyletic and together form a weakly supported clade. *Sturnira* is the sister taxon of the remaining stenodermatines. The clade of stenodermatines without *Sturnira* is strongly supported with high decay and bootstrap values (6 and 97 respectively). This group is itself composed of two large clades. One stenodermatine clade includes two smaller groups: (1) *Ametrida*, *Centurio*, and *Sphaeronycteris*, and (2) *Pygoderma*, *Phyllops*, *Stenoderma*, *Ardops*, and *Ariteus* (see fig. 49 for addtional decay and bootstrap values). Monophyly of this entire large clade is strongly supported with decay value of 9 and a bootstrap value of 98.

Within the *Centurio* group, *Centurio* and *Sphaeronycteris* are sister taxa. Within the *Pygoderma* group, *Stenoderma*, *Phyllops*, and *Pygoderma* are successive sister taxa to *Ardops* and *Ariteus* (see fig. 49 for decay and bootstrap values). A second stenodermatine clade is composed of three smaller clades: (1) *Koopmania* with the sister taxa *Artibeus* and *Dermanura*, (2) *Uroderma* with the sister taxa *Platyrrhinus* and *Vampyrodes*, and (3) the sister taxa *Mesophylla* and *Ectophylla* with the successive sister taxa *Vampyressa pusilla*, *V. nymphaea*, *V. bidens*, and *Chiroderma*. The clade including groups 2 and 3 above is moderately supported with a decay value of 3 and a bootstrap value of 53. Other moderately supported groups include: *Vampyressa pusilla*, *Ectophylla*, and *Mesophylla* (decay: 1; bootstrap: 51), and this group plus all other *Vampyressa* species and *Chiroderma* (decay value: 1; bootstrap value: 70). Other relationships within this larger clade are weakly supported (see fig. 49 for decay and bootstrap values). The *Koopmania* clade and the genus *Enchisthenes* are successive sister taxa to the *Uroderma* and *Chiroderma* groups.

# DISCUSSION

## COMPARISON OF RESULTS OF TAXONOMIC AND CHARACTER CONGRUENCE ANALYSES

The trees derived from analysis of the separate data partitions (our taxonomic congruence analyses), when compared with the results of our character congruence analysis, demonstrate the problems with relying exclusively on a taxonomic congruence approach. Many data partitions that are informative within the character congruence analysis (e.g., reproductive tract morphology) result in bushlike trees when analyzed separately. This is due in part to the small number of characters compared to the large number of taxa, but even the data partitions with the largest number of characters relative to the number of taxa appear unable to resolve relationships adequately (e.g., pelage and integument partition with 38 characters for 63 taxa, and hyoid partition with 17 characters for 27 taxa). As we noted earlier, analyzing

characters together may allow weak phylogenetic signal in some partitions to overwhelm ''noise'' in the data (Barrett et al., 1991; de Queiroz, 1993); this seems to be the case with our data set.

Our analyses highlight another problem with the taxonomic congruence approach, namely, that data partitions are often informative only in part of a tree (Hillis, 1987; de Queiroz, 1993). For example, most of our data partitions appeared to be most informative at a specific taxonomic level. We found that tongue data delimited clades that roughly correspond to subfamilies (e.g., desmodontines, glossophagines, lonchophyllines, and stenodermatines). However, relationships within these higher-level taxa remained unresolved. Furthermore, we found that data sets useful in resolving relationships within some clades were uninformative in other clades. The craniodental data appeared to be useful for resolving relationships

among glossophagine genera, but were not as useful in Phyllostominae or Stenodermatinae. Interestingly, the craniodental data suggest novel relationships for many taxa (e.g., Desmodontinae in a clade of stenodermatines), leading us to conclude that craniodental data may be more useful at lower taxonomic levels (e.g., within subfamilies) than at higher levels.

Although we have not used any statistical tests to determine whether our data sets are "heterogenous," a look at the separate trees produced for the three data sets in which at least 61 of the 63 taxa were scored for most characters (e.g., pelage and integument, craniodental, and tongue) suggests that there is some disagreement among these data sets. For example, the desmodontine clade appears in all three data sets, but its position changes in trees derived from different partitions (e.g., basal [pelage and integument], or with stenodermatines [craniodental]). Some relationships within Glossophaginae (e.g., the position of *Anoura* in craniodental vs. pelage and integument trees) and Stenodermatinae (e.g., *Sphaeronycteris* in craniodental vs. pelage and integument) are not compatible when these three trees are compared. As we noted previously, we find that there is no reliable way to divide morphological characters into groups that reflect some underlying biological reality. The incongruent areas of these partitions may merely represent an arbitrary division of evidence.

## CLASSIFICATION OF PHYLLOSTOMID BATS

**Higher-level Classification:** Our phylogenetic results indicate that many groupings of phyllostomid taxa previously recognized in formal classifications (e.g., Desmodontinae, Phyllostominae, Phyllonycterinae, Glossophaginae, Lonchophyllinae, Carolliinae, Stenodermatinae) are monophyletic. However, we suggest a somewhat different solution for taxonomic problems than those recently proposed (see table 7). We classify taxa phylogenetically (see e.g., de Queiroz and Gauthier, 1990, 1992, 1994), name only monophyletic groups, and use both ranked and unranked names in this classification

(see Simmons and Geisler [1998] for an overview of these issues). We prefer to retain most traditional subfamilial names (e.g., those used by Koopman, 1993; 1994), because these names have been extensively used in the past by systematists and researchers in fields such as ecology, behavior, and physiology.

Beginning at the base of the phyllostomid radiation (see fig. 49), we recognize Desmodontinae as the clade arising from the last common ancestor of *Desmodus*, *Diaemus*, and *Diphylla*. Desmodontinae is the basal branch of the family Phyllostomidae. Although it is possible to name the clade comprising the remaining phyllostomid taxa (e.g., Baker et al.'s [1989] use of Phyllostominae; see table 7), this group is weakly supported. Our experience suggests that the basal branching pattern of the family may change in future analyses as additional characters are added to the data matrix. Thus, we believe it would be inadvisable to apply a name to this group until basal relationships among phyllostomids are better supported.

Continuing up the tree (see fig. 49), Brachyphyllinae includes only *Brachyphylla*, pending further investigation of the relationships of this genus. Although most early investigators considered *Brachyphylla* a unique and primitive member of Stenodermatinae (e.g., Dobson, 1875; Miller, 1907; Hall and Kelson, 1959; Slaughter, 1970), later studies documented the similarity of *Brachyphylla* and Phyllonycterinae. Silva Taboada and Pine (1969) and Baker et al. (1981a) concluded that *Brachyphylla* should be placed in the subfamily Phyllonycterinae (correctly called Brachyphyllinae, which is the older name; Gray 1866d). Other workers have continued to maintain *Brachyphylla* in its own subfamily (e.g., Koopman, 1994), and based on our results, we recommend following this usage.

We recognize the clade arising from the last common ancestor of Phyllonycterinae and Glossophaginae (see below for the definitions of these taxa) as Hirsutaglossa (hirsuta = hairy [Latin]; glossa = tongue [Greek]). We propose this as an unranked taxonomic name because no rank currently exists between that of subfamily and family. Baker et al. (1989) identified this clade plus

*Brachyphylla* as Glossophagini within the subfamily Phyllostominae (see table 7). McKenna and Bell (1997) applied the name Glossophaginae to Hirsutaglossa plus *Brachyphylla*, and recognized three tribal taxa within Glossophaginae (Phyllonycterini, Lonchophyllini, and Glossophagini; see table 7). However, this arrangement leaves no name that can be used for the clade traditionally called Glossophaginae (i.e., the clade including glossophagines and lonchophyllines), a clade that is characterized by numerous synapomorphies (see appendix 4) and merits recognition. In our estimation, application of a traditional subfamilial name (e.g., Glossophaginae) to a larger, more variable group is unnecessarily confusing. Therefore, we recommend using Hirsutaglossa for the clade comprising most nectar feeders, and continue with more established usage for names like Glossophaginae (see below).

Within Hirsutaglossa, we define Phyllonycterinae as the clade arising from the last common ancestor of *Erophylla* and *Phyllonycteris*. Continued use of this name at the subfamilial level facilitates discussion and recognizes the ecological and morphological distinctiveness of these two genera. We propose that Glossophaginae be defined as the clade arising from the last common ancestor of Lonchophyllini and Glossophagini (see below for definition). This clade was consistently recognized by most authors until Griffiths (1982) recognized Lonchophyllinae. Since that time, there has been no name applied to the clade that includes lonchophyllines and glossophagines. Application of the name Glossophaginae to this group and recognition of the two clades it contains as tribes (Lonchophyllini and Glossophagini) facilitates discussion of the ecology and morphology of these bats using names recognizable to nonsystematists. Both tribes rely heavily on nectar and pollen for nutrients (Gardner, 1977b; Ferrarezzi and Gimenez, 1996) and share numerous synapomorphies including features of the pelage, face, teeth, wing, tongue, hyoid, and restriction sites. Some of these features are not found in any other phyllostomids (see appendix 4).

We define Lonchophyllini as the clade arising from the last common ancestor of *Lionycteris*, *Lonchophylla*, and *Platalina*. We recognize Glossophagini as the clade arising from the last common ancestor of *Anoura*, *Choeroniscus*, *Choeronycteris*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Monophyllus*, *Musonycteris*, and *Scleronycteris*.

We recognize Phyllostominae as the clade arising from the last common ancestor of the tribes Phyllostomini (first used as a tribal name by Baker et al., 1989), Lonchorhinini (Gray, 1866d), Vampyrini (Bonaparte, 1838), and Micronycterini (Van Den Bussche, 1992). None of these tribal names is new, although the last represents a change in rank from subfamilial to tribal level. We define Phyllostomini as the clade arising from the last common ancestor of *Phylloderma* and *Phyllostomus* (see below for comments on this relationship). Phyllostomini is therefore restricted from the definition of Baker et al. (1989), who applied this name to a larger clade that included *Lonchorhina*, *Macrophyllum*, *Mimon*, *Phylloderma*, *Phyllostomus*, and *Tonatia* (see table 7). We define Lonchorhinini as the clade arising from the last common ancestor of *Lonchorhina*, *Macrophyllum*, and *Mimon*. This group name was previously only applied to the nominate genus by Gray (1866d). We define Vampyrini as the clade arising from the last common ancestor of *Chrotopterus*, *Tonatia*, *Trachops*, and *Vampyrum*; inclusion of *Tonatia* in this group is new. Finally, we recognize Micronycterini as the clade arising from the last common ancestor of *Glyphonycteris*, *Lampronycteris*, *Macrotus*, *Micronycteris*, and *Trinycteris*. Previously, Van Den Bussche (1992) named two new subfamilies (Macrotinae and Micronycterinae) for these genera. Micronycterini is the appropriate name to apply to the clade that includes both *Macrotus* and *Micronycteris* because *Micronycteris* is the older generic name (Gray, 1866d).

The clade including Phyllostominae, Carolliinae, and Stenodermatinae is weakly supported and members share only a few derived features (see appendix 4). Given the possibility that additional data may change relationships among these taxa, we believe it would be inadvisable to apply a name to this clade until relationships among these groups are better supported.

TABLE 7
**Classifications of Phyllostomid Bats**

| Baker et al. (1989) | Koopman (1993) | McKenna and Bell (1997) |
|---|---|---|
| Phyllostomidae[a] | Phyllostomidae | Phyllostomidae |
| Desmodontinae | Desmodontinae | Desmodontinae |
| *Desmodus* | *Desmodus* | *Desmodus* |
| *Diaemus* | *Diaemus* | *Diaemus* |
| *Diphylla* | *Diphylla* | *Diphylla* |
| *Macrotus* (incertae sedis) | Brachyphyllinae | Glossophaginae |
| *Micronycteris* (incertae sedis) | *Brachyphylla* | Brachyphyllini |
| Vampyrinae | Glossophaginae | *Brachyphylla* |
| *Chrotopterus* | *Anoura* | Glossophagini |
| *Trachops* | *Choeroniscus* | *Anoura* |
| *Vampyrum* | *Choeronycteris* | *Choeroniscus* |
| Phyllostominae | *Glossophaga* | *Choeronycteris* |
| Glossophagini[b] | *Hylonycteris* | *Glossophaga* |
| *Brachyphylla* | *Leptonycteris* | *Hylonycteris* |
| *Choeroniscus* | *Lichoncyteris* | *Leptonycteris* |
| *Choeronycteris* | *Monophyllus* | *Lichonycteris* |
| *Erophylla* | *Musonycteris* | *Monophyllus* |
| *Glossophaga* | *Scleronycteris* | *Musonycteris* |
| *Hylonycteris* | Lonchophyllinae | *Scleronycteris* |
| *Leptonycteris* | *Lionycteris* | Lonchophyllini |
| *Lichonycteris* | *Lonchophylla* | *Lionycteris* |
| *Lionycteris* | *Platalina* | *Lonchophylla* |
| *Lonchophylla* | Phyllonycterinae | *Platalina* |
| *Monophyllus* | *Erophylla* | Phyllonycterini |
| *Musonycteris* | *Phyllonycteris* | *Erophylla* |
| *Phyllonycteris* | Phyllostominae | *Phyllonycteris* |
| *Platalina* | *Chrotopterus* | Phyllostominae |
| *Scleronycteris* | *Lonchorhina* | *Chrotopterus* |
| Phyllostomini | *Macrophyllum* | *Lonchorhina* |
| *Lonchorhina* | *Macrotus* | *Macrophyllum* |
| *Macrophyllum* | *Micronycteris* | *Macrotus* |
| *Mimon* | *Mimon* | *Micronycteris* |
| *Phyllostomus*[c] | *Phylloderma* | *Mimon* |
| *Tonatia* | *Phyllostomus* | *Phylloderma* |
| Stenodermatini | *Tonatia* | *Phyllostomus* |
| *Ametrida* | *Trachops* | *Tonatia* |
| *Ardops* | *Vampyrum* | *Trachops* |
| *Ariteus* | Carolliinae | *Vampyrum* |
| *Artibeus* | *Carollia* | Stenodermatinae |
| *Carollia* | *Rhinophylla* | Carolliini |
| *Centurio* | Stenodermatinae | *Carollia* |
| *Chiroderma* | Stenodermatini | *Rhinophylla* |
| *Dermanura*[d] | *Ametrida* | Stenodermatini |
| *Ectophylla* | *Ardops* | Stenodermatina |
| *Pygoderma* | *Ariteus* | *Ametrida* |
| *Phyllops* | *Artibeus* | *Artibeus* |
| *Rhinophylla* | *Centurio* | *Ardops* |
| *Sphaeronycteris* | *Chiroderma* | *Ariteus* |
| *Stenoderma* | *Ectophylla* | *Centurio* |
| *Sturnira* | *Mesophylla* | *Chiroderma* |
| *Uroderma* | *Phyllops* | *Ectophylla* |
| *Vampyressa*[e] | *Pygoderma* | *Mesophylla* |
| *Vampyrodes* | *Sphaeronycteris* | *Platyrrhinus* |
| *Vampyrops* (= *Platyrrhinus*) | *Stenoderma* | *Phyllops* |
|  | *Uroderma* | *Pygoderma* |
|  | *Vampyressa* | *Sphaeronycteris* |
|  | *Vampyrodes* | *Stenoderma* |
|  | *Vampyrops* (= *Platyrrhinus*) | *Uroderma* |
|  | Sturnirini | *Vampyressa* |
|  | *Sturnira* | *Vampyrodes* |
|  |  | Sturnirina |
|  |  | *Sturnira* |

TABLE 7
*Continued*

**This Paper**

Phyllostomidae
    Desmodontinae
        *Desmodus*
        *Diaemus*
        *Diphylla*
    Brachyphyllinae (incertae sedis)
        *Brachyphylla*
    Hirsutaglossa
        Glossophaginae
            Glossophagini
                *Anoura*
                *Choeroniscus*
                *Choeronycteris*
                *Glossophaga*
                *Hylonycteris*
                *Leptonycteris*
                *Lichonycteris*
                *Monophyllus*
                *Musonycteris*
                *Scleronycteris*
            Lonchophyllini
                *Lioncyteris*
                *Lonchophylla*
                *Platalina*
        Phyllonycterinae
            *Erophylla*
            *Phyllonycteris*

Unnamed Clade[f]
    Phyllostominae
        Lonchorhinini
            *Lonchorhina*
            *Macrophyllum*
            *Mimon*
        Micronycterini
            *Glyphonycteris*[g]
            *Lampronycteris*[h]
            *Macrotus*
            *Micronycteris*[i]
            *Neonycteris*[j]
            *Trinycteris*[k]
        Phyllostomini
            *Phylloderma*
            *Phyllostomus*
        Vampyrini
            *Chrotopterus*
            *Tonatia*
            *Trachops*
            *Vampyrum*

Nullicauda
    Carolliinae
        *Carollia*
        *Rhinophylla*
    Stenodermatinae
        Stenodermatini
            Ectophyllina
                *Artibeus*
                *Chiroderma*
                *Ectophylla*[l]
                *Enchisthenes*
                *Platyrrhinus*
                *Uroderma*
                *Vampyressa*[m]
                *Vampyrodes*
            Stenodermatina
                *Ametrida*
                *Ardops*
                *Ariteus*
                *Centurio*
                *Phyllops*
                *Pygoderma*
                *Sphaeronycteris*
                *Stenoderma*
        Sturnirini
            *Sturnira*

[a] Baker et al. (1989) placed tribes within Phyllostominae and all genera sedis mutabilis.

[b] *Anoura* appears to have been inadvertently left out of this classification.

[c] Includes *Phylloderma*.

[d] Includes *Enchisthenes*.

[e] Includes *Ectophylla*.

[f] Includes Phyllostominae and Nullicauda.

[g] *Glyphonycteris* includes *G. daviesi* and *G. sylvestris*.

[h] *Lampronycteris* contains a single species, *L. brachyotis*.

[i] *Micronycteris* includes *M. hirsuta, M. megalotis, M. microtis, M. minuta, M. sanborni*, and *M.schmidtorum*.

[j] *Neonycteris* includes a single species, *N. pusilla*.

[k] *Trinycteris* includes a single species, *T. nicefori*.

[l] Includes *Mesophylla*.

[m] Provisionally accepted, although paraphyletic, pending further investigation.

Although some recent classifications included a clade comprised of carolliines and stenodermatines named Stenodermatinae (McKenna and Bell, 1997) or Stenodermatini (Baker et al., 1989; see table 7), we have again chosen to conserve traditional subfamily names to avoid confusion and highlight the morphological and ecological distinctiveness of taxa. Therefore, we recognize the clade arising form the last common ancestor of Carolliinae and Stenodermatinae (see below for definition) as Nullicauda (nullus = no [Latin]; cauda = tail [Latin]), a new and unranked name.

We define Carolliinae as the clade arising from the last common ancestor of *Carollia* and *Rhinophylla*. This usage is entirely consistent with traditional classifications (e.g., Koopman, 1993, 1994).

We define Stenodermatinae as the clade arising from the last common ancestor of Sturnirini and Stenodermatini, two tribal level taxa that have been recognized by previous authors (e.g., Koopman 1994). We recognize

Sturnirnini as including only the genus *Sturnira*. We recognize Stenodermatini as arising from the last common ancestor of Stenodermatina and Ectophyllina (see below).

"Long-faced" and "short-faced" stenodermatines have been recognized as unique assemblages by many authors and our analysis provides support for both these groups (e.g., Miller, 1907; de la Torre, 1961; Smith, 1976; Lim, 1993; see appendix 4). We therefore propose recognition of two new subtribal taxa within Stenodermatini, Ectophyllina and Stenodermatina, for the taxa formerly known colloquially as the "long-faced" and the "short-faced" stenodermatines. We define these taxa using a stem-based approach. We define Ectophyllina as the clade of genera within Stenodermatini that share a more recent common ancestor with *Ectophylla* than with *Centurio* (these genera are *Artibeus*, *Chiroderma*, *Dermanura*, *Ectophylla*, *Enchisthenes*, *Koopmania*, *Mesophylla*, *Platyrrhinus*, *Uroderma*, *Vampyressa*, and *Vampyrodes*). We define Stenodermatina as those genera within Stenodermatini that share a more recent common ancestor with *Centurio* than with *Ectophylla* (these genera are *Ametrida*, *Ardops*, *Ariteus*, *Centurio*, *Phyllops*, *Pygoderma*, *Stenoderma*, and *Sphaeronycteris*). We use a stem-based approach here because the positions of the taxa *Artibeus*, *Dermanura*, *Enchisthenes*, and *Koopmania* are weakly supported. Use of a stem-based approach will allow the names Stenodermatina and Ectophyllina to be used in the future even if the relative positions of these four taxa should change.

The names Artibeini and Vampyressini, which appear in a tree in a paper by Ferrarezi and Gimenez (1996), are not avaliable. These names and several others appear in a classification by Owen (1987: appendix 4). Confusingly, Owen (1987) used Stenodermatini and Artibeini for both tribes and subtribes (the same name, with the same ending), making it difficult to interpret papers that use this classification. Owen (1987) also did not provide a list of characters differentiating these taxa, making these names unavailable under article 13 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1985). Furthermore, Owen (1987: 33) discounted this classification, stating ". . . I do not recommend adoption of the classification in Appendix IV."

**Generic Considerations:** Previous authors have questioned the monophyly of several phyllostomid genera including *Micronycteris*, *Mimon*, *Phyllostomus* (sensu Baker et al., 1988), *Artibeus*, and *Vampyressa* (Anderson, 1906; Miller, 1907; Straney et al., 1979; Honeycutt, 1981; Straney 1980; Koop and Baker, 1983; Owen, 1987, 1991; Baker et al., 1988a; Van Den Bussche, 1992; Lim, 1993; Van Den Bussche and Baker, 1993; Van Den Bussche et al., 1993, 1998; Simmons, 1996; Jassal and Simmons, 1996). We tested the monophyly of each of these taxa. Our results for several generic groupings do not conform to currently accepted taxonomy (e.g., Koopman, 1993, 1994). We therefore recommend adopting a revised classification that better reflects phylogenetic relationships. Although we identified additional clades that share numerous synapomorphies and are strongly supported (e.g., the clade comprising *Chrotopterus* and *Vampyrum*), we address only controversial relationships. For taxa whose classification has not been questioned, we retain traditionally used names to avoid confusion.

*Micronycteris* currently comprises five apparently monophyletic subgenera: *Glyphonycteris*, *Lampronycteris*, *Micronycteris*, *Neonycteris*, and *Trinycteris* (Simmons, 1996). A "total evidence" analysis that included allozymic, karyological, and morphological data supported the following relationships: (1) *Neonycteris* and *Trinycteris* were successive sister taxa to *Glyphonycteris*, (2) the *Neonycteris* clade was the sister taxon of *Micronycteris*, and (3) *Lampronycteris* was the basal branch within the genus (Simmons, 1996). Two karyological characters supported the monophyly of *Micronycteris* (Patton and Baker, 1978). However, the karyological study presumed that *Macrotus* exhibited the primitive karyotype, an assumption we consider flawed (see below). Our analysis indicates that *Micronycteris* as currently recognized is not monophyletic. Although we could have redefined *Micronycteris* to include *Macrotus*, we do not consider this a reasonable approach because the subgenera of *Micronycteris* are morphologically dis-

tinct, and all differ from *Macrotus* (see appendix 4). Based on the work of Simmons (1996), which supported monophyly of *Micronycteris* and *Glyphonycteris* (*Lampronycteris*, *Neonycteris* and *Trinycteris* are monotypic), we suggest that all subgenera of the genus *Micronycteris* be raised to generic rank. This approach renders all genera monophyletic without requiring any new names, and recognizes the substantial differences in morphology among these groups.

Handley (1960: 460) synonomized *Anthorhina* and *Mimon* suggesting that the two taxa were "not distinguishable even as subgenera." Although we found facial, pelage, and wing characters that distinguish the two subgenera (see appendix 4), our results support Handley's (1960) contention that *M. bennettii* and *M. crenulatum* are sister taxa. Several characters support this relationship including dental, molecular, and vibrissal features (see appendix 4).

Some authors have considered *Phylloderma* a junior synonym of *Phyllostomus* (e.g., Anderson, 1997) since Baker et al. (1988a: 12) concluded that "from the protein point of view, the inclusion of *Phylloderma* in the genus *Phyllostomus* would not add significant genetic variation to that already present in the genus." In a phylogenetic analysis of cytochrome *b* sequence data, Van Den Bussche and Baker (1993) confirmed that *Phylloderma* and *Phyllostomus* are closely related. However, examination of Van Den Bussche and Baker's (1993) shortest trees revealed that in all cases, *Phylloderma* did not nest within *Phyllostomus*, but appeared as the sister group of the clade including all traditionally recognized *Phyllostomus* species (*P. discolor*, *P. elongatus*, *P. hastatus*, and *P. latifolius*). Although *Phylloderma* could still be referred to *Phyllostomus* based on these data and our results, *Phylloderma* differs morphologically from the species of *Phyllostomus*, which share a distinct dental formula, skull shape, and noseleaf structure (see appendix 4). Thus, inclusion of *Phylloderma* in *Phyllostomus* would significantly alter the diagnosis of the genus *Phyllostomus*, but would not improve our understanding of group monophyly. Consequently, we follow traditional usage (e.g., Miller, 1907; Koop-

man, 1993, 1994) and recognize *Phylloderma* as a genus distinct from *Phyllostomus*.

Koopman (1994) recognized three subgenera of *Artibeus*: (1) the subgenus *Artibeus*, which includes large-bodied species, (2) the subgenus *Dermanura*, which includes small-bodied species and *Dermanura concolor*, and (3) the subgenus *Enchisthenes*. There was substantial disagreement concerning the relationships among these taxa and the monophyly of the group as a whole (e.g., Owen, 1987; 1991; Van Den Bussche, 1992; Lim, 1993; Van Den Bussche et al., 1993, 1998). Some authors raised each of these subgenera to generic rank (e.g., *Enchisthenes*: Miller, 1907; Baker, 1973; Gardner, 1977a; Hall, 1981; *Artibeus*: Owen, 1987; *Dermanura*: Owen, 1987). Additionally, Owen (1991) proposed a new genus, *Koopmania*, for *Dermanura concolor*. We found that *Artibeus* (s.l.) is paraphyletic because *Enchisthenes* does not group with the other three representatives of *Artibeus*, which form a clade (see fig. 49). We recommend that *Enchisthenes* be recognized as a genus distinct from *Artibeus* and that *Artibeus*, *Dermanura*, and *Koopmania* be recognized as subgenera of *Artibeus* pending further research into the relationships of these three taxa. Molecular evidence from the cytochrome *b* gene also supports these relationships (Van Den Bussche et al., 1993, 1998). Although we could recognize *Artibeus*, *Dermanura*, and *Koopmania* at the generic level as Owen (1987, 1991) recommended, there would be no convenient way to refer to these taxa as a group. Thus, we believe that the best classification option is to recognize three subgenera within *Artibeus*.

Koopman (1994) recognized five species and three subgenera of *Vampyressa*: (1) the subgenus *Vampyressa* includes *V. melissa* and *V. pusilla*, (2) the subgenus *Metavampyressa* includes *V. nymphaea* and *V. brocki*, and (3) the subgenus *Vampyriscus* includes only *V. bidens*. Recently, Owen (1987) found that these subgenera did not appear to form a monophyletic group (e.g., *Vampyressa pusilla* and *Mesophylla* formed a clade), but was unable to resolve relationships among most clades that included *Vampyressa* species. Owen (1987) recommended the following classificatory changes: (1) placing *Vampy-*

*ressa melissa* in a new unnamed subtribe, (2) placing *Vampyressa nymphaea* in the genus *Mesophylla* and recognizing the two taxa as the subtribe Mesophyllatini, (3) placing all remaining *Vampyressa* species in the subtribe Vampyressatini. More recent studies of stenodermatines (e.g., Lim, 1993) have failed to sample within *Vampyressa* and consequently did not provide a test of Owen's (1987) hypothesis. Although our results are not generally congruent with Owen's (1987), we found that *Vampyressa* is not monophyletic because *V. pusilla*, *V. nymphaea*, and *V. bidens* are successive sister taxa to *Ectophylla* and *Mesophylla*. However, we do not recommend nomenclatural changes for this taxon because there has not been a recent review of the species relationships within this genus. We did not include all species of *Vampyressa* in our analysis, so we have no way of knowing if, as Owen (1987) found, the subgenera are not monophyletic. We recommend further study of the relationships within *Vampyressa* and between this genus and other stenodermatines before changes are made in the classification of species currently referred to *Vampyressa*.

Although most previous authors recognized *Mesophylla* as a monotypic genus including only *M. macconnelli* (e.g., Starrett and Casebeer, 1968; Koopman, 1994), this genus has included members of the genus *Vampyressa* (Owen, 1987, see above). *Mesophylla* has also been placed in the genus *Ectophylla* (Laurie, 1955; Goodwin and Greenhall, 1961; Anderson et al., 1982). We found that *Mesophylla* and *Ectophylla* are sister taxa that share several synapomorphies including features of the dentition, noseleaf, and tongue (see appendix 4). Lim (1993) also found support for a sister-taxon relationship between these genera, with two synapomorphies (dental and external) uniting this node. We therefore propose that *Mesophylla* be considered a junior synonym of *Ectophylla*, the oldest name available for this clade (Allen, 1892b). We do not recommend revising *Ectophylla* to include some or all members of *Vampyressa* because relationships among *Vampyressa* species remain unclear (see above). Revising the usage of *Ectophylla* in this way would also leave no name for the clade of *Ectophylla alba* and *E. macconnelli*, which is distinct and merits recognition.

Throughout the remainder of the discussion section we employ the new classification (see table 7).

## INTERPRETATION OF CHROMOSOMAL DATA

In the 1960s and 1970s, several studies used chromosomal data to address relationships among phyllostomid bats. Attempts to produce a consensus tree of phyllostomid relationships (e.g., Honeycutt and Sarich, 1987a; Baker et al., 1989) assessed congruence between chromosomal data and other types of data (immunological and morphological). Therefore, we felt it was important to evaluate these data in the context of our phylogeny.

We agree with Gardner (1977a) who hypothesized that Desmodontinae, Phyllostominae, Phyllonycterinae, Carolliinae, and Stenodermatinae were each monophyletic, as were the subgroups we identify as Micronycterini (*Macrotus*, *Micronycteris*, and *Trinycteris*) and Phyllostomini (*Phylloderma* and *Phyllostomus*). Our analyses also agree with Patton and Baker's (1978) suggestion that *Lampronycteris*, *Micronycteris*, and *Trinycteris* form a clade. However, unlike Patton and Baker (1978) we found that *Macrotus* is also a member of this group.

Gardner (1977a) indicated that *Brachyphylla* is part of a hirsutaglossan group and forms a clade with Phyllonycterinae. Although the position of *Brachyphylla* is unresolved in our tree, the karyotypes of *Brachyphylla*, Phyllonycterinae, *Glossophaga*, *Monophyllus*, and *Leptonycteris* could be a derived feature of Hirsutaglossa plus *Brachyphylla*. However, if *Brachyphylla* is the sister taxon of Phyllostominae and Nullicauda, an alternative interpretation is that this karyotype evolved at the node joining Hirsutaglossa to the *Brachyphylla*, Phyllostominae, and Nullicauda clade. Therefore, this karyotype would represent a primitive feature retained by *Brachyphylla*. Several hirsutaglossan clades that we identified have also been supported by chromosomal data: *Glossophaga* and *Monophyllus* (Gardner, 1977a), and *Choeroniscus* and *Choeronycteris* (karyo-

types of *Musonycteris* are unknown; Baker, 1967; Gardner, 1977a).

Most authors working with karyotypes have identified Stenodermatinae as a monophyletic group (e.g., Baker, 1973; Gardner, 1977a), a finding with which we agree. Within Stenodermatinae, all authors have found Stenodermatina to be monophyletic (Baker, 1973; Greenbaum et al., 1975; Gardner, 1977a). We also agree with the findings of Baker (1973), Greenbaum et al. (1975), and Gardner (1977a) that *Chiroderma*, *Ectophylla macconnelli*, and *Vampyressa* are closely related. We also found, as these authors suggested, that *Ectophylla maconnelli* and *Vampyressa* represent the most derived group in this lineage. Additionally, Johnson (1979) found that *Ectophylla macconnelli* is karyologically very similar to *Vampyressa pusilla*. Our results agree with these findings.

There were a number of differences between our conclusions and those of previous authors who used chromosomes to investigate phyllostomid relationships. There are several possible methodological explanations for these differences. Many of the discrepancies between the results of early work using karyology and later studies were due to inaccurate homology assessments. With the advent of G- and C-banding, it became easier to discern which chromosomal arms were homologs by examining banding patterns. Nevertheless, there are still some problems with the use of karyotypes in phylogenetic reconstruction. Most investigators today use what is often termed ''global parsimony'' to investigate relationships among taxa. This method involves searching for the shortest networks, which are subsequently rooted at the node connecting the outgroup to the rest of the tree. Accordingly, this method involves no a priori assumptions about ingroup monophyly or direction of character change.

Global parsimony has not been used with karyological data in phyllostomids. Instead, most studies rely on comparisons with previously identified ''primitive'' reference taxa, typically within the ingroup, to identify homologous segments and rearrangements that are synapomorphies (see Materials and Methods). For example, it is only by comparing karyotypes of *Micronycteris nicefori* to *Macrotus waterhousi* (bearer of the pro-

posed primitive karyotype for phyllostomids [Patton and Baker, 1978]) that we can say that *M. nicefori* has ''Rearrangements of biarmed *waterhousi* chromosomes 1/2, 23/24, [and] 26/25 . . .'' (Patton and Baker, 1978: 453). We found that *Macrotus* nests well within Phyllostomidae, suggesting that chromosomal structure of *Macrotus* may have converged on the state seen in *Pteronotus* and *Noctilio*, the outgroups Patton and Baker (1978) used in their analysis. This possibility affects the interpretation of all chromosomal data reported thus far, as *Macrotus* was the primitive reference taxon for most studies.

Examination of areas where our results disagree with karyological studies suggests that these differences may also be, in part, caused by additional methodological problems. For example, Haiduk and Baker (1982) implicated limited sampling as one possible reason for their failure to support monophyly of Lonchophyllini. Autapomorphic karyotypes (i.e., those that have few recognizable arms relative to the primitive karyotype) offer additional problems and very often these taxa have been placed at the base of clades because their karyotypes offer few clues to their relationships (e.g., *Anoura*: Baker, 1967; Gardner, 1977a; *Uroderma*: Baker, 1967, 1973; Gardner, 1977a). Because autapomorphies may evolve at any point in the evolutionary history of a lineage, these taxa need not be basal. Finally, when interpreted in light of our results, it seems clear that in several cases taxa that retain primitive karyotypes have been grouped together based on shared primitive features rather than shared derived characters (e.g., *Glossophaga*, *Monophyllus*, *Leptonycteris*, Phyllonycterinae, Gardner, 1977a).

There are many areas of our tree that differ from hypotheses based on chromosomal data. For example, Johnson (1979) indicated that phyllostomines diverged from phyllostomid stem stock before other subfamilies, and subsequently were followed by desmodontines and stenodermatines, who split from a glossophagine-brachyphylline group before either of these subfamilies was distinct. Bass' (1978) examination of G-banded karyotypes suggested to her that Desmodontinae, Glossophaginae (s.l.), and Phyllonycterinae

formed a clade, with Phyllostominae as the sister group. Our results, that desmodontines and hirsutaglossans branched off prior to the divergence of phyllostomines and nullicaudans, agree with none of these findings. These differences may be due to assumptions about the primitive karyotype for the family.

Cadena and Baker (1976) suggested that *Diaemus* and *Diphylla* were less derived than *Desmodus* because they have karyotypes that are more similar to the proposed primitive karyotype for phyllostomids. Bass (1978) indicated that *Diphylla* and *Desmodus* are more closely related to each other than either is to *Diaemus*. Contra Bass (1978), we found that *Desmodus* and *Diaemus* form a clade. Within this context, it is still possible for *Desmodus* to be highly autapomorphic as Cadena and Baker (1976) suggested.

Gardner (1977a) grouped *Chrotopterus* and *Tonatia* but excluded two genera, *Vampyrum* and *Trachops*, that we include in Vampyrini. Although Gardner (1977a) identified a clade including *Phylloderma* and *Phyllostomus* (Phyllostomini), he indicated that the sister taxon of this group was *Mimon*, which we found to be a member of Lonchorhinini. Patton and Baker (1978) also identified a group of *Mimon*, *Phyllostomus*, and *Tonatia*. Our results suggest that these taxa may have been grouped together because they share primitive karyotypes.

Although Haiduk and Baker's (1982) study failed to find support for Lonchophyllini, they suggested that this may have been a sampling problem. Haiduk and Baker (1982) placed *Hylonycteris* as a sister taxon of *Choeronycteris* and *Musonycteris*, with *Choeroniscus* as the sister of this clade. We disagree with this finding, although all four genera appear to be closely related in our tree (see fig. 49). Gardner (1977a) identified *Hylonycteris*, *Lichonycteris*, *Platalina*, and *Scleronycteris* as forming a separate clade, contra our results. Gardner (1977a) also suggested that the sister taxa *Glossophaga* and *Monophyllus* formed a clade with *Leptonycteris*, and that this group and Phyllonycterinae (s.l.) formed a clade. We suggest that Gardner (1977a) grouped these four taxa on the basis of shared primitive karyotypes.

Baker and Bleier (1971) found that the karyotype of *Rhinophylla* appears most sim-ilar to those of phyllostomines, glossophagines, and stenodermatines. In contrast, we found support for a sister taxon relationship between *Rhinophylla* and *Carollia*. In the context of this hypothesis, we suggest that the similarity between the karyotype of *Rhinophylla* and other noncarolliine taxa is due to primitive retention of these karyotypic traits.

Baker and Lopez (1970) suggested that the $XX/XY_1Y_2$ sex system delineated a group consisting of *Ametrida*, *Artibeus*, *Enchisthenes*, and *Stenoderma*. Greenbaum et al. (1975) suggested that two ''short-faced'' groups could be identified: (1) *Centurio* and *Sphaeronycteris*, both of which have an XX/XY sex system, and (2) the remaining ''short-faced'' taxa, all of which have an $XX/XY_1Y_2$ system. Gardner (1977a) included *Ametrida* in a clade with *Ardops*, *Ariteus*, *Phyllops*, and *Pygoderma*. In contrast, we found that *Ametrida* is more closely related to *Centurio* and *Sphaeronycteris* and that *Artibeus* and *Enchisthenes* are basal members of Ectophyllina. According to our hypothesis, not all taxa sharing the $XX/XY_1Y_2$ system form a clade. We found that the $XX/XY_1Y_2$ system appears to be derived for Stenodermatini (and primitive for Ectophyllina and Stenodermatina). The XX/XY sex system is apparently a reversal in most members of Ectophyllina and the sister taxa *Centurio* and *Sphaeronycteris*.

Gardner (1977a) placed *Sturnira* within a large clade of Stenodermatini taxa, whereas we found that this genus was basal within Stenodermatinae. Baker (1967, 1973) and Gardner (1977a) were both unable to resolve the relationships of *Uroderma* due to its chromosomal uniqueness. We found that *Uroderma* clearly belongs in the Ectophyllina clade. Within this context, *Uroderma* remains highly autapomorphic. We also disagree with both Baker (1973) and Gardner (1977a), who indicated that *Enchisthenes* was most closely related to *Artibeus*. Our results indicate that *Enchisthenes* is a basal offshoot of Ectophyllina and is not closely related to *Artibeus*. Greenbaum et al. (1975) proposed that *Ectophylla alba* diverged from the *E. macconnelli-Vampyressa* line before a reduction in diploid number occurred. Subsequently, Gardner (1977a) placed *Ectophyl-*

*la alba* in a clade with *Artibeus*, *Enchisthenes*, *Vampyrodes*, and *Vampyrops* (= *Platyrrhinus*). In the context of our phylogeny, *Ectophylla alba*, the sister taxon of *E. macconnelli*, appears to be chromosomally autapomorphic.

## INTERPRETATION OF IMMUNOLOGICAL DATA

Although it is not possible to incorporate immunological distance data into our study, many previous workers based phylogenetic hypotheses on these data. Previous attempts to produce a consensus tree of phyllostomid relationships (e.g., Honeycutt and Sarich, 1987a; Baker et al., 1989) assessed congruence between immunological data and other types of data (chromosomal and morphological). Therefore, we felt it was important to evaluate these data in the context of our phylogeny.

Our finding that desmodontines are a basal phyllostomid lineage is congruent with some of Pierson's (1986) analyses, and all analyses from Honeycutt's (1981) and Honeycutt and Sarich's (1987a) studies. Other points of agreement include Honeycutt's (1981) and Honeycutt and Sarich's (1987a) finding that Desmodontinae and Phyllonycterinae were each monophyletic. We also agree with Straney's (1980) finding that *Artibeus*, his sole representative of Stenodermatinae, and *Carollia*, his sole representative of Carolliinae, formed a group, offering support for the clade we named Nullicauda. Honeycutt (1981) and Honeycutt and Sarich (1987a) provided additional support for Nullicauda. Gerber (1968) and Gerber and Leone's (1971) results suggested that Stenodermatinae was monophyletic, as did our study.

Honeycutt's (1981) and Honeycutt et al.'s (1981) conclusion that *Desmodus* and *Diaemus* were sister taxa, Honeycutt's (1981) finding that *Phylloderma* was strongly associated with *Phyllostomus hastatus*, and Honeycutt (1981) and Honeycutt and Sarich's (1987a) recognition of a *Vampyrum-Glyphonycteris* group all agree with our results. In these earlier studies, however, this clade did not include *Macrotus*, which we found associated with the *Vampyrum-Glyphonycteris* group. Our recognition of Vampyrini is supported by Straney's (1980) and Honeycutt's (1981) comparisons. However, in both of these earlier studies this clade did not include *Tonatia*, which we found associated with this group.

There were a number of differences between our conclusions and those of previous authors who used immunology to investigate phyllostomid relationships. There are several possible methodological explanations for these differences. Because distance data is phenetic in nature, it has been heavily criticized because, among other problems, it fails to distinguish between "primitive" and "derived" conditions, instead grouping taxa by overall similarity and increasing the number of ad hoc assumptions of homoplasy that must be made (e.g., Farris, 1983; Wiley, 1981). Thus, one possible explanation of the incongruence between our results and those of immunological studies is that some taxa may have slower rates of immunological evolution or may have retained primitive immunological features.

Arnold et al. (1982) noted that the immunological distinctiveness of phyllostomid albumins relative to other bats (the equivalent of 30 to 40 units of immunological distance) may be associated with a rate destabilization of the albumins in this group. These authors further suggested that changes in the three-dimensional structure of proteins (involving a cysteine and a possible relocation of disulfide bridges) could lead to nonequivalence of immunological distances between those caused by single amino-acid substitutions and those caused by conformational changes. Although Arnold et al. (1982: 11–12) did not discuss particular instances where this may have occurred, they concluded "We include this as final note for consideration of albumin evolution in phyllostomoid bats, where more than the usual number of interpretative problems exist."

Another problem with interpreting results of immunological distance data occurs when only unidirectional comparisons are made between taxa. Such tests allow only an "approximate" placement of taxa into the tree, which may be interpreted as "species group" relationships (Maxson and Maxson, 1990: 154). Furthermore, the relationship between sequence difference and immunological re-

activity has only been determined for microcomplement fixation, the technique used by Straney (1980), Honeycutt (1981), Honeycutt and Sarich (1987a), and in part by Pierson (1986). Other techniques, including the immunodiffusion and precipitin tests used by Gerber (1968) and Gerber and Leone (1971), and immunodiffusion and radioimmunoassay used by Pierson (1986), have a general correlation with microcomplement fixation, but use of these techniques introduces another source of error that may compromise phylogenetic studies (Maxson and Maxson, 1990).

All immunological investigations have suggested that phyllostomines are paraphyletic (e.g., Pierson, 1986; Honeycutt, 1981; Honeycutt and Sarich, 1987a; Gerber, 1968; Gerber and Leone, 1971), a finding with which we disagree. Reviewing the results of these studies, it is interesting to note that they are not only incongruent with our results, but also often with each other. Pierson (1986), Honeycutt (1981), and Honeycutt and Sarich (1987a) found that some phyllostomines were more closely related to members of Nullicauda than to other phyllostomines, and that members of Hirsutaglossa were derived from within a clade that included phyllostomines. Gerber (1968) and Gerber and Leone (1971) suggested that the phyllostomines they surveyed, which did not form a monophyletic group, were more closely related to desmodontines and some glossophagines.

Honeycutt (1981) and Honeycutt and Sarich (1987a) failed to recover Lonchorhinini and Micronycterini, and Pierson's (1986) analysis did not recover a Vampyrini-Micronycterini clade. The use of unidirectional comparisons to place *Lonchorhina*, *Macrophyllum*, *Mimon* may explain the differences between our phylogeny and that of Honeycutt (1981) and Honeycutt and Sarich (1987a). The failure of all these authors to recover Micronycterini (Honeycutt, 1981; and Honeycutt and Sarich, 1987a) and a Vampyrini-Micronycterini clade (Pierson, 1986) is due to the basal position of *Macrotus* in these trees.

Straney (1980), Honeycutt (1981), and Honeycutt and Sarich (1987a) found a relationship between *Macrotus* and the desmodontines, whereas Pierson (1986) found a re-

lationship between *Macrotus* and *Carollia*. We failed to recover any of these relationships. Pierson (1986) suggested that the association of *Macrotus* with *Carollia* was probably due to the conservative nature of the transferrin of *Carollia*. Honeycutt (1981), and Honeycutt and Sarich (1987a) postulated that a slower rate of evolution in desmodontines or equal yet independent divergence in albumins from those of other phyllostomids might have caused the association they found between *Macrotus* and desmodontines.

The association of *Tonatia* with *Phyllostomus* seems strongly supported by immunological data (Pierson, 1986; Honeycutt, 1981; Honeycutt and Sarich, 1987a). Placement of this genus was made using microcomplement fixation and two-way comparisons. Our grouping of *Tonatia* with Vampyrini genera (a novel hypothesis) is weakly supported, and there is weak support for the entire Vampyrini group. This suggests that additional data might support a relationship between *Phyllostomus* and *Tonatia*, as indicated by the immunological data. Alternatively, *Tonatia* could be immunologically primitive. If *Phyllostomus* is immunologically primitive, as suggested by its position in our tree, this might explain the persistent immunological clustering of *Tonatia* with *Phyllostomus*, a member of Phyllostomini.

Although the position of *Brachyphylla* is unresolved in the strict consensus tree from our character congruence analysis, immunological results consistently placed this genus with hirsutaglossan taxa (e.g., Baker et al., 1981a; Honeycutt, 1981; Pierson, 1986; Honeycutt and Sarich, 1987a). Placement of this genus was made using microcomplement fixation and two-way comparisons. Baker et al. (1981a), Honeycutt (1981), and Honeycutt and Sarich (1987a) identified a relationship between *Brachyphylla* and phyllonycterines (Pierson [1986] did not include phyllonycterines in her study), and the latter two studies revealed that this clade nested within Glossophagini. However, none of our most parsimonious topologies agree with the immunological data in this respect, although trees in which *Brachyphylla* is the sister taxon of Hirsutaglossa are only two steps longer than the most parsimonious topology. *Bra-*

*chyphylla*, like *Tonatia*, may be immunologically conservative.

Gerber (1968) and Gerber and Leone (1971) reported that *Choeronycteris* associated more closely with phyllostomines and desmodontines than with other glossophagines. We found that Glossophagini is monophyletic. The relationships we found within Glossophagini differ from those found by Honeycutt (1981). Honeycutt's (1981) unidirectional tests suggested that there were two major groups within Glossophagini: (1) *Glossophaga* and *Leptonycteris* and (2) *Anoura*, *Choeroniscus*, and *Monophyllus*. The position of *Hylonycteris* was equivocal with respect to the two reference taxa (*Glossophaga* and *Monophyllus*). The use of unidirectional comparisons to place these taxa may explain the differences between our phylogeny and that of Honeycutt (1981).

Gerber (1968) and Gerber and Leone (1971) found that *Carollia* had the greatest affinity for *Glossophaga* species, not for stenodermatines as we found. Gerber (1968) and Gerber and Leone (1971) found that Stenodermatini, Sturnirini, *Artibeus* (*Artibeus*), and *Artibeus* (*Dermanura*) were not monophyletic. They also failed to recover the *Platyrrhinus-Uroderma* clade that we found. Instead, their results suggested that *Chiroderma* and *Uroderma* were closest relatives and formed a clade with a group comprised of *Artibeus phaeotis*, *Platyrrhinus helleri*, and *Sturnira lilium*. As we noted above, immunodiffusion and precipitin tests introduce additional sources of error into phylogenetic analysis. This may be responsible for the discrepencies between our tree and that of Gerber (1968) and Gerber and Leone (1971).

## UTERINE FUSION: PROGRESSIVE AND UNIDIRECTIONAL?

Many mammalian orders have uterine morphologies that are shared by all group members (e.g., all edentates have a simplex uterus, all perissodactyls have a bicornuate uterus; Mossman, 1987). In contrast, chiropterans show a diversity of uterine morphologies with duplex, bicornuate, and fully simplex uteri, and varying degrees of internal uterine fusion; most of these morphologies occur in Phyllostomidae (Robin, 1881, Wood Jones, 1917; Wimsatt, 1975, 1979; Mossman, 1977, 1987; see characters 131 and 132 above).

In most mammalian orders, simplex uteri are correlated with small litters (Wimsatt, 1975, 1979; Mossman 1977). Bats typically produce single young regardless of uterine structure although multiple births occur in members of a few bat families, (e.g., vespertilionids like *Lasiurus*). Because cases of multiple births occur in taxa that nest well within the microchiropteran clade, small litter size appears to be primitive for Microchiroptera (and Phyllostomidae) and therefore does not provide an explanation for the evolution of a simplex uterus in these chiropteran groups (Hood and Smith, 1983).

Previous hypotheses concerning uterine evolution in mammals suggested that evolutionary changes in fusion of the uterine horns and internal uterine spaces were progressive, passing through intermediate states to reach more derived states, and unidirectional (Wood Jones, 1923; Mossman, 1953, 1977; Le Gros Clark, 1959; Lillegraven, 1969, 1976; Luckett, 1980; Hood and Smith, 1982, 1983). Under this scenario, a duplex uterus was considered primitive, the simplex uterus was derived, and the bicornuate condition represented an intermediate stage. Reversals were not thought to occur at any point in this evolutionary process.

Hood and Smith (1982, 1983) tested the progressive fusion hypothesis of uterine evolution for phyllostomid bats and concluded that it was correct. More primitive phyllostomids (e.g., desmodontines) have bicornuate uteri with a small common lumen, whereas more derived taxa have fully simplex uteri with a single lumen (e.g., carolliines and stenodermatines). Hood and Smith (1982) found no reversals.

Our results suggest a different pattern of uterine evolution (figs. 50, 51)[5]. We found that, as Hood and Smith (1982, 1983) indicated, the last common ancestor of all phyllostomids had uterine horns that were rough-

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[5] Although we lack data for these characters (see table 4) for many taxa included in our analysis, we have used the character state assignments reconstructed in MacClade as predictions of these states. Further work is needed to be confident of these interpretations.

ly half the length of the common uterine body. After the split with the desmodontines, the last common ancestor of the remaining phyllostomids had a more derived degree of external uterine fusion: a fully simplex uterus (fig. 50). The ''intermediate'' condition of external uterine fusion (uterine horns ¼ the length of the common uterine body) only occurs within the phyllostomine part of the tree, as a synapomorphy of Micronycterini plus Vampyrini (possibly also including Lonchorhinini, for which data is currently unavailable). Thus, external uterine fusion is clearly not progressive in phyllostomids when these data are optimized on our tree.

Patterns of variation in internal uterine fusion (character 132) appear to be slightly more congruent with the progressive fusion hypothesis (fig. 51). The last common ancestor of all phyllostomids was characterized by a distinct cornual lumina. After the split with the desmodontines, the last common ancestor of the remaining phyllostomids had a more derived state: cornual lumina that were reduced to intramural uterine cornua. In stenodermatines, the cornual lumina are absent, an even more derived condition. However, the evolution of internal uterine fusion in phyllostomids was not unidirectional as distinct cornual lumina evolved secondarily in the last common ancestor of Micronycterini plus Vampyrini (and possibly Lonchorhinini; data is currently unavailable for this clade). This represents a reversal to a more primitive condition.

We explored the possibility that the outcome of Hood and Smith's (1982) study was the result of testing the progressive fusion hypothesis with characters that had predetermined ordered transformation series (i.e., passage from the primitive state to the most derived state requires passage through the intermediate condition). Our comparison of analyses of the four female reproductive tract characters included in our study as ordered and unordered (characters 131–134) indicates that running characters unordered results in the collapse of the *Macrotus*-group node that Hood and Smith (1982) identified (i.e., *Macrotus*, *Trachops*, *Micronycteris hirsuta*, *M. megalotis* and *Desmodus* form a polytomy with the clade containing the remaining phyllostomids; see fig. 8 above). Thus, ordering

the characters in a manner that reflected the progressive fusion hypothesis appears to have partly biased the outcome of Hood and Smith's (1982) analysis. With the collapse of the *Macrotus*-group node, no claim can be made that the fusion of the external uterus proceeded in a progressive fashion.

Our character congruence analysis, and the reanalyzed data of Hood and Smith (1982, 1983) suggest that fusion of the external uterus was not progressive. In our tree the ''intermediate'' condition occurs only as a synapomorphy of Micronycterini plus Vampyrini. Although patterns of variation in internal uterine fusion appear to be more compatible with the hypothesis that uterine fusion proceeded in a progressive fashion, the reversal seen in Micronycterini and Vampyrini suggests that unidirectionality may not always characterize the evolution of internal uterine fusion.

## EVOLUTION OF FACIAL FEATURES: A PHYLOGENETIC PERSPECTIVE

**Vibrissae:** Most mammals possess vibrissae, long, stiff hairs that occur in discrete groups on the face. The locations of various groups of facial vibrissae are highly conservative (Pocock, 1914; Brown, 1971; Wineski, 1985; fig. 17A). Many and perhaps all facial vibrissae have separate representations in both the spinal trigeminal nucleus and the somatosensory cortex (Zucker and Welker, 1969; Waite, 1973a, 1973b; Woolsey, 1978), confirming a tactile role for these hairs.

A single superciliary vibrissa occurs above the eye on each side of the face in several phyllostomids (see fig. 17A). This trait appears to have evolved independently at least five times within the family (see character 11; fig. 52). Unambiguous transformations occurred in: (1) the last common ancestor of *Desmodus* and *Diaemus*, (2) the last common ancestor of *Lampronycteris*, *Macrotus*, and *Micronycteris*, (3) within *Lonchorhina* (*L. marinkellei*), and (4) in *Centurio*. There are two alternative interpretations of superciliary vibrissal evolution in Vampyrini. These vibrissae either evolved in the last common ancestor of *Chrotopterus* and *Vampyrum* (DELTRAN), or in the last common ancestor of *Tonatia* and these two genera (ACCT-
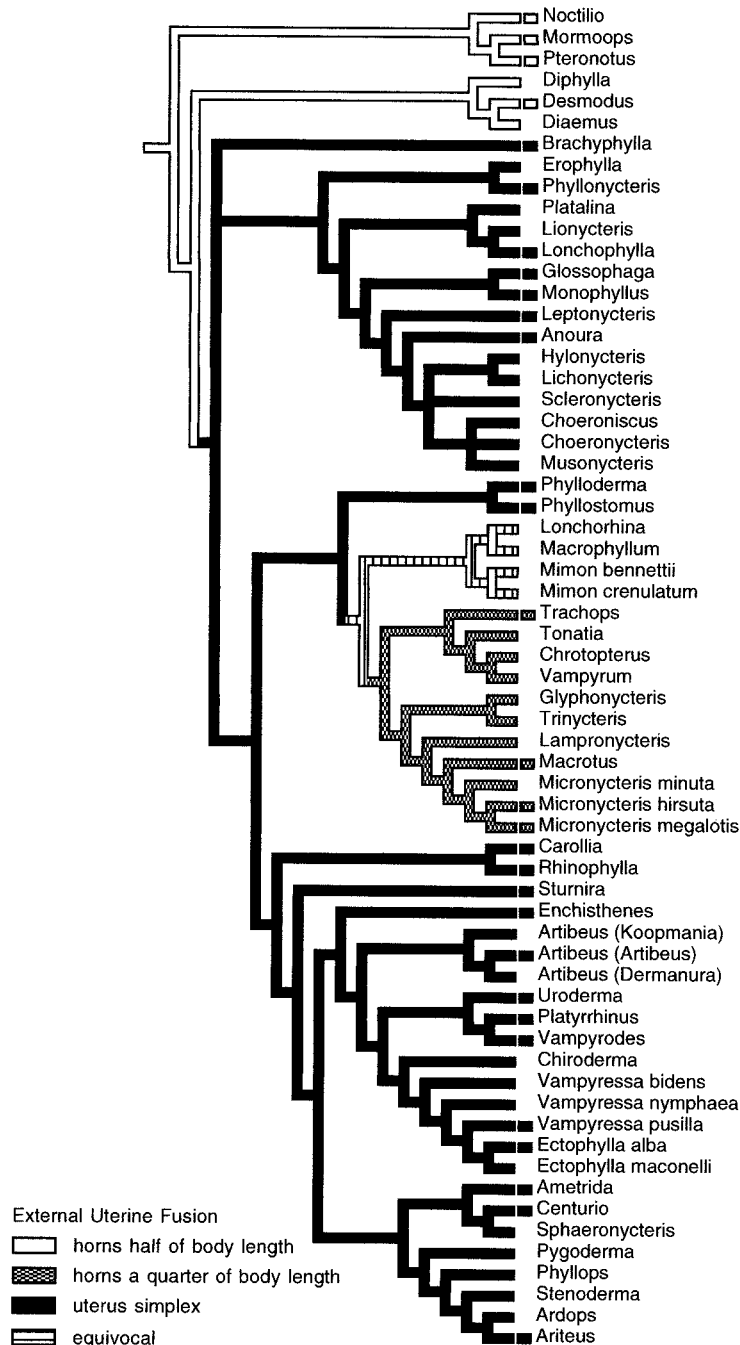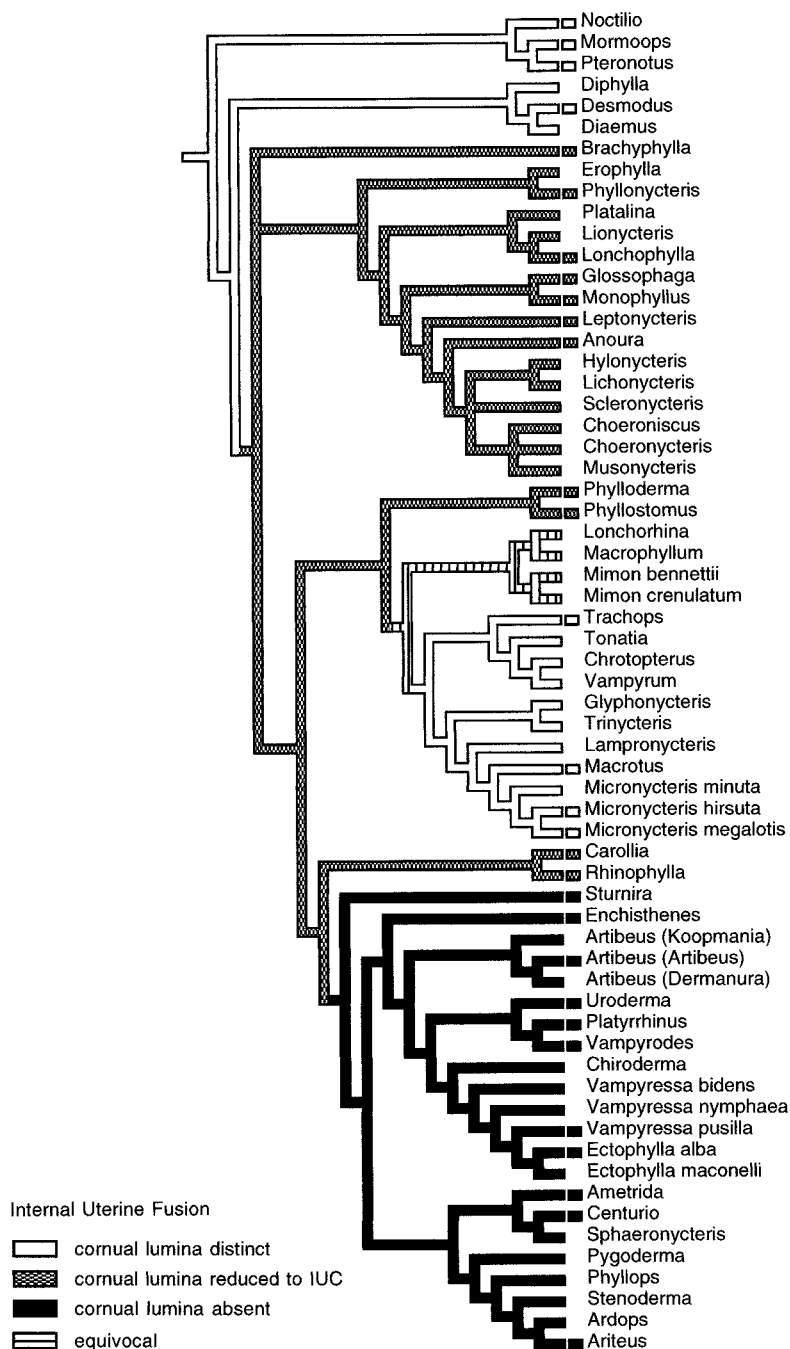
Fig. 50.　Degree of external uterine fusion (character 131) optimized onto the strict consensus tree from our character congruence analysis. The "intermediate" state of external uterine fusion (character 131: horns one quarter the length of uterine body) is derived from the simplex condition, suggesting that external uterine fusion is not progressive. The equivocal optimization within Phyllostominae is due to missing data in Lonchorhinini. To prevent an equivocal reconstruction for the base of the clade that includes all phyllostomids except desmodontines, we examined trees in which the position of *Brachyphylla* was resolved and fixed the node at the base of the clade that includes all phyllostomids except desmodontines with the state that occurred under the two alternative placements for this genus.

Fig. 51. Degree of internal uterine fusion (character 132) optimized onto the strict consensus tree from our character congruence analysis. There is a reversal to distinct cornual lumina from reduced cornual lumina (character 132) in some phyllostomines, suggesting that internal uterine fusion is not unidirectional. The equivocal optimization within Phyllostominae is due to missing data in Lonchorhinini. To prevent an equivocal reconstruction for the base of the clade that includes all phyllostomids except desmodontines, we examined trees in which the position of *Brachyphylla* was resolved and fixed the node at the base of the clade that includes all phyllostomids except desmodontines with the state that occurred under the two alternative placements for this genus.
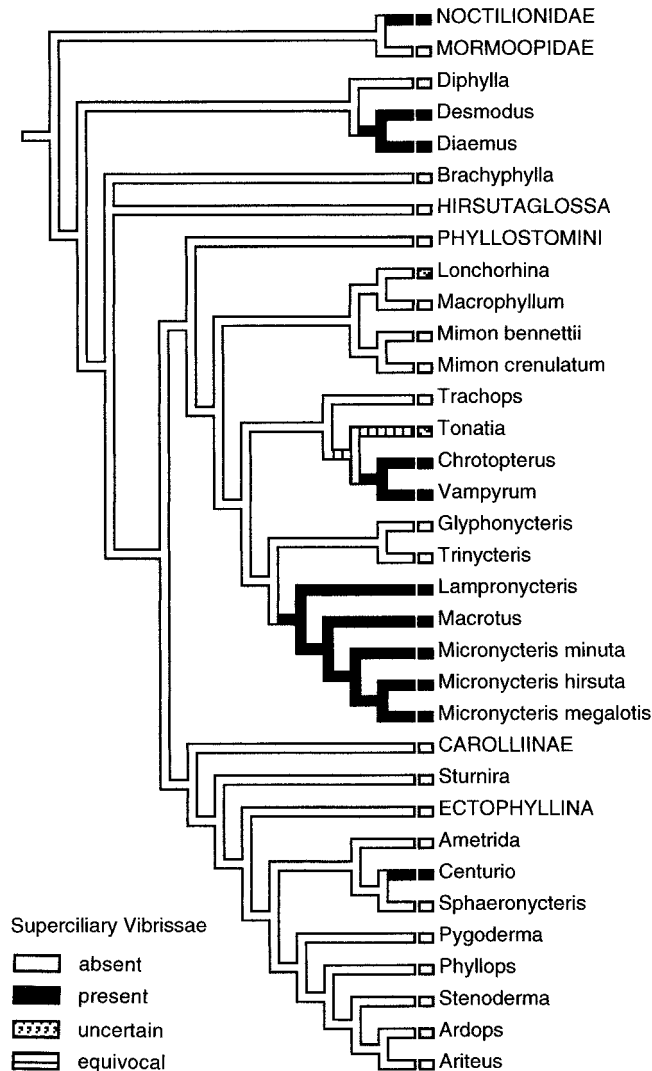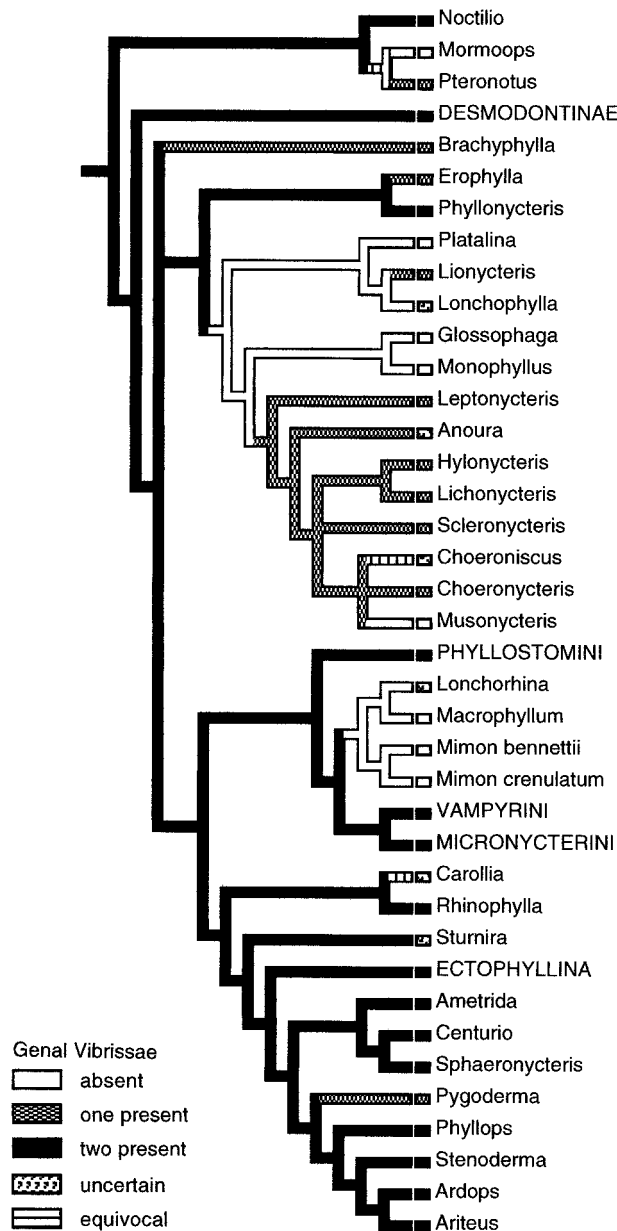
Fig. 52. Evolution of superciliary vibrissae inferred from optimization of character 11 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction for the clade including *Tonatia*, *Chrotopterus*, and *Vampyrum* is due to the presence of taxonomic polymorphism in *Tonatia* and has two possible resolutions. The state for *Lonchorhina* and *Tonatia* is ''uncertain'' because of taxonomic polymorphism in these genera (see character 11).

RAN). Under the former alternative, the superciliary vibrissae present in some species of *Tonatia* (e.g., *T. silvicola*, and *T. schulzi*) are derived within the genus.

Possession of two genal vibrissae ventral to and/or posterior to the eye on each side of the face (see figure 17A) appears to be the primitive state in phyllostomid bats (see character 12; fig. 53). The reconstruction for the base of Mormoopidae has two resolu-

tions: under ACCTRAN the reconstruction is equivocal, whereas under DELTRAN two superciliary vibrissae are primitive for Mormoopidae. All desmodontines, most phyllostomines, and most members of Nullicauda retain the primitive complement of two genal vibrissae. Members of Lonchorhinini share, as a synapomorphy, the absence of these vibrissae. *Pygoderma* is characterized by a reduction in vibrissal number to one, as are

many species of *Carollia*. However, other *Carollia* species lack these vibrissae, making the reconstruction equivocal.

In Hirsutaglossa, many genera also have a reduced number of genal vibrissae. Although *Phyllonycteris* retains two genal vibrissae in each cluster, *Erophylla* is autapomorphic with a single genal vibrissa on each side of the face. The genal vibrissae were completely lost in the last common ancestor of glossophagines. Within Lonchophyllini, *Lionycteris* has a single vibrissa on each side of the face. A single genal vibrissa on each side of the face unites the clade of *Anoura*, *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Musonycteris*, and *Scleronycteris*. Within this group there is additional variation: *Choeroniscus* species either retain the primitive complement (one vibrissa) or have no genal vibrissae, whereas *Musonycteris* has no genal vibrissae. The possible resolutions of the *Musonycteris* clade affect the reconstruction of the state changes. A single vibrissa on each cheek is primitive for *Choeroniscus* under all possible optimizations except when *Choeroniscus* and *Musonycteris* are sister taxa and ACCTRAN is used. Under this optimization absence of these vibrissae is primitive for the *Choeroniscus-Musonycteris* clade.

Possession of two vibrissae between the rami of the lower jaws well posterior to the mandibular symphysis appears to be the primitive state for phyllostomids (''interramal vibrissae;'' see character 13; fig. 54). This condition is present basally in all subfamilies. Within Phyllostominae, considerable vibrissal evolution occurred within tribes, except Micronycterini. Within Phyllostomini, the reconstruction for *Phyllostomus* is equivocal because some species have a single vibrissa, whereas others are polymorphic (absent or one vibrissa). Within Lonchorhinini, few genera retain the primitive number of interramal vibrissae. *Mimon* has lost the interramal vibrissae completely, whereas *Macrophyllum* is characterized by a reduction in vibrissal number to either none or one. Within Vampyrini, *Trachops* is uniquely characterized by the presence of a polymorphic condition (zero or one interramal vibrissa). *Chrotopterus* and *Vampyrum* have lost the interramals. However, within Vampyrini, the reconstruction of the primitive state for the tribe is equivocal as there are two possible resolutions of this character. Under ACCTRAN, absence of interramal vibrissae is primitive for the group of *Chrotopterus*, *Tonatia* (presence of these vibrissae in *T. silvicola* is derived within the genus), and *Vampyrum*. The base of Vampyrini remains equivocal, however. Under DELTRAN, presence of two interramal vibrissae is primitive for all of Vampyrini and this condition is retained by *Tonatia* (absence of these vibrissae in *T. saurophila* is derived within the genus).

Within Hirsutaglossa, Lonchophyllini is uniquely diagnosed by the presence of three interramal vibrissae. Additional changes within Hirsutaglossa occurred in the clade comprising *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, where there has been a reduction to a single interramal vibrissa.

The interramal vibrissae were lost in the last common ancestor of Stenodermatina, as well as in the last common ancestor of all members of Ectophyllina except *Artibeus* and *Enchisthenes*. Within the Ectophyllina group, a reversal to the primitive condition of two vibrissae occurs in *Vampyrodes*. *Artibeus* (*Koopmania*) has either one or two interramal vibrissae, a condition that is unique to this subgenus.

Lateral vibrissal columns, consisting of two vibrissae, were primitively present in phyllostomids (character 14; fig. 55). These vibrissae have been lost in *Phyllostomus*, Lonchorhinini, and Nullicauda. However, the reconstruction of this character is equivocal because there are two alterantive optimizations of the character. If ACCTRAN is used, loss of the lateral columns is a synapomorphy of the phyllostomine and nullicaudan clade. Reversal to the primitive condition (lateral vibrissal column present) occurs in *Phylloderma* and the clade comprising Vampyrini and Micronycterini. The DELTRAN alternative indicates that loss of the lateral vibrissal column evolved independently three times (once each in *Phyllostomus*, Lonchorhinini, and Nullicauda). One unambiguous character that uniquely diagnoses a stenodermatine group is the number of vibrissae in each medial vibrissal column (character 15; fig. 55). A reduction to three medial vi-
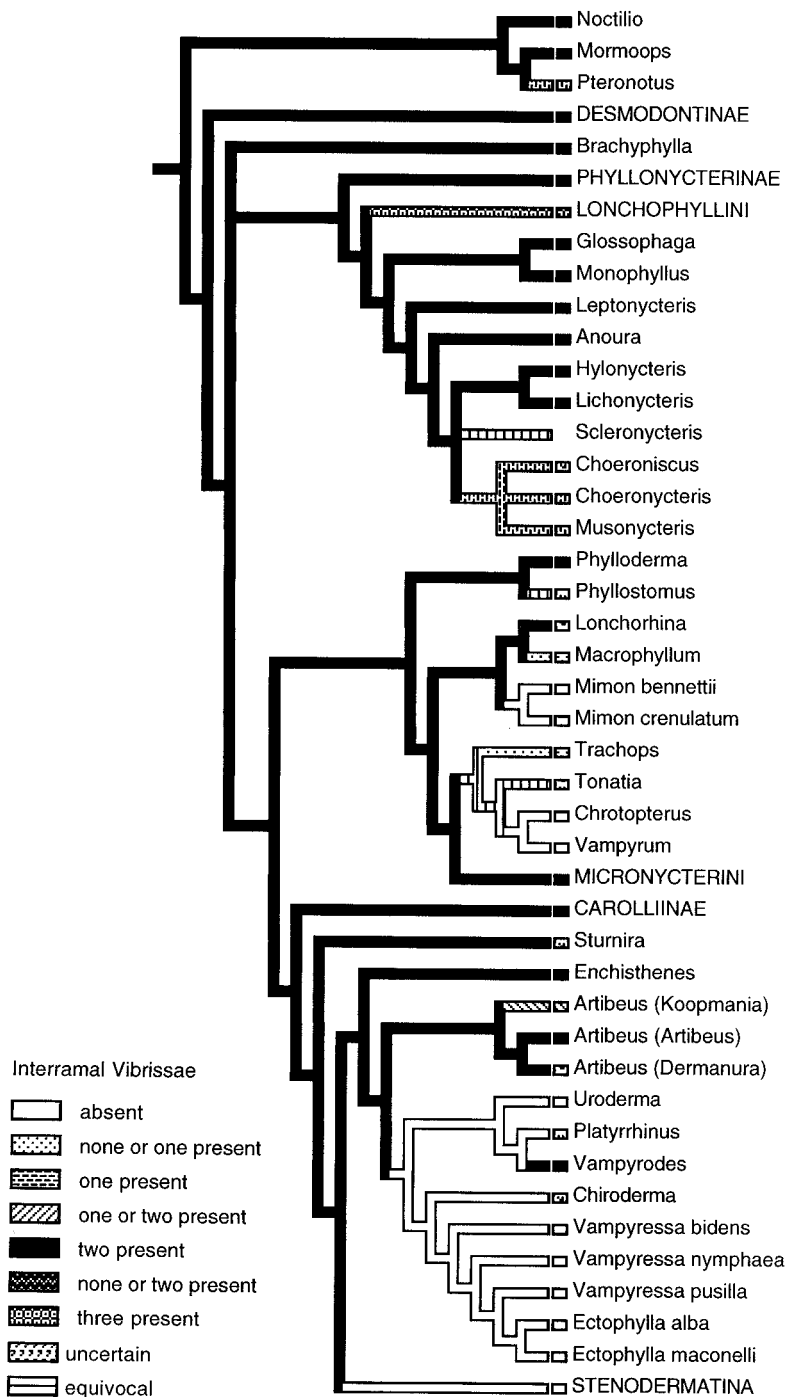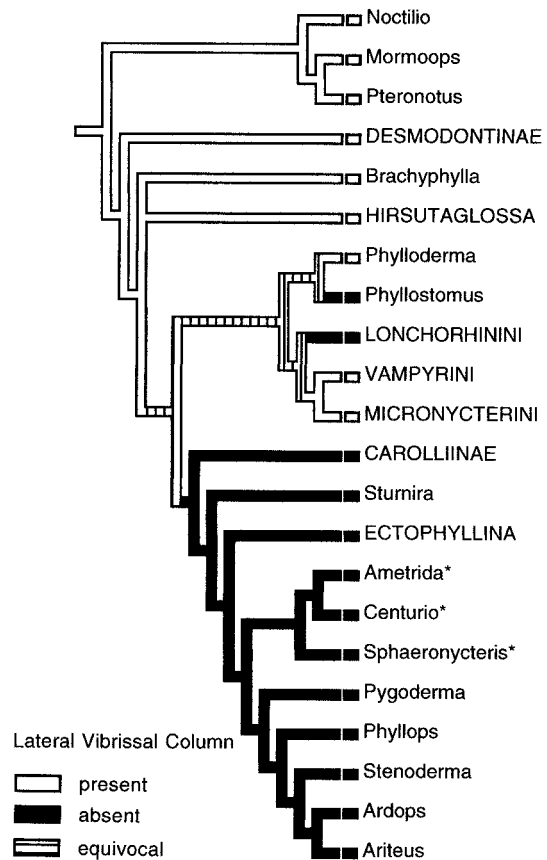
Fig. 53. Evolution of the number of genal vibrissae inferred from optimization of character 12 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction for the base of Mormoopidae is due to differences in interpretation under ACCTRAN and DELTRAN. The equivocal reconstructions for both *Choeroniscus* and *Carollia* are due to the presence of taxonomic polymorphism, and, in the case of *Choeroniscus*, different resolutions of the clade including this genus, *Choeronycteris*, and *Musonycteris*. The "uncertain" state, which appears for several taxa (e.g., *Loncho-phylla*, *Lonchorhina*), is due to taxonomic polymorphism (see character 12). To prevent an equivocal reconstruction for the base of Hirsutaglossa, we examined trees in which the position of *Brachyphylla* was resolved and fixed the node at the base of Hirsutaglossa with the state that occurred under the two alternative placements for this genus.

Fig. 54.   Evolution of the number of interramal vibrissae inferred from optimization of character 13 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction for *Scleronycteris* is due to missing data, while in *Phyllostomus* it is caused by taxonomic polymorphism. The equivocal reconstruction of this character in Vampyrini is due to the occurence of taxonomic polymorphism in *Tonatia*; there are two possible resolutions of this character in this clade under ACCT-

brissae in each medial row occurred in the last common ancestor of *Ametrida*, *Centurio*, and *Sphaeronycteris*.

Although vibrissal characters have not been previously used in phylogenetic analysis of phyllostomid bats, they appear to be informative at many taxonomic levels. Vibrissal characters diagnose numerous groups within Phyllostomidae (e.g., Lonchorhinini, Lonchophyllini, Stenodermatina). Even the interramal vibrissae character, which includes much polymorphism and is highly homoplastic (character 13: ci = .417), diagnoses several groups (e.g., *Mimon*, Lonchophyllini, the *Choeroniscus* clade, Stenodermatina). The utility of this character is reflected in its high retention index (ri = .731).

Vibrissal patterns may be related to foraging behavior in phyllostomids. Brown (1971) noted that facial vibrissae are well developed in predatory mammals. Thus, a high number of vibrissae would be expected in insectivorous and carnivorous bats, and a low number in nonpredatory bats. Our reconstructions indicate that, for most groups of vibrissae, the full complement is present primitively. Superciliary vibrissae, which are absent primitively in phyllostomids, evolved in predatory lineages (e.g., some Desmodontinae, Vampyrini, and Micronycterini) and the genus *Centurio*, a frugivore. Loss of vibrissae in some clusters (e.g., interramal, the lateral column) occurred most frequently in nullicaudans, suggesting these vibrissae may be less important in frugivorous taxa. Curiously, many of these vibrissae were also lost in members of Lonchorhini, a group of primarily insectivorous species.

**The Noseleaf:** The noseleaf of phyllostomid bats appears to be a uniquely derived feature of this group, despite the appearance of noseleaves in other bat families (e.g., Rhinolophidae, Megadermatidae; interpreted in the context of Simmons, 1998, and Sim-



Fig. 55. Evolution of the lateral vibrissal column inferred from optimization of character 14 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction that begins with the last common ancestor of Phyllostominae and Nullicauda is due to differences in interpretation of the character under ACCTRAN or DELTRAN. The three taxa with asterisks after their names have only three vibrissae in each medial vibrissal column (character 15).

←

RAN and DELTRAN. The "uncertain" state in some taxa (e.g., *Choeroniscus*, *Lonchorhina*) is due to taxonomic polymorphism (see character 13). To prevent an equivocal reconstruction for the base of the clade including *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, we examined trees in which the position of *Scleronycteris*, and the polytomy consisting of *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, was resolved and fixed the node at the base of *Choeroniscus*, *Choeronycteris*, and *Musonycteris* with the state that occurred under all alternative placements for these genera.

mons and Geisler, 1998). Noseleaves appear to function in directing nasally emitted echolocation calls (Fenton, 1984, 1985; Novick, 1977), but few studies have documented the role that these structures play in echolocation or addressed how differences in noseleaf structure affect nasal emission.

Hartley and Suthers (1987) investigated the role of the spear (which they termed the lancet) in *Carollia perspicillata*. These authors found that the spear acts to direct echolocation pulses in the vertical dimension, but does not affect emission in the horizontal dimension. Interference between the emission from each nostril is apparently used to direct sound in the horizontal dimension (Hartley and Suthers, 1987). These results are similar to those for other species of bats in which the role of the noseleaf was studied (e.g., *Megaderma* and *Rhinolophus*; Möhres and Neuwiler, 1966; Strother and Mogus, 1970; Sokolov and Makarov, 1971; Schnitzler and Grinnell, 1977). Although other features of the noseleaf and horseshoe have not been studied in relation to their affect on echolocation pulses, it seems likely that these characters influence some aspects of pulse emissions. Here, we explore the evolution of features of the noseleaf used in our phylogenetic analysis and evaluate synapomorphies and various optimization options for characters of both the spear and horseshoe. We also briefly examine the correlation between noseleaf morphology and mode of foraging.

Our phylogenetic analysis indicates that the last common ancestor of phyllostomids had a truncated (short) noseleaf (see characters 19, 20; fig. 56). In desmodontines, the spear is short and has a U-shaped indentation. The spear is also short in *Brachyphylla*. Because the position of *Brachyphylla* is unresolved in the strict consensus tree, there are two possible interpretations for the evolution of spear length in Hirsutaglossa based on the position of this genus. If *Brachyphylla* is the sister taxon of the clade that includes Hirsutaglossa, Phyllostominae, and Nullicauda (fig. 56A), the reconstruction for Hirsutaglossa is equivocal because there are two alternative optimizations. Under ACCTRAN, the long noseleaf evolved once in the last common ancestor of Hirsutaglossa, Phyllostominae, and Nullicauda, and the shortened

noseleaf of phyllonycterines is convergent with that in desmodontines and *Brachyphylla*. Under DELTRAN, the shortened noseleaf evolved once in phyllostomids and the longer spear of Glossphaginae is convergent with that of the phyllostomine and nullicaudan clade. If *Brachyphylla* is the sister taxon of Phyllostominae and Nullicauda (fig. 56B), then a short noseleaf is primitive for Hirsutaglossa. This, in turn, suggests that a long spear evolved twice, once in Glossophaginae and once in the clade comprising Phyllostominae and Nullicauda.

The position of *Brachyphylla* also influences the interpretation of the evolution of the U-shaped notch in the tip of the spear. If *Brachyphylla* is the sister taxon of Hirsutaglossa and the clade of Phyllostominae and Nullicauda (fig. 56C), the presence of a rounded or pointed spear tip (and absence of the U-shaped notch) is a synapomorphy uniting the latter three taxa. However, if *Brachyphylla* is the sister taxon of Phyllostominae and Nullicauda (fig. 56D), the reconstruction is equivocal. Under ACCTRAN, the reconstruction suggests that the presence of the U-shaped notch evolved convergently in desmodontines and *Brachyphylla*. Using DELTRAN, the reconstruction remains equivocal, exactly as it appears in figure 56D.

Interestingly, some phyllostomids that have a truncated spear and a U-shaped notch at the tip also have a well-developed skin ridge posterior to the spear that could possibly assist in directing echolocation pulses in the vertical dimension (see character 28). Although this structure, which evolved in the last common ancestor of the three desmodontine genera, is more posterior to the nostrils than the spear, its function has never been investigated in relation to the emission of echolocation calls.

Several phyllostomid taxa have structures posterior to the spear that differ from those in the desmodontines (see character 29). *Sphaeronycteris* is characterized by the presence of a large, visorlike structure, a feature apparently uniquely evolved in this genus. The visor is much larger in males than in females, suggesting that sexual selection may have played a role in its evolution. *Ectophylla macconnelli* and *Vampyressa pusilla* have small outgrowths (''leaflets'') posterior

Fig. 56. Evolution of spear length and spear tip shape inferred from the optimization of characters 19 and 20, respectively, on the strict consensus tree from our character congruence analysis. Optimization of spear length **A.** with *Brachyphylla* as the sister taxon of Hirsutaglossa, Phyllostominae, and Nullicauda. The equivocal reconstruction beginning with the last common ancestor the clade including Hirsutaglossa, Phyllostominae, and Nullicauda is due to alternative optimizations under ACCTRAN and DELTRAN. **B.** with *Brachyphylla* as the sister taxon of Phyllostominae and Nullicauda. Optimizations of spear tip shape **C.** with *Brachyphylla* as the sister taxon of Hirsutaglossa, Phyllostominae, and Nullicauda, and **D.** with *Brachyphylla* as the sister taxon of Phyllostominae and Nullicauda. The equivocal reconstruction beginning with the last common ancestor of Phyllostomidae is due to alternative reconstructions under ACCTRAN and DELTRAN.

to the spear that probably do not function in directing echolocation pulses because they are completely hidden behind the large spear. There are two alternative explanations for the origin of these leaflets. They may be a synapomorphy of the clade that includes both species of *Ectophylla* and *Vampyressa pusilla*, or they may be the result of convergent evolution in *Ectophylla macconnelli* and *Vampyressa pusilla*.

The interpretation of variation in the central rib is also somewhat ambiguous (see character 21, fig. 57). In the most basal phyllostomid taxa (e.g., desmodontines, *Brachyphylla*, phyllonycterines, and most glossophagines), the rib is undifferentiated. A proximally restricted rib, which does not reach

the tip of the spear, evolved at least four times in Phyllostomidae. A proximally restricted rib is a synapomorphy of the sister taxa *Lionycteris* and *Lonchophylla*. Within Phyllostominae, a proximally restricted rib appears as a synapomorphy of all Micronycterini. However, within this clade, *Macrotus* lacks a rib. Similarly, all members of Stenodermatini have, as a synapomorphy, a rib which extends to the tip of the spear, except *Sphaeronycteris*, which has a proximally restricted rib. The reconstruction in the phyllostomine-nullicaudan clade is equivocal because there are two alternative optimizations of this character for this group. Regardless of the position of *Brachyphylla* (as the sister taxon of Hirsutaglossa, Phyllostomi-
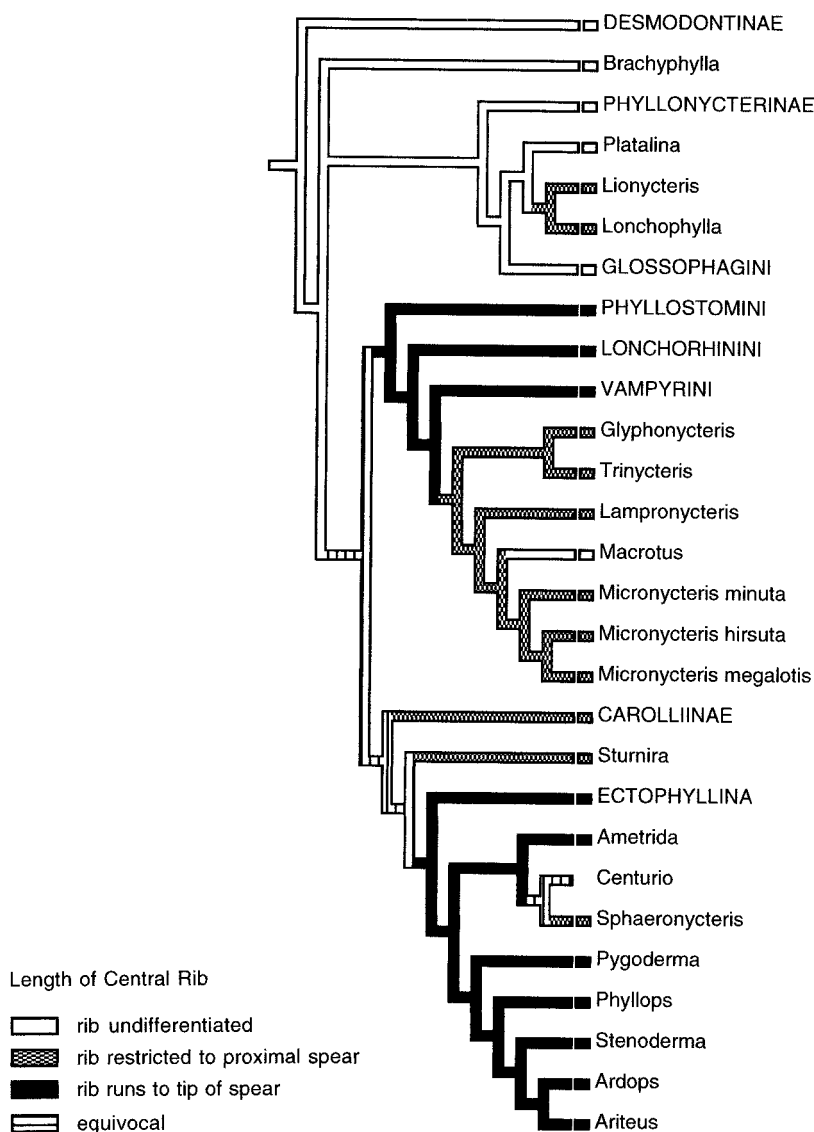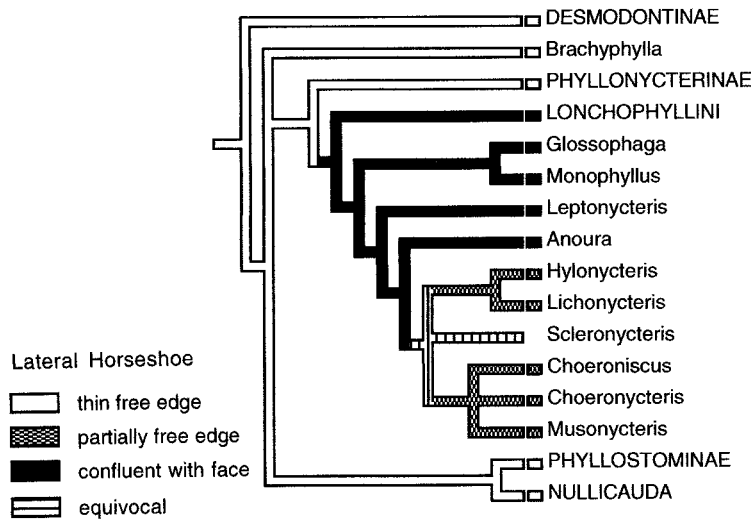
Fig. 57. Evolution of length of the central rib inferred from optimization of character 21 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction for the base of the clade including phyllostomines and nullicaudans is due to alternative interpretations under ACCT-RAN and DELTRAN. The reconstruction for *Centurio* is equivocal due to missing data (see character 18). See text for discussion.

nae, and Nullicauda, or as the sister taxon of Phyllostominae and Nullicauda), the optimization for this clade is similar. Under ACCT-RAN, the resolution for the base of the phyllostomine-nullicaudan clade is equivocal. Under DELTRAN, the absence of a rib is primitive for the clade uniting Phyllostominae and Nullicauda. For Nullicauda, the

ACCTRAN reconstruction suggests that having a proximally restricted rib is primitive, whereas the DELTRAN reconstruction remains equivocal.

Other features of the noseleaf have only slightly less ambiguous origins. The internarial ridge evolved within Phyllostomidae either five or six times (see character 22, fig.
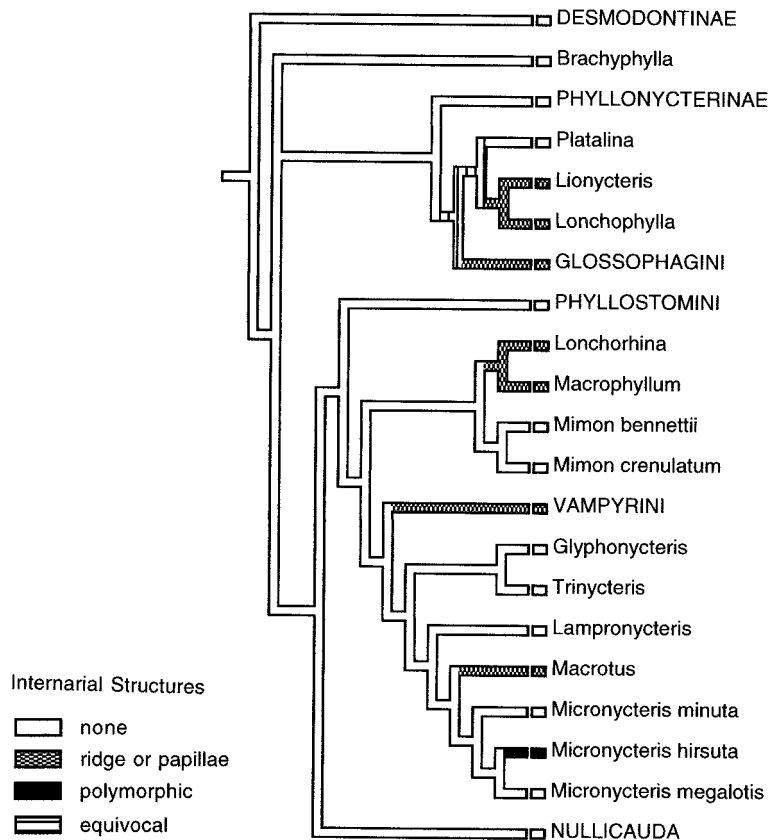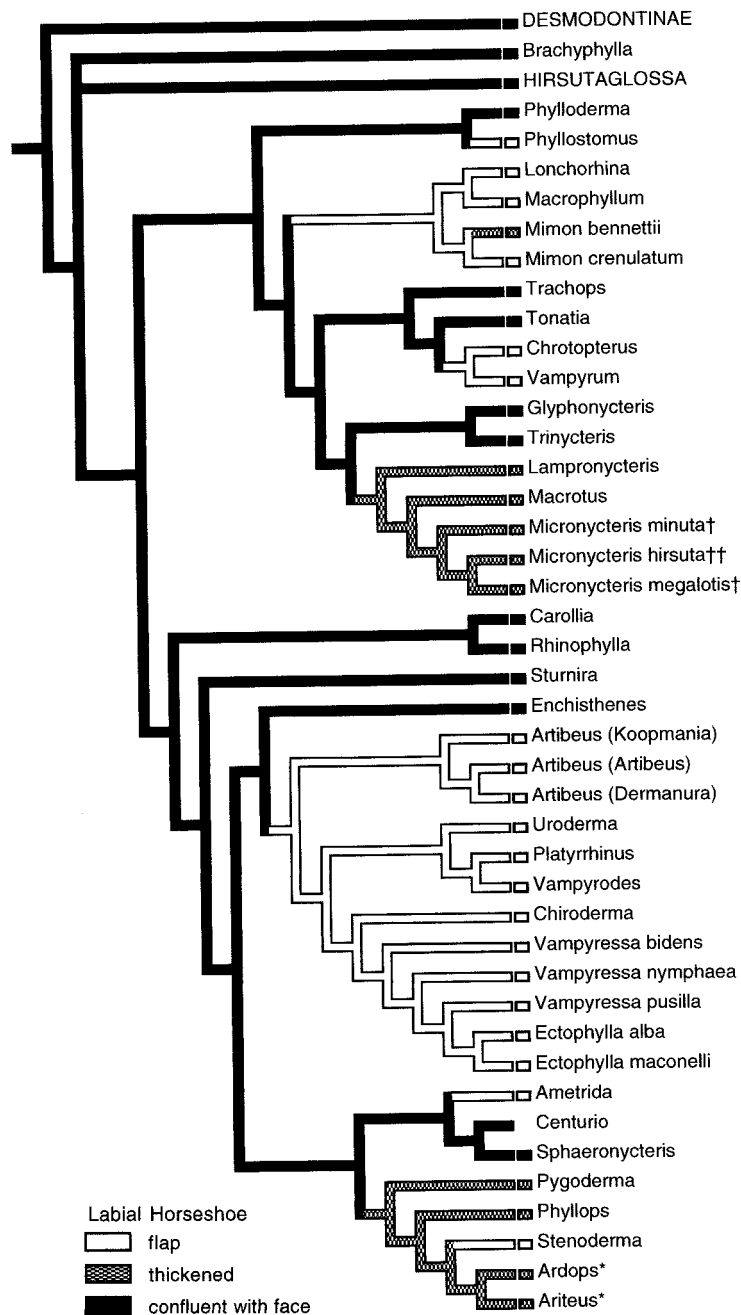
Fig. 58. Evolution of the internarial structures inferred from optimization of character 24 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction within Hirsutaglossa is due to alternative interpretations under ACCTRAN and DELTRAN. Note that "polymorphic" indicates that some individuals in a species have a ridge or papillae, whereas others do not.

58). This feature appears as a synapomorphy of the sister taxa *Lonchorhina* and *Macrophyllum*, as well as all members of Vampyrini. The presence of an internarial ridge is an autapomorphy of *Macrotus*. The appearance of this ridge in some individuals of *Micronycteris hirsuta* uniquely characterizes this species. In addition, depending on the optimization used, the internarial ridge is either a synapomorphy of Glossophaginae with a reversal in *Platalina* (ACCTRAN), or it evolved convergently, once in the last common ancestor of Glossophagini and once in the last common ancestor of *Lionycteris* and *Lonchophylla* (DELTRAN).

A unique feature of the noseleaf appears in three other phyllostomid taxa. *Chrotopterus* and *Vampyrum* have a sella, a rounded globular structure that we initially hypothe-

sized was homologous with a pommel-shaped structure in *Lonchorhina* (see character 23). The sella appears to have evolved twice, once in the last common ancestor of *Chrotopterus* and *Vampyrum* and a second time in *Lonchorhina*, and thus is not homologous in all three taxa.

The lateral boundary of the phyllostomid horseshoe was primitively thin and free (see character 24, fig. 59). Within Hirsutaglossa, the last common ancestor of all glossophagines apparently evolved a horseshoe that was fully fused to the face. Subsequently, a horseshoe that was only partly fused to the face (superior part is free, inferior part is fused to the skin of the face) probably evolved in the last common ancestor of *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, *Lichonycteris*, *Musonycteris*, and *Scleronycter-*

Fig. 59. Evolution of the lateral horseshoe inferred from optimization of character 24 on the strict consensus tree from our character congruence analysis. The equivocal reconstruction for the evolution of a ''partly free edge'' is due to the missing data for *Scleronycteris*.

*is*. Only when *Scleronycteris* appears as the sister taxon of the other genera that have a partially free horseshoe is the reconstruction at the base of the clade equivocal due to missing data.

The labial boundary of the horseshoe appears to have been undifferentiated from the upper lip primitively, as this condition occurs basally in the family as well as all subfamilies (see character 25, fig. 60). The presence of the thin, free edge is highly homoplastic, having evolved six times within the family (see below). In Phyllostominae, the lip and horseshoe were undifferentiated primitively within Phyllostomini (a more derived condition, a thin, free flap, occurs in *Phyllostomus*), Vampyrini (a more derived condition, a thin, free flap, occurs in *Chrotopterus* and *Vampyrum*), and Micronycterini. Within Micronycterini, the thickened condition of the labial horseshoe evolved in the last common ancestor of *Lampronycteris*, *Macrotus*, and *Micronycteris*, making this feature a synapomorphy of this group. Lonchorhinini is characterized by a derived condition, a thin, free edge. A thickened edge apparently evolved subsequently in *Mimon bennettii*.

Similarly, the presence of an undifferentiated labial horseshoe border was primitive in Nullicauda, appearing in Carolliinae, *Enchis-*

*thenes*, *Sphaeronycteris*, and *Sturnira*, (see fig. 60). Within Stenodermatina, a thickened boundary evolved in the last common ancestor of *Ardops*, *Ariteus*, *Stenoderma*, *Phyllops*, and *Pygoderma*. In *Stenoderma*, a thin, free flap has evolved. A thin, free flap also appears as autapomorphy of *Ametrida*. A thin, free flap also evolved in the last common ancestor of all Ectophyllina save *Enchisthenes*, making this feature a synapomorphy of this group.

Among taxa that have a thickened labial border of the horseshoe, *Ardops* and *Ariteus* share, as a synapomorphy, the presence of a V-shaped labial projection (see character 27, fig. 60). The presence of a V-shaped notch in some individuals appears in *Micronycteris megalotis* and *M. minuta*, whereas the presence of this feature in all individuals of *Micronycteris hirsuta* is uniquely derived in this taxon. The other taxa with a thickened labial border all possess a smooth rounded border (e.g., *Macrotus*, *Mimon bennettii*, *Lampronycteris*, *Phyllops*, and *Pygoderma*).

Finally, two genera, *Chrotopterus* and *Vampyrum*, have a horseshoe in which the thin, free edges are cupped around the nostrils (see character 26; reconstruction not shown). This feature is unique to these two phyllostomids; in all other genera with free

Fig. 60. Evolution of the labial horseshoe inferred from optimization of character 25 on the strict consensus tree from our character congruence analysis. The morphology of the thickened labial horseshoe (character 27) is also indicated: asterisks indicate taxa with a V-shaped labial projection; a single cross indicates taxa in which all individuals have a V-shaped notch; a double cross indicates taxa in which some individuals have a V-shaped notch. The state for *Centurio* is not indicated because we scored this taxon "?" for all characters related to the noseleaf (see character 18).

edges on the horseshoe, the labial edge lies flat over the upper lip.

Noseleaf morphology appears to be useful in phylogenetic reconstruction at many taxonomic levels. Noseleaf characters diagnose numerous groups within Phyllostomidae (e.g., Glossophaginae, Lonchorhinini, Vampyrini). In addition, congruence of these characters with those of other systems indicates that our hypotheses of homology for the various structures seem to be valid. One notable exception is the sella of *Chrotopterus*, *Lonchorhina*, and *Vampyrum* (see above).

The noseleaf became a much more elaborate and complex structure within phyllostomids over evolutionary time. Primitively within the family, the spear was short, the internarial region was flat, and the horseshoe was undifferentiated from the upper lip. Subsequently, within the various subfamilies, the spear became more elongate, the central rib and other internarial structures evolved, and the labial horseshoe became flaplike or cupped in some taxa.

The evolutionary forces shaping noseleaf morphology in phyllostomids remain unknown. Earlier researchers proposed that noseleaf morphology was related to foraging behavior and that echolocation played some role in this relationship. However, many phyllostomids rely on passive auditory cues, olfaction, vision, or touch to detect and select food items (e.g., Tuttle and Ryan, 1981; Laska, 1990; Kalko and Condon, 1993). In addition, the link between morphology and echolocation is unclear. For example, in the group with the most variable noseleaves, the phyllostomines (Bogdanowicz et al., 1997), echolocation calls of the different species are surprisingly similar (Belwood, 1988). Thus, it is difficult to envision how foraging behavior and diet are linked to phyllostomid noseleaf morphology through echolocation (Bogdanowicz et al., 1997).

Arita (1990) suggested that bats that rely on senses other than echolocation to locate food (e.g., olfaction, vision, thermoperception) may require less directionality in echolocation calls than those that rely primarily on echolocation. He suggested that this may explain the truncated spears seen in desmodontines, *Brachyphylla*, and phyllonycteri-

nes. Our analysis suggests that this short structure may have originally evolved in the last common ancestor of phyllostomids to improve echolocating ability as a supplement to other senses (e.g., vision, olfaction, and thermoperception). The factors related to foraging behavior that are involved in the evolution of a longer spear are not clear. Because many phyllostomids rely so heavily on other senses for prey detection, it seems unlikely that the longer spear seen in these bats parallels an increasing reliance on echolocation for detection of food items.

## TRACING THE DIVERSIFICATION OF FEEDING HABITS

Phyllostomids show a remarkable diversity of feeding specializations. However, data on the feeding ecology of phyllostomids are very incomplete. The diet of most species has been poorly studied, and seasonal and geographical variation in the diet has been inadequately documented. One example of seasonal dietary change involves *Carollia perspicillata*, the phyllostomid whose diet has been perhaps most thoroughly investigated. Several studies have suggested that this bat consumes more insects, nectar, and pollen during the dry season than during the rainy season (Fleming et al., 1972; Heithaus et al., 1975; Sazima, 1976; Fleming and Heithaus, 1986). Fleming et al. (1972) found that insects make up 40% of the diet of *Carollia perspicillata* during the dry season, but only 10% during the wet season.

Other serious problems with collecting dietary data involve over- or underestimation of various food types. *Carollia perspicillata* reportedly consumes only the soft inner parts of hard-bodied insects that it feeds upon, resulting in few recognisable insect remains in fecal samples (Ayala and d'Allessandro, 1973). Therefore, the proportion of insects in the diet may be underestimated. Similarly, many bats discard large seeds without swallowing them. Consequently, fecal sampling underestimates the proportion of these large-seeded fruits in the diet (Thomas, 1988). Collecting samples from night and day roosts may provide a different picture of bat diets (Thomas, 1988). In addition, geographic variation in dietary habits may be important in

widespread taxa that occupy different habitats in different parts of their range. For example, *Carollia perspicillata* is found in thorn scrublands, dry deciduous forests, and lowland rainforests (Pine, 1972; Fleming, 1988; Cloutier and Thomas, 1992; Koopman, 1993, 1994; Voss and Emmons, 1996), and in arid regions this species may feed on cactus fruits that are not available in moister habitats (Santos et al., 1996).

Despite such problems, Ferrarezi and Gimenez (1996) made the first explicitly phylogenetic attempt to consider the evolution of feeding specializations in the family as a whole. These authors compiled a dietary data set based on previously published literature accounts and mapped eight diet characters (one composite, seven multistate; see table 8 for multistate) onto a phylogeny they assembled from several studies (see fig. 61; Honeycutt and Sarich, 1987a; Baker et al., 1989; Lim, 1993; Owen, 1991; Gimenez et al., 1996). The composite character combined all seven multistate characters in a complex transformation series (not shown). The terminal taxa used in this analysis included species, genera, tribes, and families of noctilionoids (see table 8).

After assessing the relative importance of food types in the diet, Ferrarezi and Gimenez (1996: table 1; see our table 8) defined one character for insectivory using the following states (in addition to ''absent''): strict, predominant, and complementary. ''Strict insectivory'' indicates that no foods other than insects are consumed. ''Predominant insectivory'' indicates that insects are a primary food source, but are not the only foods eaten. A ''complementary'' reliance on insects indicates that this food source is a secondary component of the diet. Ferrarezi and Gimenez (1996) defined two similar characters for frugivory (absent, complementary, predominant, strict; other states in the original character do not occur in phyllostomids), and nectarivory/palynivory (absent, complementary, predominant). Finally, Ferrarezi and Gimenez (1996) included three presence/absence characters for sanguivory, carnivory, and folivory. They defined the derived state of the carnivory character as ''predominant carnivory,'' indicating that taxa with the derived state of the character primarily feed on

small vertebrates, but supplement this diet with insects and fruits (Ferrarezi and Gimenez, 1996).

Coding dietary data for use as characters is not always straightforward. For example, Ferrarezzi and Giminez (1996) coded *Pteronotus* as a stict insectivore, despite evidence that more than 10% of the dietary samples in one study of *P. quadridens* included pollen (Rodriguez-Duran and Lewis, 1987). We follow Ferrarezzi and Giminez (1996), because other authors have suggested that *P. quadridens* inadvertently consumed pollen while eating insects, its primary food source (Rodriguez-Duran and Kunz, 1992). Although similar problems are found in other areas of the data set (e.g., reports of frugivory in the sanguivorous *Desmodus*), we have only slightly modified the original codings of Ferrarezi and Gimenez (1996; see our table 8).

In the context of the phylogeny used by Ferrarezzi and Gimenez (1996; fig. 61), predominant insectivory appeared to be primitive for Phyllostomidae. In addition, it appeared that most of the major shifts in diet had occurred a single time each. Sanguivory evolved once in the last common ancestor of the three desmodontine genera. A predominantly carnivorous way of life evolved in the last common ancestor of Vampyrinae, and strict insectivory may have evolved once or twice due to the unresolved relationships of *Lonchorhina* and *Macrophyllum*. The last common ancestor of all nectarivores and frugivores primarily consumed fruit, indicating a single evolution of predominant frugivory. Predominant nectarivory and strict frugivory both evolved once.

Our results are similar to those of Ferrarezi and Gimenez (1996). In the context of our phylogeny, strict insectivory appears to be primitive for Noctilionoidea (this cannot be inferred unless noctilionoids are considered in the context of Simmons and Geisler's [1998] microchiropteran phylogeny; see fig. 62). However, the primitive condition for Phyllostomidae is equivocal: either strict insectivory is primitive (DELTRAN) or the reconstruction remains equivocal(ACCTRAN), and either the absence of insectivory or the complementary state could be primitive for the family. Sanguivory (reconstruction not

TABLE 8
**Data Matrix for Feeding Habits Based on Ferrarezzi and Gimenez (1996)[a]**

| Taxon[b] | Insectivory[c] | Carnivory[d] | Sanguivory[e] | Frugivory[f] | Nectarivory[g] | Folivory[h] |
|---|---|---|---|---|---|---|
| *Desmodus* | 0[i] | 0 | 1 | 0[i] | 0 | 0 |
| *Diaemus* | 0 | 0 | 1 | 0 | 0 | 0 |
| *Diphylla* | 0 | 0 | 1 | 0 | 0 | 0 |
| *Brachyphylla*[j] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Erophylla*[k] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Phyllonycteris*[k] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Anoura*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Choeroniscus*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Choeronycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Glossophaga*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Hylonycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Leptonycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Lichonycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Lionycteris*[m] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Lonchophylla*[m] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Monophyllus*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Musonycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Platalina*[m] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Scleronycteris*[l] | 1 | 0 | 0 | 1 | 2 | 0 |
| *Chrotopterus* | 1 | 1 | 0 | 1 | 0 | 0 |
| *Glyphonycteris*[n] | 2 | 0 | 0 | 1 | 0 | 0 |
| *Lampronycteris*[n] | 2 | 0 | 0 | 1 | 0 | 1 |
| *Lonchorhina* | 3 | 0 | 0 | 1[o] | 0 | 0 |
| *Macrophyllum* | 3 | 0 | 0 | 0 | 0 | 0 |
| *Macrotus* | 2 | 0 | 0 | 1 | 0 | 0 |
| *Micronycteris*[n] | 2 | 0 | 0 | 1 | 0 | 0 |
| *Mimon* | 2 | 1[p] | 0 | 1 | 0 | 0 |
| *Phylloderma* | 2 | 0 | 0 | 1 | 1 | 0 |
| *Phyllostomus* | 2 | 0/1[q] | 0 | 1 | 1 | 0/1[q] |
| *Tonatia* | 2 | 0/1[r] | 0 | 1 | 1 | 0 |
| *Trachops* | 1 | 1 | 0 | 1 | 0 | 0 |
| *Trinycteris*[n] | 2 | 0 | 0 | 1 | 0 | 0 |
| *Vampyrum* | 1 | 1 | 0 | 1 | 0 | 0 |
| *Carollia* | 1 | 0 | 0 | 2 | 1 | 1[s] |
| *Rhinophylla* | 1 | 0 | 0 | 2 | 1 | 0 |
| *Ametrida*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Ardops*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Ariteus*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Artibeus (Artibeus)*[u] | 1 | 0 | 0 | 2 | 1 | 0/1[v] |
| *Artibeus (Dermanura)*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Artibeus (Koopmania)*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Centurio*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Chiroderma*[u] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Ectophylla alba*[u] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Ectophylla macconelli*[u] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Enchisthenses*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Phyllops*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Platyrrhinus*[u] | 1 | 0 | 0 | 2 | 1 | 1[v] |
| *Pygoderma* | 0 | 0 | 0 | 3 | 0 | 0 |
| *Stenoderma*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Sturnira* | 1 | 0 | 0 | 2 | 1 | 0 |
| *Sphaeronycteris*[t] | 0 | 0 | 0 | 3 | 0 | 0 |
| *Uroderma*[u] | 1 | 0 | 0 | 2 | 1 | 0 |

TABLE 8
*Continued*

| Taxon[b] | Insectivory[c] | Carnivory[d] | Sanguivory[e] | Frugivory[f] | Nectarivory[g] | Folivory[h] |
|---|---|---|---|---|---|---|
| *Vampyressa bidens*[w] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Vampyressa nymphaea*[w] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Vampyressa pusilla*[w] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Vampyrodes*[u] | 1 | 0 | 0 | 2 | 1 | 0 |
| *Mormoops*[x] | 3 | 0 | 0 | 0 | 0 | 0 |
| *Pteronotus*[x] | 3 | 0 | 0 | 0 | 0 | 0 |
| *Noctilio*[y] | 3/2 | 0/1 | 0 | 0 | 0 | 0 |

[a] We have not presented all characters and character states initially included by Ferrarezzi and Gimenez (1996). Specifically, we excluded the composite character they constructed and character states that do not appear in any ingroup taxa (see text for discussion). We also, in this preliminary analysis, used their character coding but, in a few cases, supplemented this with additional data. States that they applied to higher-level taxa, we applied to all genera within the clade, even if no data existed for a particular taxon.

[b] Genera are arranged alphabetically by subfamily.

[c] (0) Absent, (1) complementary (secondary food source), (2) predominant (most important or primary food source), (3) strict (only type of food consumed). Character 1 of Ferrarezzi and Gimenez (1996: table 1).

[d] (0) Absent, (1) present. Ferrarezzi and Gimenez (1996: table 1, character 2) only defined two states of carnivory, they defined present as "predominant."

[e] (0) Absent, (1) present. Character 4 of Ferrarezzi and Gimenez (1996: table 1).

[f] (0) Absent, (1) complementary, (2) predominant, (3) strict. Character 5 of Ferrarezzi and Gimenez (1996: table 1) included an additional state (state "2," intermediate) which did not occur in any of our taxa and was excluded.

[g] (0) Absent, (1) complementary, (2) predominant. Character 6 of Ferrarezzi and Gimenez (1996: table 1). Note that this character includes the consumption of pollen and petals.

[h] (0) Absent, (1) complementary. Character 7 of Ferrarezzi and Gimenez (1996: table 1), included an additional state ("3," predominant), which did not occur in any of our taxa and was excluded.

[i] Ferrarezzi and Gimenez (1996) scored *Desmodus* "1" for both insectivory and frugivory; however, Greenhall (1972) suggested that the insects some investigators observed in the stomachs of *Desmodus* were accidentally swallowed. Pieces of flesh that have been observed in the stomachs of these bats were also probably accidentally ingested. Trajano (1985) is the only author to find that fruit was included in the diet of Desmodus. Because it seems unlikely that insects, flesh, and fruit are truly complementary components of the diet of *Desmodus*, we have scored this taxon with "0" for insectivory, carnivory, and frugivory.

[j] This taxon was called Brachyphyllini by Ferrarezzi and Gimenez (1996).

[k] We split Phyllonycterini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera.

[l] We split Glossophagini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera.

[m] We split Lonchophyllini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera.

[n] Ferrarezzi and Gimenez (1996) included *Glyphonycteris*, *Lampronycteris*, and *Trinycteris* in *Micronycteris*. We took our data on the diet of *Glyphonycteris* from Medellín et al. (1985) and for *Lampronycteris*, *Micronycteris*, and *Trinycteris* from Gardner (1977b).

[o] Emmons (1997) notes that this genus includes some fruit in its diet.

[p] Emmons (1997) notes that *Mimon* feeds on small lizards.

[q] Ferrarezzi and Gimenez (1996) scored *Phyllostomus* with "0" for both carnivory and frugivory; however, both *P. discolor* and *P. hastatus* are known to include small vertebrates and plant products in their diet (Gardner, 1977b).

[r] Ferrarezzi and Gimenez (1996) scored *Tonatia* with "0" for this character; however, Emmons (1997) notes that *T. bidens* eats birds.

[s] Gardner (1977b) reported that *Carollia* species often feed on flowers.

[t] We split Stenodermatini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera following Owen (1987). We have assumed that Ferrarezzi and Gimenez (1996) used this taxon at the tribal, not subtribal level.

[u] We split Artibeini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera, following Owen (1987). We have assumed that Ferrarezzi and Gimenez (1996) used this taxon at the tribal, not subtribal level.

[v] Although Ferrarezzi and Gimenez (1996) scored Artibeini with state "1" for this character and Vampyressini with "1?", it appears that only two genera in either group include species that feed on plant parts. We therefore score those two genera with state "1" and other members of both tribes with state "0."

[w] We split Vampyressini, the taxon used by Ferrarezzi and Gimenez (1996), into its composite genera, following Owen (1987), who named this taxon Vampyressatini. We assumed that Ferrarezzi and Gimenez (1996) raised Vampyressatini to tribal level, because in Owen's (1987) classification it appears as a subtribe of Artibeini.

[x] We divided Mormoopidae, the taxon used by Ferrarezzi and Gimenez (1996), into two genera.

[y] Ferrarezzi and Gimenez (1996) used both *Noctilio leporinus* and *N. albiventris*. *N. leporinus* was scored with state "2" (predominant) for the insectivory character and state "1" (complementary) for a piscivory character that we have not used, because it occurred only in this species. Consequently, to reflect the partial reliance of *N. leporinus* on fish, we scored this species with state "1" for the carnivory character. *N. albiventris* was scored with state "3" (strict) for the insectivory character by Ferrarezzi and Gimenez and with state "0" (absent) for the piscivory character.
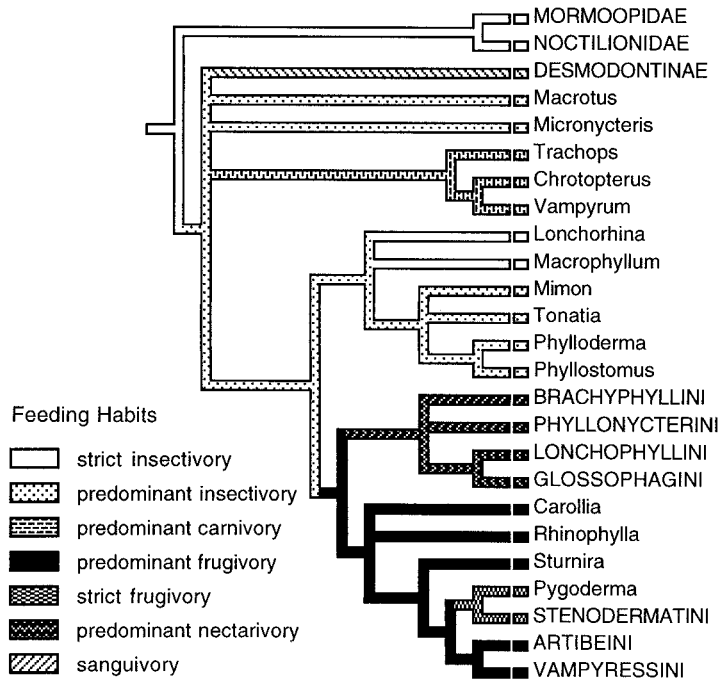
Fig. 61. Tree used by Ferrarezi and Gimenez (1996; redrawn from fig. 4) with their feeding-habits character optimized on the topology. This character was ordered such that predominant insectivory evolved from strict insectivory; predominant carnivory, predominant frugivory, or sanguivory evolved from predominant insectivory; and predominant nectarivory or strict frugivory evolved from predominant frugivory.

shown) is a synapomorphy of Desmodontinae. At the node uniting Brachyphyllinae, Hirsutaglossa, and the clade of Phyllostominae plus Nullicauda, insects appear to have become a less important part of the diet as the importance of plant parts (fruits, nectar, and pollen) increased (regardless of the position of *Brachyphylla*; see figs. 63, 64).

Despite the importance of plants to most phyllostomids, many phyllostomines rely principally on insects and small vertebrates for food (see figs. 62, 65). Predominant insectivory evolved in the last common ancestor of Phyllostominae, with a strict habit evolving in the last common ancestor of the sister taxa *Lonchorhina* and *Macrophyllum*. In Vampyrini, species of *Tonatia* may rely more on insects for nutrients than do other members of this clade (this condition represents either retention of the primitive condition [DELTRAN] or a reversal [ACCT-RAN]). Predominant carnivory appears as a synapomorphy uniting all four Vampyrini

genera, although this is not the only evolutionary origin of this character, which also occurs in *Mimon* (see fig. 65).

Fruits appear to supplement the diet of most phyllostomids (see fig. 63). However, frugivory has become most important in Nullicauda; many members of this group rely almost exclusively on fruit and may not include any insects in their diet. Predominant frugivory evolved three times in phyllostomids: (1) in the last common ancestor of Nullicauda, (2) in the last common ancestor of all Ectophyllina genera except *Artibeus* and *Enchisthenes*, and (3) in *Artibeus* (*Artibeus*). In contrast, strict frugivory evolved only in the last common ancestor of Stenodermatini. Although most phyllostomids apparently do not feed on plant products such as stems, leaves, and flowers, folivory has apparently evolved five times in the family (in *Lampronycteris*, *Glossophaga*, *Carollia*, *Artibeus*, and *Platyrrhinus*; reconstruction not shown; see table 8).
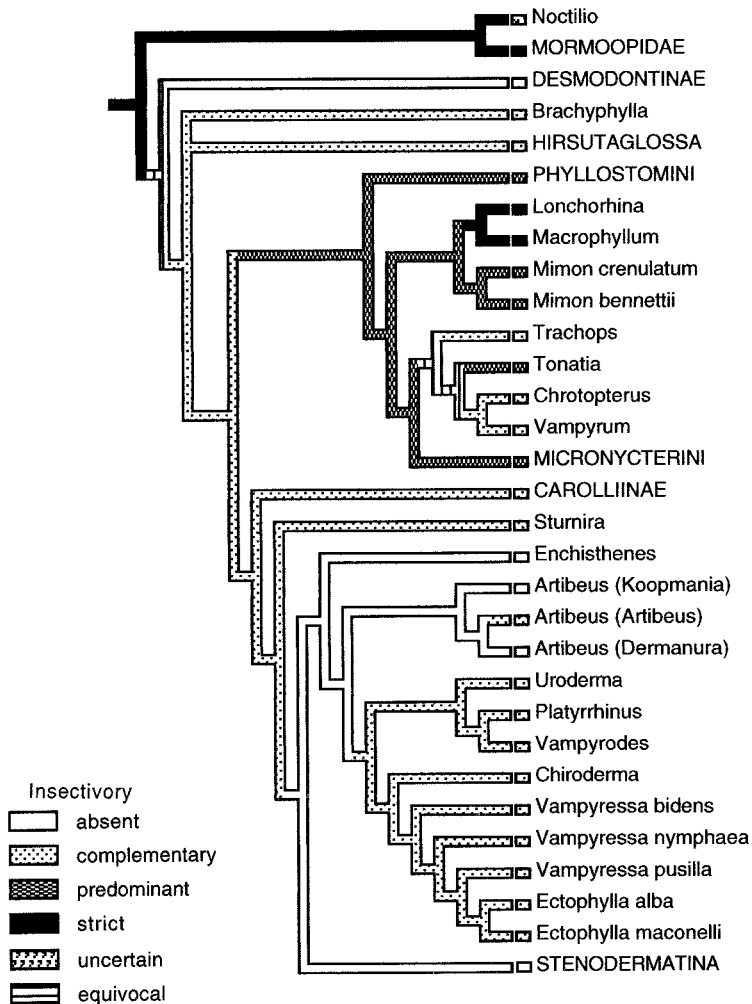
Fig. 62. Evolution of different types of insectivory (see text for description of character states) inferred from our optimization of the insectivory character of Ferrarezi and Gimenez (1996: table 1; see our table 8) on our strict consensus tree from the character congruence analysis. We inferred the state at the root with reference to a phylogeny of Microchiroptera (Simmons, 1998). The equivocal optimizations for Phyllostomidae and Vampyrini are due to differences in interpretation of the character under ACCTRAN or DELTRAN. The "uncertain" state for *Noctilio* is due to taxonomic polymorphism (see table 8).

A reliance on nectarivory/palynivory evolved in the last common ancestor of the clade comprising *Brachyphylla*, Hirsutaglossa, Phyllostominae, and Nullicauda. The reconstruction is similar regardless of the position of *Brachyphylla*: predominant nectarivory is primitive for clade including all phyllostomids except the desmodontines. Complementary nectarivory evolved four times (see fig. 64).

We found that sanguivory, strict insectivory, predominant nectarivory, and strict frugivory all have single evolutionary origins within Phyllostomidae. However, carnivory, predominant frugivory, and possibly predominant insectivory all may have evolved more than once (see figs. 63–65). These differences between our conclusions and those of Ferrarezi and Gimenez (1996) are due to a change we made in the coding of *Mimon*
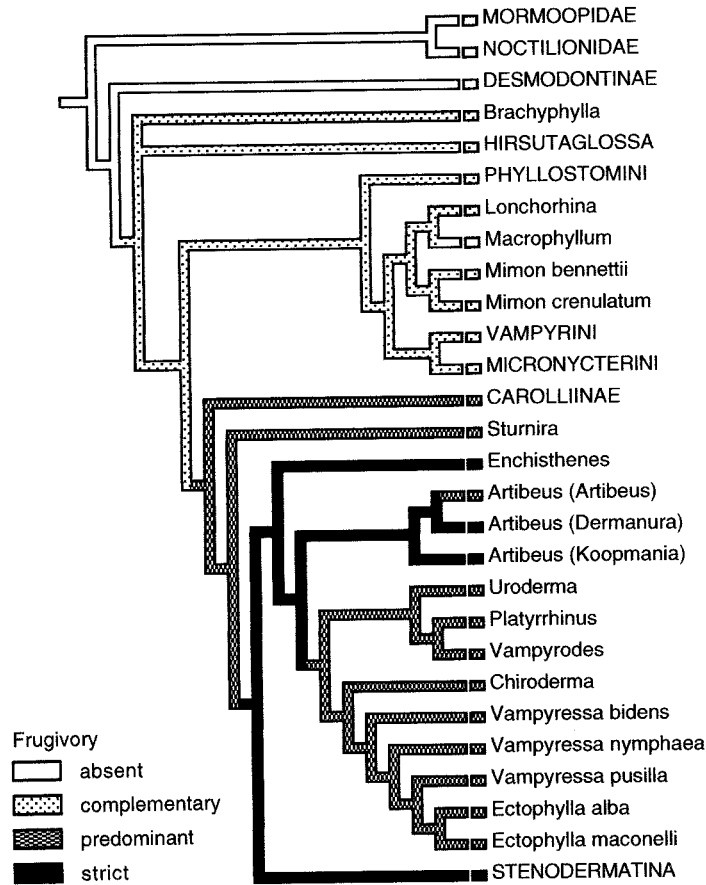
Fig. 63. Evolution of different types of frugivory inferred from our optimization of the frugivory character of Ferrarezi and Gimenez (1996: table 1; see our table 8) on our strict consensus tree from the character congruence analysis. To prevent an equivocal reconstruction for the base of the clade that includes all phyllostomids except desmodontines, we examined trees in which the position of *Brachyphylla* was resolved and fixed the node at the base of the clade that includes all phyllostomids except desmodontines with the state that occurred under the two alternative placements for this genus.

for the carnivory character and the different tree topology we used (see table 8).

We found that plant products became an important food source for phyllostomids earlier in their evolutionary history than Ferrarezi and Gimenez (1996) suggest. In our tree the switch to herbivory appears to characterize the clade that includes all phyllostomids except desmodontines (see figs. 63–64). Concomitant with the increasing importance of plants is a reduction in reliance on insects (fig. 62). In contrast, the topology used by Ferrarezi and Gimenez (1996; fig. 61) suggests that a reliance on plant products evolved only in the last common ancestor of

*Brachyphylla*, Hirsutaglossa, and Nullicauda (fig. 61).

Despite the growing consensus concerning the number of evolutionary origins of feeding specializations in phyllostomids, few hypotheses have been advanced to describe the evolutionary steps neccessary to derive these specializations from their evolutionary precursors. Gillette (1975) put forth perhaps the only model to describe the evolution of feeding strategies in bats. He based his hypothesis on the following statement by Jepsen (1970: 56), ''some forms preferred fruit, after finding initially that it was a good source for worms and bugs, and
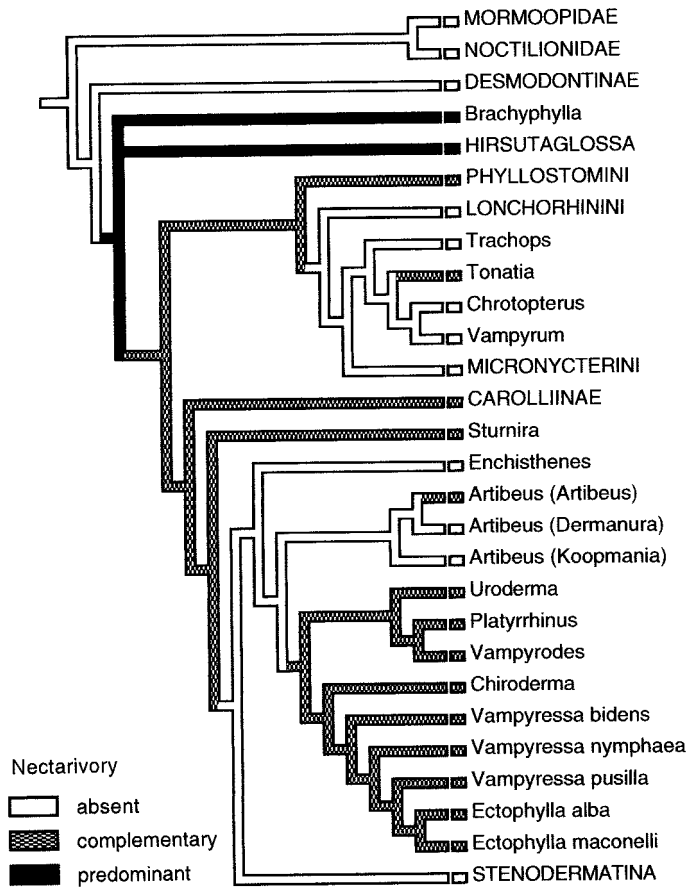
Fig. 64. Evolution of different types of nectarivory inferred from our optimization of the nectarivory character of Ferrarezi and Gimenez (1996: table 1; see our table 8) on our strict consensus tree from the character congruence analysis. Note that the nectarivory character, as defined by Ferrarezi and Gimenez (1996) includes the consumption of pollen and petals. To prevent an equivocal reconstruction for the base of the clade that includes all phyllostomids except desmodontines, we examined trees in which the position of *Brachyphylla* was resolved and fixed the node at the base of the clade that includes all phyllostomids except desmodontines with the state that occurred under the two alternative placements for this genus.

in accord with such dietary changes, new dental types appeared.''

Gillette's (1975) model relied on what he called ''food source duality.'' From a condition of generalized insectivory, he suggested that bats evolved to specialized insectivory, gleaning insects from fruit or flowers. At some point, these animals shifted to using the substrate (the plant material) as a food source in conjunction with the insects they had originally fed upon, thus relying on dual food sources. The culmination of this evolutionary sequence involved sole exploitation of the alternative (plant) food source. As Ferrarezi and Gimenez (1996) found, this model accurately describes their hypothesis of feeding specializations on their composite tree (see fig. 61).

Food source duality is also compatible with many parts of our hypothesis. For example, food source duality (predominant frugivory) is characteristic of basal nullicaudans, although some derived nullicaudans are strictly frugivorous (fig. 63). However, the two possible resolutions of predominant nectarivory/palynivory on our tree indicate that
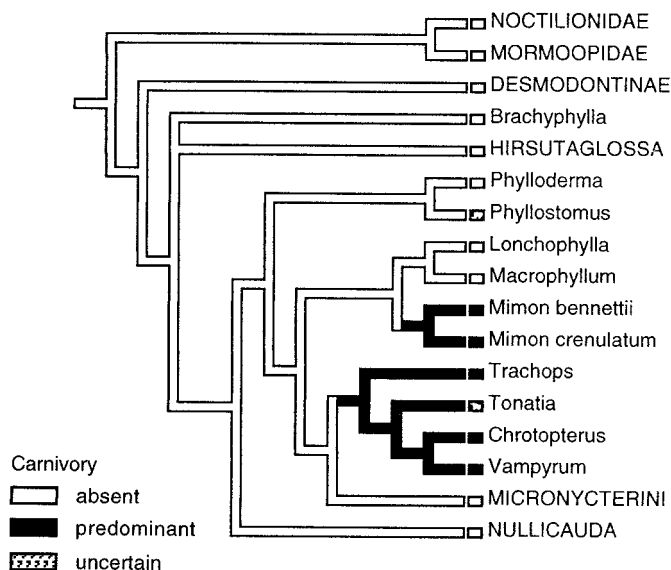
Fig. 65. Evolution of carnivory inferred from our optimization of the carnivory character of Ferrarezi and Gimenez (1996: table 1; see our table 8) on our strict consensus tree from the character congruence analysis. The ''uncertain'' states for *Phyllostomus* and *Tonatia* are due to taxonomic polymorphism.

this condition did not always arise from the less specialized condition involving some reliance on both plants and insects (fig. 64). Instead, our tree indicates that predominant nectarivory/palynivory may have arisen from strict insectivory.

For desmodontines, there is no direct evidence of food source duality. To explain the evolution of blood feeding in this group five hypotheses have been advanced: (1) desmodontines evolved from frugivorous species of phyllostomids that were capable of piercing thick fruit rinds (Slaughter, 1970); (2) desmodontines intially fed on the ectoparasites of large mammals (Gillette, 1975; Turner, 1975); (3) desmodontines intially fed on insects attracted to the wounds of large mammals (Fenton, 1992); and (4) desmodontines initially fed on small vertebrates (Schmidt, 1978), and may have specialized on small arboreal prey items (e.g., *Diaemus*; Sazima, 1978), (5) desmodontines were arboreal om-

nivores that began ingesting pieces of flesh along with blood from these wound sites (Schutt, 1998). Only Slaughter's (1970) and Schutt's (1998) hypotheses were made in the context of a phylogeny.

Ferrarezi and Gimenez (1996) noted that hypotheses proposing that blood feeding evolved from food source duality on mammalian hosts (hypotheses 2 and 3) are not the most parsimonious interpretations. Given the relationships among the three desmodontine genera (*Diphylla*(*Diaemus*, *Desmodus*)), the most parsimonious interpretation is that the last common ancestor of extant desmodontines was arboreal, as Sazima (1978) and Schutt (1998) have suggested, and fed on the blood of birds as do *Diaemus* and *Diphylla* today. Hypotheses that blood feeding evolved from frugivory and carnivory currently lack any corroborating phylogenetic evidence.

## SUMMARY AND CONCLUSIONS

Phyllostomidae is a large (more than 140 species), diverse clade of Neotropical bats that includes species that feed on blood, insects, vertebrates, nectar, pollen, and fruits. This group offers a number of problems for systematists at many taxonomic levels. Pre-

vious attempts to resolve phylogenetic problems in phyllostomids were hampered by limited taxonomic sampling, limited data sets, and use of taxonomic congruence. The result was a poorly resolved picture of phyllostomid relationships. Our total evidence analysis of 150 morphological and molecular characters resulted in a well-resolved hypothesis of relationships within this family. Results of parsimony analyses of our combined data set (appendix 2) indicate that all traditionally recognized phyllostomid subfamilies are monophyletic and that most taxa sharing feeding specializations form clades. These results largely agree with studies that have used a taxonomic congruence approach to evaluate karyological, immunological, and limited sets of morphological characters, although our finding that Phyllostominae is monophyletic is novel. Our results indicate that several genera (*Micronycteris*, *Artibeus*, and *Vampyressa*) are not monophyletic.

Based on our phylogenetic results, we propose a new classification for Phyllostomidae that better reflects hypothesized relationships. Important features of this new classification include: (1) formal recognition of Hirsutaglossa and Nullicauda to group nectarivorous and frugivorous subfamilies, respectively, (2) redefinition of Glossophaginae and inclusion of Glossophagini and Lonchophyllini within this subfamily, (3) recognition of Phyllostomini, Lonchorhinini, Vampyrini, and Micronycterini as tribes within Phyllostominae, (4) formal recognition of Stenodermatina ("short-faced" stenodermatines) and Ectophyllina ("long-faced" stenodermatines), (5) elevation of *Glyphonycteris*, *Lampronycteris*, *Neonycteris*, *Trinycteris*, and the nominate subgenus of *Micronycteris* to generic rank, (6) recognition of *Mesophylla* as a junior synonym of *Ectophylla*, (7) recognition of *Enchisthenes* as a distinct genus, and (8) retention of *Dermanura* and *Koopmania* as subgenera of *Artibeus*.

Our comparison of character congruence and taxonomic congruence indicates that character congruence provides improved resolution of relationships among phyllostomids. Many of the data partitions we identified and analyzed separately are informative only at limited hierarchical levels or in certain portions of the phyllostomid tree, and several traditionally recognized clades (e.g., Carolliinae, Stenodermatinae) do not appear in any of the strict consensus trees of the separate data partitions. In addition to these problems, we find no compelling evidence that partitioning morphological data reflects any underlying biological reality. We therefore recommend character congruence or "total evidence" to make classificatory recommendations and to provide a phylogenetic framework.

Although both chromosomal and immunological data provide additional support for several clades that we identified (e.g., Desmodontinae, Stenodermatinae, Nullicauda, Hirsutaglossa, Phyllonycterinae), these data sets are incongruent with many aspects of our phylogenetic results, especially our finding of phyllostomine monophyly. These conflicts may be due to methodological constraints associated with the use of karyological and immunological data (e.g., problems with assessing homologies and distinguishing primitive from derived traits). Among other observations, we find that *Macrotus waterhousii*, which has been thought to have the primitive karyotype for Phyllostomidae (Patton and Baker, 1978), nests well within the phyllostomine clade. This suggests that results of previous analyses of chromosomal data may require reevaluation.

Mapping characters and behaviors on our phylogenetic tree provides a context for evaluating hypotheses of evolution in Phyllostomidae. Although previous studies of uterine evolution in phyllostomids and other mammals have generally supported the unidirectional progressive fusion hypothesis, our results indicate that intermediate stages of uterine fusion are often derived relative to the fully simplex condition, and that reversals occur with respect to internal uterine fusion. Uterine fusion therefore appears to be neither completely unidirectional nor progressive in Phyllostomidae.

Evolution of the vibrissae and noseleaf are also complex and homoplasy is commonly seen in the evolutionary history of these structures; however, many of these features diagnose clades of phyllostomids (see appendix 4) and appear to be phylogenetically informative, indicating that they may be useful

in other mammalian and chiropteran groups. There is considerable reduction in numbers of vibrissae present in various clusters within Phyllostomidae. These reductions occurred principally in Nullicauda, but also occurred in Lonchorhinini and Hirsutaglossa, and may be related to foraging behavior.

Within Phyllostomidae, the noseleaf seems to have become a much more elaborate and complex structure over evolutionary time. Primitively within the family, the spear was short, the internarial region was flat, and the horseshoe was undifferentiated from the upper lip. Subsequently, within the various subfamilies, the spear became more elongate, the central rib and other internarial structures evolved, and the labial horseshoe became flaplike or cupped in some taxa.

Presumably, noseleaf morphology is related to foraging behavior in phyllostomids. We suspect, as have others (e.g., Neuweiler, 1984; Arita, 1990; Bogdanowicz et al., 1997), that many characters of the noseleaf influence echolocation-emission patterns and may be related to foraging strategies and habitat exploitation; however, most features of the noseleaf have not been explored in this context.

We suggest that the primitively short noseleaf may have originally functioned to improve echolocating ability as a supplement to other senses (e.g., vision, olfaction, and thermoperception). Because many phyllostomids rely so heavily on other senses for prey detection, it is unlikely that the larger spear seen in more derived taxa parallels an increasing reliance on echolocation for detection of food items.

Dietary evolution in phyllostomids appears somewhat more complex than previously thought. We find that most of the major dietary guilds (e.g., frugivory, sanguivory) are represented by a single large clade within Phyllostomidae indicating that each feeding specialization evolved once. However, reversals do occur (e.g., loss of nectar and pollen feeding in many phyllostomines and stenodermatines), and some specializations may have evolved more than once (e.g., carnivory).

Additional research effort needs to be expended on resolving some remaining systematic problems. The position of *Brachyphylla* is unresolved in our most parsimonious topology, and it is not clear how immunological and karyological data that support placement of this genus with Hirsutaglossa should be interpreted. The status of the genus *Vampyressa* is also not clear. We agree with the results of some previous investigations that indicated that this genus may not be monophyletic (e.g., Owen, 1987); however, our analysis did not include all *Vampyressa* species. Therefore, the genus should be reviewed before any nomenclatural change is made. Finally, several studies have suggested that Mormoopidae, not a clade comprising Mormoopidae and Noctilionidae, may be the sister taxon of Phyllostomidae (Van Valen, 1979; Novacek, 1991; Kirsch et al., 1998; Simmons and Conway, MS). In the future, we hope to resolve this question by performing a global parsimony analysis that intensively samples all noctilionoids. It is not clear exactly how many of the weakly and moderately supported clades we have identified will be recovered in additional analyses that add new data to our existing data matrix. As our study built upon those of many previous workers, we hope that the data and hypotheses presented here will provide a starting point for new and productive investigations of phyllostomid relationships and evolution.

## ACKNOWLEDGMENTS

# REFERENCES

Allen, H. A.
  1892a. On a new family of phyllostome bats. Proc. U.S. Natl. Mus. 15: 437–439.
  1892b. Description of a new genus of phyllostome bats. Ibid. 15: 441–442.
  1898. On the Glossophaginae. Trans. Am. Philos. Soc. 19: 237–266.

Altenbach, J.S.
  1979. Locomotor morphology of the vampire bat, *Desmodus rotundus*. Spec. Publ. Am. Soc. Mammal. 6: 1–137.

Anderson, K.
  1906. On the bats of the genus *Micronycteris* and *Glyphonycteris*. Ann. Mag. Nat. Hist. ser. 7, 18: 50–63.
  1912. Catalogue of the Chiroptera in the collection of the British Museum, vol. I: Megachiroptera. London: British Museum.

Anderson, S. A.
  1997. Mammals of Bolivia, taxonomy and distribution. Bull. Am. Mus. Nat. Hist. 231: 1–652.

Anderson, S. A., K. F. Koopman, and G. K. Creighton
  1982. Bats of Bolivia: an annotated checklist. Am. Mus. Novitates 2750: 24 pp.

Arita, H. T.
  1990. Noseleaf morphology and ecological correlates in phyllostomid bats. J. Mammal. 71: 36–47.

Arnold, M. L., R. L. Honeycutt, R. J. Baker, V. M. Sarich, and J. K. Jones, Jr.
  1982. Resolving a phylogeny with multiple data sets: a systematic study of phyllostomoid bats. Occas. Pap. Mus. Texas Tech Univ. 77: 1–55.

Ayala, S. C., and A. d'Allessandro
  1973. Insect feeding behavior of some Colombian fruit-eating bats. J. Mammal. 54: 266–267.

Baker, R. J.
  1967. Karyotypes of bats of the family Phyllostomidae and their taxonomic implications. Southwest. Nat. 12: 407–428.
  1970. The role of karyotypes in phylogenetic studies of bats. *In* B. H. Slaughter and W. D. Walton (eds.), About bats: 303–312. Dallas: Southern Methodist Univ. Press.
  1973. Comparative cytogenetics of the New World leaf–nosed bats (Phyllostomatidae). Period. Biol. 75: 37–45.
  1979. Karyology. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. III. Spec. Publ. Mus. Texas Tech Univ. 16: 1107–155.

Baker, R. J., and R. A. Bass
  1979. Evolutionary relationship of the Brachyphyllinae to the glossophagine genera *Glossophaga* and *Monophyllus*. J. Mammal. 60: 364–372.

Baker, R. J., and W. J. Bleier
  1971. Karyotypes of bats of the subfamily Carolliinae (Mammalia; Phyllostomatidae) and their evolutionary implications. Experientia 27: 220–222.

Baker, R. J., and T. C. Hsu
  1970. Further studies on the sex–chromosome systems of the American leaf-nosed bats (Chiroptera, Phyllostomatidae). Cytogenetics 9: 131–138.

Baker, R. J., and G. Lopez
  1970. Karyotypic studies of the insular populations of bats on Puerto Rico. Caryologia 23: 465–472.

Baker, R. J., H. H. Genoways, W. J. Bleier, and J. W. Warner
  1973. Cytotypes and morphometrics of two phyllostomatid bats, *Micronycteris hirsuta* and *Vampyressa pusilla*. Occas. Pap. Mus. Texas Tech Univ. 17: 1–10.

Baker, R. J., R. A. Bass, and M. A. Johnson
  1979.  Evolutionary implications of chromosomal homology in four genera of stenodermatine bats (Phyllostomatidae: Chiroptera). Evolution 33: 220–226.

Baker, R. J., R. L. Honeycutt, M. L. Arnold, V. M. Sarich, and H. H. Genoways
  1981a. Electrophoretic and immunological studies on the relationship of the Brachyphyllinae and the Glossophaginae. J. Mammal. 62: 665–672.

Baker, R. J., H. H. Genoways, and P. A. Seyfarth
  1981b. Results of the Alcoa Foundation–Suriname Expeditions. VI. Additional chromosomal data for bats (Mammalia: Chiroptera) from Suriname. Ann. Carnegie Mus. 50: 333–344.

Baker, R. J., M. W. Haiduk, L. W. Robbins, A. Cadena, and B. F. Koop
  1982.  Chromosomal studies of South American bats and their systematic implications. In M. A. Mares and H. H. Genoways (eds.), Mammalian biology in South America. Spec. Publ. Ser. Pymatuning Lab. Ecol. 6: 303–327.

Baker, R. J., M. B. Qumsiyeh, and C. S. Hood
  1987.  Role of chromosomal banding patterns in understanding mammalian evolution. In H. H. Genoways (ed.), Current mammalogy: 67–96. New York: Plenum.

Baker, R. J., C. G. Dunn, and K. Nelson
  1988a. Allozymic study of the relationships of Phylloderma and four species of Phyllostomus. Occas. Pap. Mus. Texas Tech Univ. 125: 1–14.

Baker, R. J., R. L. Honeycutt, and R. A. Bass
  1988b. Genetics. In A. M. Greenhall and U. Schmidt(eds.), Natural history of vampire bats, pp. 31–40. Boca Raton, LA: CRC Press.

Baker, R. J., C. S. Hood, and R. L. Honeycutt
  1989.  Phylogenetic relationships and classification of the higher categories of the New World bat family Phyllostomidae. Syst. Zool. 38: 228–238.

Baron, G., H. Stephan, and H. D. Frahm
  1996a. Comparative neurobiology in Chiroptera, vol. 2. Boston: Birkhauser.
  1996b. Comparative neurobiology in Chiroptera, vol. 3. Boston: Birkhauser.

Barrett, M., M. J. Donoghue, and E. Sober
  1991.  Against consensus. Syst. Zool. 40: 486–493.

Bass, R. A.
  1978.  Systematics of the Desmodontinae and Phyllonycterinae (Chiroptera: Phyllostomatidae) based on G–band chromosomal homologies. M.S. thesis, Texas Tech Univ., Lubbock.

Belwood, J. J.
  1988.  Foraging behavior, prey selection, and echolocation in phyllostomine bats (Phyllostomidae). In P. E. Nachtigall and P.W.B. Moore (eds.), Animal sonar: 601–605. New York: Plenum.

Benedict, F. A.
  1957.  Hair structure as a generic character in bats. Univ. California Publ. Zool. 59: 285–548.

Bhatnager, K. P.
  1980.  The chiropteran vomeronasal organ: its relevance to the phylogeny of bats. In D. E. Wilson and A. L. Gardner, (eds.), Proceedings of the fifth international bat research conference: 289–315. Lubbock: Texas Tech Univ.
  1985.  Comparative morphology of the vomeronasal receptor-free epithelium of some phyllostomid bats: light micorscopic observations. Aust. J. Mammal. 8: 265–270.
  1988.  Anatomy. In A. M. Greenhall and U. Scmidt (eds.), Natural history of vampire bats: 41–70. Boca Raton, LA: CRC Press.

Bhatnager, K. P., and F. C. Kallen
  1974.  Morphology of the nasal cavities and associated structures in Artibeus jamaicensis and Myotis lucifugus. Am. J. Anat. 139: 167–190.

Bhatnager, K. P., D. H. Matulionis, and W. Breipohl
  1982.  Fine structure of the vomeronasal neuroepithelium of bats: a comparative study. Acta Anat. 112: 158–177.

Bogdanowicz, W., R. D. Csada, M. B. Fenton
  1997.  Structure of the noseleaf, echolocation, and foraging behavior in the Phyllostomidae (Chiroptera). J. Mammal. 78: 942–953.

Bonaparte, C. L.
  1831.  Saggio di una distribuzione metodica degli animali vertebrati. Rome: Antonio Boulzaler.
  1838.  Synopsis vertebratorum systematis. Nuovi Ann. Sci. Nat., Anno I Tomo II: 105–133.

Brown, J. C.
  1971.  The description of mammals. 1. The external characters of the head. Mammal Rev. 1: 151–167.

Bull, J. J, J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford, and P. J. Waddell
  1993.  Partitioning and combining data in phy-

logenetic analysis. Syst. Biol. 42: 384–397.

Cabrera, A.
1958.   Catálogo de los mamiferos de America del Sur. Rev. Mus. Argent. Cienc. Nat.''Bernardino Rivadavia'' 4: iv–308.

Cadena, A., and R. J. Baker
1976.   Cariotipos de los murcielagos vampiros (Chiroptera: Desmodinae). Caldasia 11: 159–163.

Chippendale, P. T., and J. J. Wiens
1994.   Weighting, partitioning, and combining characters in phylogenetic analysis. Syst. Biol. 43: 278–287.

Cloutier, D., and D. W. Thomas
1992.   *Carollia perspicillata*. Mamm. Species 417: 1–9.

Cooper, J. G., and K. P. Bhatnager
1976.   Comparative anatomy of the vomeronasal organ complex in bats. J. Anat. 122: 571–601.

Corbet, G. B., and J. E. Hill
1980.   A world list of mammalian species, 1st ed. London: British Museum.
1986.   A world list of mammalian species, 2nd ed. London: British Museum.

Cracraft, J., and D. P. Mindell
1989.   The early history of modern birds: a comparison of molecular and morphological evidence. *In* B. Fernholm, K. Bremer, and H. Jörnvall (eds.), The hierarchy of life: molecules and morphology in phylogenetic analysis: 389–403. Amsterdam: Elsevier.

Cuvier, G.
1817.   Le règne animal distribue d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, tomus 1. Paris: Deterville.

Dalquest, W. W., and H. J. Werner
1954.   Histological aspects of the faces of North American bats. J. Mammal. 35: 147–160.

Davis, D. E., D. C. Carter, and R. H. Pine
1964.   Noteworthy records of Mexican and Central American bats. J. Mammal. 45: 375–387.

de la Torre, L.
1961.   The evolution, variation, and systematics of the neotropical bats of the genus *Sturnira*. Ph.D. diss., Univ. Illinois, Urbana.

de Queiroz, A.
1993.   For consensus (sometimes). Syst. Biol. 42: 368–372.

de Quieroz, K., and J. Gauthier
1990.   Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39: 307–322.
1992.   Phylogenetic taxonomy. Annu. Rev. Ecol. Syst. 23: 449–480.
1994.   Toward a phylogenetic system of biological nomenclature. Trends Ecol. Evol. 9: 27–31.

de Queiroz, A., M. J. Donoghue, and J. Kim
1995.   Separate versus combined analysis of phylogenetic evidence. Annu. Rev. Ecol. Syst. 26: 657–681.

Desmarest, A. G.
1820.   Mammalogie, ou description des espèces de mammifères, partie 1. Paris: Mme. Veuve Agasse.

Dobson, G. E.
1875.   Conspectus of the suborders, families, and genera of Chiroptera, arranged according to their natural affinities. Ann. Mag. Nat. Hist. ser. 4, 16: 345–357.
1878.   Catalogue of the Chiroptera in the collection of the British Museum. London: British Museum.

Dumeril, A. M. C.
1806.   Zoologie analytique, ou méthode naturelle de classification des animaux, rendu plus facile à l'aide de tableaux synoptiques. Paris: Allais.

Eernisse, D. J., and A. G. Kluge
1993.   Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. Mol. Biol. Evol. 10: 1170–1195.

Emmons, L. H.
1997.   Neotropical rainforest mammals: a field guide, 2nd ed. Chicago: Univ. Chicago Press.

Farris, J. S.
1983.   The logical basis of phylogenetic analysis. *In* N. I. Platnick and V. A. Funk (eds.), Advances in cladistics, vol. 2. Proceedings of the second meeting of the Willi Hennig Society: 1–36. New York: Columbia Univ.

Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult
1995.   Testing significance of incongruence. Cladistics 10: 315–319.

Felsenstein, J.
1978.   Cases in which parsimony and compatibility methods will be positively misleading. Syst. Zool. 27: 401–410.

Fenton, M. B.
1984.   Echolocation: implications for ecology and evolution of bats. Q. Rev. Biol. 59: 33–53.

1985. Communication in the Chiroptera. Bloomington: Indiana Univ. Press.

1992. Wounds and the origin of blood–feeding in bats. Biol. J. Linn. Soc. 47: 161–171.

Ferrarezzi, H., and E. d. A. Gimenez
1996. Systematic patterns and the evolution of feeding habits in Chiroptera (Archonta: Mammalia). J. Comp. Biol. 1: 75–94.

Fischer von Waldheim, G.
1813. Zoognosia tabulis synopticus illustrata, in usum praelectionum Academiae imperialis medico–chirugicae mosquensis edita. Moscow: Nicolai S. Vsevolozsky.

Fleming, T. H.
1988. The short–tailed fruit bat: a study in plant–animal interactions. Chicago: Univ. Chicago Press.

Fleming, T. H., and E. R. Heithaus
1986. Seasonal foraging behavior of *Carollia perspicillata* (Chiroptera: Phyllostomidae). J. Mammal. 67: 660–671.

Fleming, T. H., E. T. Hooper, and D. E. Wilson
1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. Ecology 53: 555–569.

Flower, W. H., and R. Lydekker
1891. An introduction to the study of mammals living and extinct. London: Adam and Charles Black.

Forman, G. L.
1971. Gastric morphology in selected mormoopid and glossophagine bats as related to systematic problems. Trans. Illinois Acad. Sci. 64: 273–282.

1973. Studies of gastric morphology in North American Chiroptera (Emballonuridae, Noctilionidae, and Phyllostomatidae). J. Mammal. 54: 909–923.

Forman, G. L., R. J. Baker, and J. D. Gerber
1968. Comments on the systematic status of vampire bats (family Desmodontidae). Syst. Zool. 17: 417–425.

Forman, G. L., C. J. Phillips, and C. S. Rouk
1979. Alimentary tract. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. III. Spec. Publ. Mus. Texas Tech Univ. 16: 205–227.

Frahm, H. D.
1981. Volumetric comparison of the accessory olfactory bulb in bats. Acta Anat. 109: 173–183.

Frahm, H. D., and K. P. Bhatnager
1980. Comparative morphology of the accessory olfactory bulb in bats. J. Anat. 130: 349–365.

Gardner, A. L.
1977a. Chromosomal variation in *Vampyressa* and a review of chromosomal evolution in the Phyllostomidae (Chiroptera). Syst. Zool. 26: 300–318.

1977b. Feeding habits. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. II. Spec. Publ. Mus. Texas Tech Univ. 16: 293–350.

Gardner, A. L. and C. S. Ferrell
1990. Comments on the nomenclature of some Neotropical bats (Mammalia: Chiroptera). Proc. Biol. Soc. Washington 103: 501–508.

Gerber, J. D.
1968. Electrophoretic and immunologic comparisons of the serum proteins of bats. Ph.D. diss., Univ. Kansas, Lawrence.

Gerber, J. D., and C. A. Leone
1971. Immunologic comparisons of the sera of certain phyllostomid bats. Syst. Zool. 20: 160–166.

Gervais, P.
1854. Histoire naturelle des mammifères, partie I. Paris: L. Curmer.

1856. Deuxième mémoire. Documents zoologiques pour servir à la monographie des chéiroptères Sud–Américains. *In* P. Gervais (ed.), Mammifères: 25–88. *In* F. Castelnau (ed.) Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para; executée par ordre du gouvernement français pendant les années 1843 à 1847, sous la direction du Comte Francis Castelnau. 1(2): 1–116. Paris: P. Bertran. [dated 1855, but published 1856; see Ann. Mag. Nat. Hist. ser 7, 8: 164.].

Gill, T.
1872. Arrangement of the families of mammals. Washington, D.C.: Smithsonian Inst..

1884. Animalivora. *In* J. S. Kingsley (ed.), The standard natural history 5: 163–177. Boston: S. E. Cassino.

Gillette, D. D.
1975. Evolution of feeding strategies in bats. Tebiwa 18: 39–48.

Gimenez, E. d. A.
1993. Morfologia lingual comparada, fili-

ogenia e evolução dos hábitos alimentares na superfamilia Phyllostomoidea (Mammalia: Chiroptera). M.S. thesis, Univ. Estadual Paulista, São Paulo.

Gimenez, E. d. A., H. Ferrarezzi, and V. A. Taddei
1996. Lingual morphology and cladistic analysis of the New World nectar-feeding bats (Chiroptera: Phyllostomidae). J. Comp. Biol. 1: 41–64.

Goldfuss, G. A.
1820. Handbuch der zoologie, theil. 2. Nurnberg: Johann Leonhard Schrag.

Goodwin, G. G., and A. M. Greenhall
1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infection, and ecology. Bull. Am. Mus. Nat. Hist. 122: 187–302.

Gray, J. E.
1821. On the natural arrangement of vertebrose animals. London Med. Repos. 15: 296–310.
1826. An attempt at a division of the family Vespertilionidae into groups. Zool. J. 2: 242–243.
1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species. Mag. Zool. Bot. 2: 483–505.
1866a. Synopsis of the genera of Vespertilionidae and Noctilionidae. Ann. Mag. Nat. Hist. ser. 3, 17: 89–93.
1866b. A revision of the genera of pteropine bats (Pteropidae) and descriptions of some apparently undescribed species. Proc. Zool. Soc. London 1866: 62–67
1866c. A revision of the genera of Rhinolophidae, or horseshoe bats. Proc. Zool. Soc. London 1866: 81–83.
1866d. Revision of the genera of Phyllostomidae, or leaf-nosed bats. Proc. Zool. Soc. London 1866: 111–118.

Greenbaum, I. F., and C. J. Phillips
1974. Comparative anatomy and general histology of tongues of long-nosed bats (*Leptonycteris sanborni* and *L. nivalis*) with reference to infestation of oral mites. J. Mammal. 55: 489–504.

Greenbaum, I. F., R. J. Baker, and D. E. Wilson
1975. Evolutionary implications of the karyotypes of the stenodermine genera *Ardops*, *Ariteus*, *Phyllops*, and *Ectophylla*. Bull. S. California. Acad. Sci. 74: 156–159.

Greenhall, A. M.
1972. The biting and feeding habits of the vampire bat, *Desmodus rotundus*. J. Zool., (London) 168: 451–461.

Griffin, D. R., and A. Novick
1955. Acoustic orientation of neotropical bats. J. Exp. Zool. 130: 251–300.

Griffiths, T. A.
1978. Muscular and vascular adaptations for nectar-feeding in the glossophagine bats *Monophyllus* and *Glossophaga*. J. Mammal. 59: 414–418.
1982. Systematics of the New World nectar-feeding bats (Mammalia, Phyllostomidae), based on the morphology of the hyoid and lingual regions. Am. Mus. Novitates 2742: 45 pp.
1983a. On the phylogeny of the Glossophaginae and the proper use of outgroup analysis. Syst. Zool. 32: 283–285.
1983b. Comparative laryngeal anatomy of the Big Brown bat, *Eptesicus fuscus* and the Mustached bat *Pteronotus parnellii*. Mammalia 47: 377–394.
1985. Molar cusp patterns in the bat genus *Brachyphylla*: some functional and systematic observations. J. Mammal. 66: 544–549.

Griffiths, T. A., and B. B. Criley
1989. Comparative lingual anatomy of the bats *Desmodus rotundus* and *Lonchophylla robusta* (Chiroptera: Phyllostomidae). J. Mammal. 70: 606–613.

Haiduk, M. W., and R. J. Baker
1982. Cladistical analysis of G–banded chromosomes of nectar-feeding bats (Glossophaginae: Phyllostomidae). Syst. Zool. 31: 252–265.

Hall, E. R.
1981. The mammals of North America, 2nd ed. New York: Wiley.

Hall, E. R., and K. R. Kelson
1959. The mammals of North America. New York: Ronald Press.

Handley, C. O., Jr.
1959. A revision of American bats of the genera *Euderma* and *Plecotus*. Proc. U.S. Natl. Mus. 110: 95–246.
1960. Descriptions of new bats from Panama. Proc. U.S. Natl. Mus. 112: 459–479.
1980. Inconsistencies in formation of family-group and subfamily-group names in Chiroptera. *In* D. E. Wilson and A. L. Gardner (eds.), Proceedings of the fifth international bat research conference: 9–13. Lubbock: Texas Tech Univ.

Hartley, D. J., and R. A. Suthers
1987. The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat *Carollia perspicillata*. J. Acoust. Soc. Am. 82: 1892–1900.

Heithaus, E. R., T. H. Flemming, and P. A. Opler
  1975.  Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56: 841–854.
Hernandez, J., and A. Cadena
  1978.  Notas para la revision del genero Lonchorhina (Chiroptera: Phyllostomidae). Caldasia 12: 199–251.
Hill, J. E., and J. D. Smith
  1984.  Bats: a natural history. Austin: Univ. Texas Press.
Hillis, D. M.
  1987.  Molecular versus morphological approaches to systematics. Ann. Rev. Ecol. Syst. 18: 23–42.
Honeycutt, R. L.
  1981.  Molecular evolution in New World leaf-nosed bats of the family Phyllostomidae with comments on the superfamily Noctilionoidea. Ph.D. diss., Texas Tech Univ., Lubbock.
Honeycutt, R. L., and V. M. Sarich
  1987a.  Albumin evolution and subfamilial relationships among New World leaf-nosed bats (family Phyllostomidae). J. Mammal. 68: 508–517.
  1987b.  Monophyly and molecular evolution within three phyllostomid bat genera. J. Mammal. 68: 518–525.
Honeycutt, R. L., R. J. Baker, and H. H. Genoways
  1980.  Results of the Alcoa Foundation-Suriname expeditions. III. Chromosomal data for bats (Mammalia: Chiroptera) from Suriname. Ann. Carnegie Mus. 49: 237–250.
Honeycutt, R. L., I. F. Greenbaum, R. J. Baker, and V. M. Sarich
  1981.  Molecular evolution of vampire bats. J. Mammal. 62: 805–811.
Hood, C. S., and J. D. Smith
  1982.  Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. Syst. Zool. 31: 241–251.
  1983.  Histomorphology of the female reproductive tract in phyllostomoid bats. Occas. Pap. Mus. Texas Tech Univ. 86: 1–38.
Hsu, T. C., R. J. Baker, and T. Utakoji
  1968.  The multiple sex chromosome system of American leaf-nosed bats (Chiroptera, Phyllostomidae). Cytogenetics 7: 27–38.
Huelsenbeck, J. P., J. J. Bull, and C. W. Cunningham
  1996.  Combining data in phylogenetic analysis. Trends Ecol. Evol. 11: 152–157.
International Commission on Zooloogical Nomenclature
  1985.  International code of zoological nomenclature, 3rd ed. London: Int. Trust Zool. Nomencl.
Jassal, M., and N. B. Simmons
  1996.  Phylogenetic relationships of "phyllostomine" bats: results of an analysis using a dense-sampling approach. Bat Res. News 37: 136.
Jepsen, G. L.
  1970.  Bat origins and evolution. In W.A. Wimsatt (ed.), Biology of bats, vol. 1: 1–64. New York: Academic.
Johnson, M. A.
  1979.  Evolutionary implications of G- and C-banded chromosomes of 13 species of stenodermine bats. M.S. thesis, Texas Tech Univ., Lubbock.
Jones, J. K., Jr., and R. J. Baker
  1980.  Chiroderma improvisum. Mamm. Species 134: 1–2.
Jones, J. K., Jr., and D. C. Carter
  1976.  Annotated checklist, with keys to subfamilies and genera. In R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. I. Spec. Publ. Mus. Texas Tech Univ. 10: 7–38.
Kalko, E.K.V., and M. Condon
  1993.  Bat-plant interactions: how frugivorous leaf-nosed bats find their food. Bat. Res. News 34: 115.
Kirsch, J.A.W., J. M. Hutcheon, D.G.P. Byrnes, and B. D. Lloyd
  1998.  Affinities and historical zoogeography of the New Zealand short-tailed bat, Mystacina tuberculata Gray 1843, inferred from DNA hybridization comparisons. J. Mamm. Evol. 5: 33–64.
Kluge, A. G.
  1989.  A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). Syst. Zool. 38: 7–25.
Kluge, A. G., and A. J. Wolf
  1993.  Cladistics: what's in a word? Cladistics 9: 183–199.
Koch, C.
  1862–63. Das Wesentliche der Chiropteren mit besonder Beschreibung der in dem Herzogthum Nassau und den angranzenden Landestheilen vorkomenden Fledermäuse. Jahrg. Ver. Naturk. Herzogthum Nassau 17–18: 261–593.
Koop, B. F., and R. J. Baker.
  1983.  Electrophoretic studies of relationships of six species of Artibeus (Chiroptera:

Phyllostomidae). Occas. Pap. Mus. Texas Tech Univ. 83: 1–12.

Koopman, K. F.
1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Am. Mus. Novitates 2651: 33 pp.
1984. Bats. In S. Anderson and J. K. Jones Jr. (eds.), Orders and families of Recent mammals of the world: 145–186. New York: Wiley.
1993. Order Chiroptera. In D. E. Wilson and D. M. Reeder (eds.), Mammal species of the world, a taxonomic and geographic reference, 2nd ed.: 137–241. Washington, D.C.: Smithsonian Inst.
1994. Chiroptera: systematics. Handb. der Zool., vol. 7, p. 60, Mammalia: 1–217.

Koopman, K. F., and E. L. Cockrum
1967. Bats. In S. Anderson and J. K. Jones Jr. (eds.), Recent mammals of the world: 109–150. New York: Ronald Press.

Koopman, K. F., and J. K. Jones, Jr.
1970. Classification of bats. In B. H. Slaughter and W. D. Walton (eds.), About bats: 22–28. Dallas: Southern Methodist Univ. Press.

Koopman, K. F., and G. T. MacIntyre
1980. Phylogenetic analysis of chiropteran dentition. In D. E. Wilson and A. L. Gardner (eds.), Proceedings of the fifth international bat research conference: 279–288. Lubbock: Texas Tech Univ.

Lacépède, B. G.
1799. Tableau des divisions, sous-divisions, ordres, et genres des mammifères. Tabl. Div. Subd. Order Genres Mammifères Paris: Chez Plasson [1797].

Lanyon, S. M.
1993. Phylogenetic frameworks: towards a firmer foundation for the comparative approach. Biol. J. Linn. Soc. 49: 45–61.

Laska, M.
1990. Olfactory sensitivity to food odor components in the short-tailed fruit bat, Carollia perspicillata (Phyllostomatidae: Chiroptera). J. Comp. Physiol. (166A): 395–399.

Laurie, E.M.O.
1955. Notes on some mammals from Ecuador. Ann. Mag. Nat. Hist. ser. 12, 8: 268–276.

Le Gros Clark, W. E.
1959. The antecedents of man. Edinburgh: Edinburgh Univ. Press.

Lesson, R. P.
1827. Manuel de mammalogie. Paris: Librairie de Roret.
1842. Nouveau table du règne animal. Paris: Arthus Bertrand.

Lillegraven, J. A.
1969. Latest Cretaceous mammals of upper part of Edmonton formation of Alberta, Canada, and a review of the marsupial-placental dichotomy in mammalian evolution. Univ. Kans. Paleontol. Contrib. Vertebr. 50(12): 1–222.
1976. Biological considerations of the marsupial-placental dichotomy. Evolution 29: 707–722.

Lim, B. K.
1993. Cladistic reapprisal of Neotropical stenodermatine bat phylogeny. Cladistics 9: 147–165.

Linnaeus, C.
1758. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis, vol. 1, 10th ed. Stockholm: Laurentii Salvii.

Luckett, W. P.
1980. The use of fetal membrane data in assessing chiropteran phylogeny. In D. E. Wilson and A. L. Gardner (eds.), Proceedings of the fifth international bat research conference: 245–264. Lubbock: Texas Tech Univ.

Machado-Allison, C. E.
1967. The systematic position of the bats Desmodus and Chilonycteris, based on host-parasite relationships (Mammalia; Chiroptera). Proc. Biol. Soc. Washington. 80: 223–226.

Maddison, W. P.
1993. Missing data versus missing characters in phylogenetic analysis. Syst. Biol. 42: 576–581.

Maddison, W. P., and D. R. Maddison
1992. MacClade: analysis of phylogeny and character evolution, version 3.0. Computer program distributed by Sinauer, Sunderland, MA.

Marques-Aguiar, S. A.
1994. A systematic review of the large species of Artibeus Leach, 1821 (Mammalia: Chiroptera), with some phylogenetic inferences. Bol. Mus. Para. Emilio Goeldi ser. Zool. 10: 3–83.

Maxson, L. R., and R. D. Maxson
1990. Proteins II: immunological techniques. In D. M. Hillis and C. Moritz (eds.), Molecular systematics, 1st ed.: 127–155. Sunderland, MA: Sinaeuer.

McDaniel, V. R.
1976. Brain Anatomy. In R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Bi-

ology of the bats of the New World family Phyllostomatidae, p. I. Spec. Publ. Mus. Texas Tech Univ. 10: 147–200.

McKenna, M. C., and S. K. Bell
1997. Classification of mammals above the species level. New York: Columbia Univ.

Medellín, R. A.
1988. Prey of *Chrotopterus auritus*, with notes on feeding behavior. J. Mammal. 69: 841–844.

Miller, G. S.
1907. The families and genera of bats. Bull. U.S. Natl. Mus. 57: 1–282.
1924. List of North American recent mammals. Bull. U.S. Natl. Mus. 128: 1–673.

Miyamoto, M. M.
1985. Consensus cladograms and general classifications. Cladistics 1: 186–189.

Miyamoto, M. M., and W. M. Fitch
1995. Testing species phylogenies and phylogenetic methods with congruence. Syst. Biol. 44: 64–76.

Möhres, F. P., and G. Neuweiler
1966. Die Ultraschallorientung der Gloss-blatt-Fledermäuse (Chiroptera-Megadermatidae). Z. Vergl. Physiol. 53: 195–227.

Mossman, H. W.
1953. The genital system and the fetal membranes as criteria for mammalian phylogeny and taxonomy. J. Mammal. 34: 289–298.
1977. Comparative anatomy. *In* R. M. Wynn (ed.), The biology of the uterus, 2nd ed.: 19–34. New York: Plenum.
1987. Vertebrate fetal membranes. New Brunswick: Rutgers Univ.

Myers, P.
1981. Observations on *Pygoderma bilabiatum* (Wagner). Z. Säugetierkd. 46: 146–151.

Nagorsen, D.W., and R.L. Peterson.
1975. Karyotypes of six species of bats (Chiroptera) from the Dominican Republic. R. Ont. Mus. Life Sci. Occas. Pap. 28: 1–28.

Neuweiler, G.
1984. Foraging ecology and audition in bats. Naturwissenschaften 71: 446–455.

Novacek, M. J.
1991. Aspects of morphology of the cochlea in microchiropteran bats: an investigation of character transformation. Bull. Am. Mus. Nat. Hist. 206: 84–100.

Novick, A.
1963. Orientation in Neotropical bats. II.

Phyllostomatidae and Desmodontidae. J. Mammal. 44: 44–56.
1977. Acoustic orientation. *In* W. A. Wimsatt (ed.), Biology of bats, vol. 3: 73–289. New York: Academic Press.

Nowak, R. M.
1991. Walker's mammals of the world. Baltimore: Johns Hopkins Univ.

Oken, L.
1816. Lehrbuch der Naturgeschichte, theil 3, abt., 2. Jena: August Schmidt.

Owen, R. D.
1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Spec. Publ. Mus. Texas Tech Univ. 26: 1–65.
1991. The systematic status of *Dermanura concolor* (Peters, 1865) (Chiroptera: Phyllostomidae), with description of a new genus. Bull. Am. Mus. Nat. Hist. 206: 18–25.

Paradiso, J. L.
1967. A review of the wrinkled-faced bats (*Centurio senex* Gray), with a description of a new subspecies. Mammalia 31: 595–604.

Park, H., and E. R. Hall
1951. The gross anatomy of the tongues and stomachs of eight New World bats. Trans. Kansas Acad. Sci. 54: 64–72.

Patton, J. C., and R. J. Baker
1978. Chromosomal homology and evolution of phyllostomatoid bats. Syst. Zool. 27: 449–462.

Patton, J. L, and A. L. Gardner
1971. Parallel evolution of multiple sex-chromosome systems in the phyllostomatid bats, *Carollia* and *Choeroniscus*. Experientia 27: 105–106.

Peters, W.C.H.
1865. Vorlage von Abbildungen zu einer Monographie der Chiropteren, und Übersicht der von ihm befolgten systematischen Ordnung der hieher gehörigen Gattungen. Monatsber. K. Preuss. Akad. Wiss. Berlin 1865: 265–258.

Peterson, R. L.
1965. A review of the bats of the genus *Ametrida*, family Phyllostomidae. R. Ont. Mus. Life Sci. Contrib. 65: 1–13.

Phillips, C. J.
1971. The dentition of glossophagine bats: development, morphological characteristics, variation, pathology, and evolution. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 54: 1–138.

Pierson, E. D.
1986. Molecular systematics of the Microchi-

roptera: higher taxon relationships and biogeography. Ph.D. diss., Univ. of California, Berkeley.

Pine, R. H.
1972. Bats of the genus *Carollia*. Texas Agric. Exp. Tech. Monogr. 8: 1–125.

Platnick, N. I., C. E. Griswold, and J. A. Coddington
1991. On missing entries in cladistic analysis. Cladistics 7: 337–343.

Pleijel, F.
1995. On character coding for phylogeny reconstruction. Cladistics 11: 309–315.

Pocock, R. I.
1914. On the facial vibrissae of Mammalia. Proc. Zool. Soc. London 1914: 889–912.

Rehn, J. A. G.
1901. A study of the genus *Centurio*. Proc. Acad. Nat. Sci. Philadelphia. 53: 295–302.

Robin, H. A.
1881. Recherches anatomiques sur les mammifères de l'ordre des chéiroptères. Ann. Sci. Nat., ser. 6 Zool., 12: 1–180.

Rodrigo, A. G., M. Kelly-Borges, P. R. Bergquist, and P. L. Bergquist.
1993. A randomisation test of the null hypothesis that two cladograms are sample estimates of a parametric phylogenetic tree. New Zealand J. Bot. 31: 257–268.

Rodriguez-Duran, A., and T. H. Kunz
1992. *Pteronotus quadridens*. Mamm. Species 395: 1–4.

Rodriguez-Duran, A., and A. R. Lewis
1987. Patterns of population size, diet, and activity time for a multispecies assemblage of bats at a cave in Puerto Rico. Caribb. J. Sci. 23: 352–360.

Santos, M., A. Ruiz, J. Cavalier, and P. Soriano
1996. The phenology of cacti and its relationships with the bat community in a tropical dry forest–thorn shrubland of Colombia. Bat Res. News 36: 105–106. [Dated 1995 but published in 1996].

Savage, D. E.
1951. A Miocene phyllostomatid bat from Colombia, South America. Univ. California Publ. Geol. Sci. 28: 357–366.

Sazima, I.
1976. Observations on the feeding behavior of some phyllostomatid bats (*Carollia*, *Anoura*, and *Vampyrops*) in Southeastern Brazil. J. Mammal. 57: 381–382.
1978. Aspectos do comportamento alimentar do morcêgo hematófago, *Desmodus ro-*

*tundus*. Bol. Zool. Univ. São Paulo 3: 97–119.

Schmidt, U.
1978. Vampirfledermäuse; familie Desmodontidae (Chiroptera). Wittenberg Luterhstadt: A. Zimsen.

Schnitzler, H. -U., and A. D. Grinnell
1977. Directional sensitivity of echolocation in the horseshoe bat *Rhinolophus ferrumequinum*. I. Directionality of sound emission. J. Comp. Physiol. 116: 51–61.

Schober, W., and K. Brauer
1974. Makromorphologie des Zentralnervensystems. *In* J. G. Helmcke, D. Starck, H. Wermuth (eds.), Handbuch der Zoologie. Eine Naturgeschichte der Stamme des Tierreiches. 8. Band/52. Liefrung: 1–296. New York: Walter de Gruyter.

Schutt, W. A., Jr.
1998. Chiropteran hindlimb morphology and the origin of blood-feeding in bats. *In* T. H. Kunz, and P. A. Racey (eds.), Bat biology and conservation: 157–168. Washington D.C.: Smithsonian Inst.

Silva-Taboada, G. S., and R. H. Pine
1969. Morphological and behavioral evidence for the relationship between the bat genus *Brachyphylla* and the Phyllonycterinae. Biotropica 1: 10–19.

Simmons, N. B.
1993. The importance of methods: archontan phylogeny and cladistic analysis of morphological data. *In* R.D.E. MacPhee (ed.), Primates and their relatives in phylogenetic perspective: 1–61. New York: Plenum.
1996. A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Northeastern Brazil, with comments on phylogenetic relationships. Am. Mus. Novitates 3158: 34 pp.
1998. A reappraisal of interfamilial relationships of bats. *In* T. H. Kunz and P. A. Racey (eds.), Bats: biology and conservation: 3–26. Washington D.C.: Smithsonian.

Simmons, N. B., and T. M. Conway
MS. Phylogenetic relationships of mormoopid bats (Chiroptera: Mormoopidae) based on morphological data.

Simmons, N. B., and J. H. Geisler
1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strat-

egies in Microchiroptera. Bull. Am. Mus. Nat. Hist. 235: 1–182.

Simmons, N. B., and C. O. Handley, Jr.
1998. A revision of *Centronycteris* Gray (Chiroptera: Emballonuridae) with notes on natural history. Am. Mus. Novitates 3239: 28 pp.

Simpson, G. G.
1945. The principles of classification and a classification of the mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.

Sites, J. W., Jr., J. W. Bickham, and M. W. Haiduk
1981. Conservative chromosomal change in the bat family Mormoopidae. Can. J. Genet. Cytol. 23: 459–467.

Slaughter, B. H.
1970. Evolutionary trends of chiropteran dentitions. *In* B. H. Slaughter and W. D. Walton (eds.), About bats: 51–83. Dallas: Southern Methodist Univ. Press.

Smith J. D.
1972. Systematics of the chiropteran family Mormoopidae. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 56: 1–132.
1976. Chiropteran evolution. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. I. Spec. Publ. Mus. Texas Tech Univ. 10: 49–69.

Smith, J. D., and C. S. Hood
1984. Geneology of New-World nectar-feeding bats reexamined: a reply to Griffiths. Syst. Zool. 33: 435–460.

Snow, J. L., J. K. Jones, and W. D. Webster
1980. *Centurio senex*. Mamm. Species 138: 1–3.

Sokolov, B. V., and A. K. Makarov
1971. Direction of the ultrasonic radiation and the role of the nasal leaf in *Rhinolophus ferrumequinum*. J. Biol. Sci. Moscow Univ. 7: 37–44.

Solmsen, E.-H.
1994. Vergleichende Untersuchungen zur Schädelkonstruktion der neuweltlichen Blütenfledermäuse sowie zu ihrer systematischen Ordnung unter besonderer Berücksichtigung der Glossophaginae (Phyllostomatidae, Chiroptera, Mammalia). Ph.D. Diss., Univ. Hamburg, Hamburg.

Sonntag, C. F.
1920. The comparative anatomy of the tongues of the Mammalia—I. general description of the tongue. Proc. Zool. Soc. London 1920: 115–129.
1925. The comparative anatomy of the tongues of the Mammalia—XII. summary, classification, and phylogeny. Proc. Zool. Soc. London 1925: 701–762.

Spix, J. B.
1823. Simiarum et vespertilionum brasiliensum: species novae ou histoire naturelle des espèces nouvelles des singes et de chauve-souris, observées et recueilles pendant le voyage dans l'intérieur du Brésil. Monachii: F.S. Hubschmann.

Sprague, J. M.
1943. The hyoid region of placental mammals with especial reference to the bats. Am. J. Anat. 72: 385–472.

Starett, A., and R. S. Casebeer
1968. Records of bats from Costa Rica. Los Angeles Cty. Mus. Contrib. Sci. 148: 1–21.

Stock, A. D.
1975. Chromosome banding pattern homology and its phylogenetic implications in the bat genera *Carollia* and *Choeroniscus*. Cytogenet. Cell Genet. 14: 34–41.

Straney, D. O.
1980. Relationships of phyllostomatine bats: evaluation of phylogenetic hypotheses. Ph. D. diss., Univ. of California, Berkeley.

Straney, D. O., M. H. Smith, I. F. Greenbaum, and R. J. Baker
1979. Biochemical genetics. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (eds.), Biology of the bats of the New World family Phyllostomatidae, p. III. Spec. Publ. Mus. Texas Tech Univ. 16: 157–176.

Strickler, T. L.
1978. Functional osteology and the myology of the shoulder in the Chiroptera. Contrib. Vertebr. Evol. 4: 1–198.

Strother, G. K., and M. Mogus
1970. Acoustical beam patterns for bats some theoretical considerations. J. Acoust. Soc. Am. 48: 1430–1432.

Swofford, D. L.
1991. When are phylogeny estimates from molecular and morphological data incongruent? *In* M. M. Miyamoto and J. Cracraft (eds.), Phylogenetic analysis of DNA sequences: 295–333. New York: Oxford Univ. Press.
1998. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b1. Computer program distributed by Sinauer, Sunderland, MA.

Swofford, D. L., and D. P. Begle
1993. PAUP: Phylogenetic analysis using

parsimony, version 3.1.1. User's manual distributed by the Smithsonian Institution, Washington, D.C.

Thomas, D. W.
1988.   Analysis of diets of plant-visiting bats and methods of estimating fruit availability to frugivorous bats. *In* T. H. Kunz (ed), Ecological and behavioral methods for the study of bats: 211–231. Washington, D.C.: Smithsonian Inst.

Thomas, O.
1903.   Two new glossophagine bats from Central America. Ann. Mag. Nat. Hist. ser. 7, 11: 286–289.
1908.   The missing premolar of the Chiroptera. Ann. Mag. Nat. Hist. ser. 8: 346–348

Trajano, E.
1985.   Ecologia de populações de morcêgos cavernícolas em uma região cárstica do sudeste do Brasil. Rev. Bras. Zool. 2: 255–820.

Trouessart, E. L.
1897.   Catalogus mammalium tam viventum quam fossilium. Nova edito (prima completa). 1: 1–218. Berlin: R. Friedländer.

Turner, D. C.
1975.   The vampire bat, a field study of behavior and ecology. Baltimore: Johns Hopkins Univ. Press.

Tuttle, M. D., and M. J. Ryan
1981.   Bat predation and the evolution of frog vocalizations in the Neotropics. Science 214: 677–678.

Uchikawa, K.
1987.   Myobiid mites (Trombidiformes: Myobiidae) associated with the vampire bats (Chiroptera: Pyllostomatidae) and information on host taxonomy deduced from them. J. Parasitol. 73: 640–645.

Van Den Bussche, R. A.
1991.   Phylogenetic analysis of restriction site variation in the ribosomal DNA complex of New World leaf-nosed bat genera. Syst. Zool. 40: 420–432.
1992.   Restriction-site variation and molecular systematics of New World leaf-nosed bats. J. Mammal. 73: 29–42.

Van Den Bussche, R. A., and R. J. Baker
1993.   Molecular phylogenetics of the New World bat genus *Phyllostomus* based on cytochrome *b* DNA sequence variation. J. Mammal. 74: 793–802.

Van Den Bussche, R. A., R. J. Baker, H. A. Wichman, and M. J. Hamilton
1993.   Molecular phylogenetics of Stenodermatini bat genera: congruence of data

from nuclear and mitochondrial DNA. Mol. Biol. Evol. 10: 944–959.

Van Den Bussche, R. A., J. L. Hudgeons, and R. J. Baker
1998.   Phylogenetic accuracy, stability, and congruence: relationships within and among the New World bat genera *Artibeus*, *Dermanura*, and *Koopmania*. *In* T. H. Kunz and P. A. Racey (eds.), Bats: biology and conservation: 59–71. Washington D.C.: Smithsonian Inst.

Van Valen, L.
1979.   The evolution of bats. Evol. Theory 4: 104–121.

Vaughan, T. A.
1959.   Functional morphology of three bats: *Eumops*, *Myotis*, and *Macrotus*. Univ. Kansas Publ. Mus. Nat. Hist. 12: 1–153.
1986.   Mammalogy, 3rd ed. Philadelphia: W. B. Saunders.

Vaughan, T. A., and G. C. Bateman
1970.   Functional morphology of the forelimb of mormoopid bats. J. Mammal. 51: 217–235.

Vierhaus, V. H.
1983.   Wie Vampirfledermäuse (*Desmodus rotundus*) ihre Zähne schärfen. Z. Säugetierkd. 48: 269–277.

Voss, R. S., and L. H. Emmons
1996.   Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bull. Am. Mus. Nat. Hist. 230: 1–115.

Wagner, J. A.
1840.   Die Säugethiere in Abbildungen nach der Natur mit Beschriebungen von Dr. Johann Christian Daniel von Schreber, Supplementband, Erst Abtheilung. [Part one of Wagner's supplement to Schreber's multivolume work]. Erlangen: in der Expedition des Schreber'schen Säughthier[e] und des Esper'schen Schmetterlingwerkes, etc.

Waite, P.M.E.
1973a.   Somatotropic organization of vibrissal responses in the ventro-basal complex of the rat thalamus. J. Physiol. (London) 228: 527–540.
1973b.   The responses of cells in the rat thalamus to mechanical movements of whiskers. J. Physiol. (London) 228: 541–561.

Walton, D. W., and G. M. Walton
1968.   Comparative osteology of the pelvic and pectoral girdles of the Phyllostomatidae (Mammalia: Chiroptera). J.

Grad. Res. Cent. South. Methodist Univ. 37: 1–35.

Warner, R. M.
1983. Karyotypic megaevolution and phylogenetic analysis: New World nectar-feeding bats revisited. Syst. Zool. 32: 279–282.

Weber, M.
1904. Die Säugetiere. Jena: Gustav Fischer.

Wenzel, R. L., V. J. Tipton, and A. Kiewlicz
1966. The streblid batflies of Panama (Diptera Calypterae: Streblidae). *In* R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama: 405–675. Chicago: Field Museum.

Wible, J. R., and K. P. Bhatnager
1996. Chiropteran vomeronasal complex and the interfamilial relationships of bats. J. Mamm. Evol. 3: 285–314.

Wilder, B. D.
1976. Comparative histology and ultrastructure of the epithelial elements of the parotid glands of selected glossophagine bats with reference to evolution and systematics. Ph.D. diss., St. John's Univ., New York.

Wiley, E. O.
1981. Phylogenetics: the theory and practice of phylogenetic systematics. New York: Wiley.

Wilkinson, M.
1995. A comparison of two methods of character construction. Cladistics 11: 297–308.

Wille, A.
1954. Muscular adaptation of the nectar eating bats (subfamily Glossophaginae). Trans. Kansas Acad. Sci. 57: 315–325.

Wimsatt, W. A.
1975. Some comparative aspects of implantation. Biol. Reprod. 12: 1–40.
1979. Reproductive asymmetry and unilateral pregnancy in Chiroptera. J. Reprod. Fertil. 56: 345–357.

Wineski, L. E.
1985. Facial morphology and vibrissal movement in the golden hamster. J. Morphol. 183: 199–217.

Winge, H.
1892. Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa, Minas Geraes, Brasilien. Museo Lundii 2: 1–66.
1941. The interrelationships of the mammalian genera, trans. E. Deichmann and G. M. Allen. Copenhagen: C. A. Reitzels.

Winkelmann, J. R.
1971. Adaptations for nectar-feeding in glossophagine bats. Ph.D. diss., Univ. of Michigan, Ann Arbor.

Wood Jones, F.
1917. The genitalia of the Chiroptera. J. Anat. Phys. London 51: 36–60.
1923. The mammals of South Australia. Pt. I: The monotremes and carnivorous marsupials. Adelaide: Gov. Printer.

Woolsey, T. A.
1978. Some anatomical bases of cortical somatotropic organization. Brain Behav. Evol. 15: 325–371.

Zucker E., and W. I. Welker
1969. Coding of somatic sensory input by vibrissae neurons in the rat trigeminal ganglion. Brain Res. 12: 128–156.

## APPENDIX 1: SPECIMENS EXAMINED

The following list includes all specimens examined in this study; see individual character discussions for published data sources. All taxa are arranged alphabetically. See Materials and Methods for abbreviations. The dagger (†) indicates that the noseleaf of a skin was rehydrated.

**Mormoopidae**: *Mormoops megalophylla* (AMNH 25090–25091, 25097–25100, 25121, 27301, 27303, 27305, 144509–144511, 170194, 170196–170197, 175564, 175575, 177423, 183315, 187842–187843, 187848, 187850–187852, 204472–204473, 205340, 205342, 205344, 205347–205348, 206692–206693, 214414, 239231–239232, 249066; USNM 37484/8311, 314677, 407207, 417184). *Mormoops blan-* *villii* (AMNH 39559, 39561, 213894–213897, 236656). *Pteronotus davyi* (AMNH 2698/2324, 26981, 27296, 29694, 29703–29704, 32083–32085, 32089–32091, 32093–32094, 170201, 170204, 175276, 178479–178481, 178487, 179954, 180437, 202316, 203563–203566, 204407, 204960, 204963, 204965, 207060, 214405–214407, 214410, 214412–214413, 234961, 249065; USNM 6325, 362096, 508373, 508376). *Pteronotus parnellii* (AMNH 23656, 31570–31571, 31574–31576, 135245, 135249, 238140, 267851).

**Noctilionidae:** *Noctilio leporinus* (AMNH 2757, 39574, 91936–91937, 91945, 92373, 92378–92380, 92530, 93434, 93808, 173912, 175534, 175536, 175538, 213201–213202,

213956–213957, 230111-230112, 234277, 243719–243724, 243905–243906, 244904, 249993, 260049, 261372, 265974, 267398, 267408; USNM 391025, 508370, 522063, 523006).

**Phyllostomidae: Brachyphylliinae:** *Brachyphylla cavernarum* (AMNH 39287, 72278–72280, 72283, 72293–72295, 72297, 72299–72300, 149367, 208181, 213706, 213731, 213735, 213737, 213740, 213742, 213899, 213907–213909, 214203, 214251, 214258 235646, 239064–239065, 246997–247005; USNM 544829, 544830, 544832–544833, 544866). *Brachyphylla nana* (AMNH 175972–175973). **Carolliinae:** *Carollia perspicillata* (AMNH 130722, 202299, 202750–202752, 209407, 212944, 217534–217535, 217537–217538, 217540, 236043, 236047, 246206, 246210, 246212–246215, 248017, 260006–260007, 266125, 266130, 266134, 266138–266139, 266141, 266143–266145, 266147, 266149, 266152–266153, 266155–266162, 266164, 266378, 267453–267454; USNM 536900–536901, 536905, 537910, 537912–537914, 537916, 537918–537919). *Carollia subrufa* (AMNH 164023, 186375, 235717, 244091, 249087, 254622). *Rhinophylla pumilio* (AMNH 233521, 233523–233525, 236056, 237950, 239918, 239920, 262421–262423, 262468–262469, 262471, 266165, 266167, 266169, 266171–266172, 266178, 266186–266187, 266189–266194, 266196, 267158–267160, 267162–267164, 267455, 267971; USNM 361632, 393015, 574529). *Rhinophylla fischerae* (AMNH 76094, 94557, 230483, 230485–230496, 230500, 233863, 239918, 262469, 266190). *Rhinophylla alethina* (AMNH 217032). **Desmodontinae:** *Desmodus rotundus* (AMNH 172293, 174303, 183304, 189215, 190149, 190152–190154, 202296, 203764, 205410, 205414, 207903, 208894, 208897, 208899, 208904, 209748, 210955–210956, 210962, 213654, 214423, 235326–235327, 235353–235354, 237373, 237375, 239943, 249100, 249102, 249193, 254670, 256983, 263625–263626, 267503–267505, 267211; USNM 114977, 245140, 363077, 441621, 508828, 523438, 536939, 549500, 565049, 574562). *Diaemus youngi* (AMNH 78285, 94559, 175654, 175997, 209100, 209742, 209744–209747, 215026, 237920, 246230–246232, 260249, 263182, 266347, 267297, 267299, 267301; USNM 335399–335400, 361772, 393029–393030, 536938, 553710). *Diphylla ecaudata* (AMNH 63841, 66800–66801, 91283–91284, 126464, 129041, 142201, 165640, 175000, 175004, 203837–203843, 203846, 206694, 213423, 239944, 256847, 261777; USNM 315733,

335401, 338091, 372482, 441630, 542757, 549502). **Glossophaginae:** *Anoura geoffroyi* (AMNH 60536, 60538, 78288, 203622–203624, 203636–203637, 203678, 230270–230271, 233346, 235649, 237932–237933, 243758, 244620, 244947, 246191–246194, 246196, 246198–246199, 246473, 283347; USNM 49356, 385799, 523116–523117, 548093, 549371). *Anoura caudifera* (AMNH 176347, 212261, 246468–246471, 248013, 261393, 261395–261396). *Anoura cultrata* (AMNH 233257). *Choeroniscus godmani* (AMNH 172779, 186162). *Choeroniscus intermedius* (AMNH 95778, 179956, 185314, 207065, 230285–230286, 246156, 266120–266124, 266377, 267152–267153, 267946–267947). *Choeroniscus minor* (AMNH 67626, 140471, 207824, 248759; USNM 361575, 385925, 460101–460103). *Choeroniscus periosus* (AMNH 217038). *Choeronycteris mexicana* (AMNH 27306, 27314–27316, 74465–74468, 173664–173665, 173871–173872, 173874, 180350, 212359, 212362, 212364, 213762, 237361–237362, 239233–239234, 243862–243863; USNM 21903, 52178, 52181, 52342, 52348, 52355–52358, 54354–54358, 96492). *Glossophaga commissarisi* (AMNH 189605, 235715). *Glossophaga leachii* (AMNH 97545, 135277, 189626). *Glossophaga longirostris* (AMNH 182724–182725, 182904). *Glossophaga soricina* (AMNH 9755, 15157, 91238, 91926, 91929, 91932, 97553, 209354, 214137, 214139, 214415, 214417, 217530, 237911–237912, 247984, 247989–247990, 254619, 260958, 260960, 260964–260965, 266090–266091, 266099, 267133–267134, 267136–267143, 267448–267449, 267956; USNM 312995, 313000–313003, 313119, 313121–313122, 545156, 545159). *Hylonycteris underwoodi* (AMNH 178904, 189687–189688, 238199; FMNH 69728; USNM 336355, 336455, 349922, 506578, 523119, 559562, 562787–562791, 562793–562796, 562798–562799, 562802–562805, 563276–563278, 566441). *Leptonycteris curasoae* (AMNH 7402–7403, 27321, 149385–149390, 169966, 173667, 173669, 180347, 180349, 189699, 189701, 189708–189709, 189711, 189714–189715, 189724–189725, 204976–204979, 205353, 205355, 205357; USNM 314690, 389140, 389142–389143, 389147–389150, 444719, 444722–444723, 444732, 456798, 456800, 456804, 483373, 511721). *Leptonycteris nivalis* (AMNH 172039, 249086). *Lichonycteris obscura* (AMNH 131769, 244621, 267960; USNM 51546, 309402–309403, 315310, 319377, 319493, 331257–331258, 335187, 338727, 362595, 396476, 432194, 483374, 506578, 514961, 519891–519892, 537520, 537589, 575499–575500). *Lionycteris*

*spurrelli* (AMNH 78431, 78433–78434, 97221, 97264, 97267–97269, 145504, 202295, 230207, 230209, 236006, 236010, 236014, 236016, 236019, 236022, 236024–236027, 239391, 260004, 265336; USNM 335186, 491672, 491675–491676). *Lonchophylla handleyi* (AMNH 230214). *Lonchophylla mordax* (AMNH 235608). *Lonchophylla robusta* (AMNH 143761–143763, 185380, 207820, 233761, 233177–233179, 235760–235761, 243993, 267452; USNM 306589, 311999, 313749, 362539, 362544, 362546, 483361–483362, 498827, 562767–562773, 563275). *Lonchophylla thomasi* (AMNH 95493, 95772, 97271–97272, 209358, 210688, 237930, 262429, 262434, 266100, 266104–266105, 266107–266108, 266117, 267452, 267942; USNM 339568, 446481, 554625). *Monophyllus plethodon* (AMNH 72367). *Monophyllus redmani* (AMNH 19106, 23782–23783, 39431, 39436, 39439–39440, 39444, 39447, 39505–39506, 39519, 39522, 39525, 41157, 176154–176157, 219658–219660, 236659–236660, 236662–236668, 236671; USNM 520514, 534895, 534899, 534900, 543893, 545161). *Musonycteris harrisoni* (AMNH 235179; USNM 314639, 314689, 324971–324972; photo from *Walker's Mammals of the World*). *Platalina genovensium* (AMNH 257108; FMNH 54980, 69728; USNM 268765–268766). *Scleronycteris ega* (USNM 407889; photo from *Walker's Mammals of the World*). **Phyllonycterinae:** *Erophylla sezekorni* (AMNH 4824, 39341, 41056–41057, 41059–41060, 41065–41066, 41091, 41096, 102059, 102061, 164280, 167115, 167117–167118, 167124–167125, 167127, 176100, 186976–186977, 194201–194203, 208979, 212998, 214945, 219702, 245691–245692, 247595–247597; USNM 538180–538183, 538185, 539744, 539746–539747). *Phyllonycteris poeyi* (AMNH 10749–10750, 23758, 23762, 103545, 176019–176022, 176024–176029, 186987–186988, 214130, 236697–236698, 256331; USNM 49568, 103445, 103542, 103573–103575, 535321, 535323, 535326). **Phyllostominae:** *Chrotopterus auritus* (AMNH 32139, 36987–36988, 175021–175022, 209353, 248306, 255714–255715, 256351, 256824, 260867, 260953, 261373, 267130–267131, 267443–267444, 267852; USNM 113852, 335152, 362400, 370090, 371568, 517315, 519868–519869, 549357–549358, 554691). *Glyphonycteris sylvestris* (AMNH 183297, 183299, 183846, 207061, 214316, 245656, 267879; USNM 335101, 362394, 388734, 396399, 407260, 534240). *Lampronycteris brachyotis* (AMNH, 28336, 69969, 94601, 169020, 175628–175633, 175637–175641, 182703–182704, 185856; MVZ 118762–118763). *Lonchorhina aurita* (AMNH 31517–31519, 62940, 149217–149218, 149233, 183850, 184700–184701, 230121–230122, 249947–249948, 256292–256293, 265950–265951; USNM 313101, 313105–313106, 313726–313727, 313731, 313733, 491172, 491174, 562890). *Lonchorhina orinocensis* (USNM 491177, 491179). *Macrophyllum macrophyllum* (AMNH 42744, 78747, 78750, 94551, 96018, 97252, 98761, 119462–119463, 177662, 177664-177666, 178137, 178140, 178165, 178169, 178179, 209320–209321, 222040, 235703–235706, 243730, 243908, 243974–243976, 262424, 266039–266041; USNM 312931, 312935, 312940, 312942–312943, 312946–312947, 312951, 312958, 312960). *Macrotus waterhousii* (AMNH 2148, 2160/2146, 2659/2145, 2661/2147, 4116, 22799, 41098, 41100–41101, 41103, 41130, 41133–41134, 41140–41143, 41159, 41172, 41176, 45229–45231, 120970, 139569–139572, 139574, 166770–166771, 170844–170845, 170847, 176162–176163, 180523, 182518, 185074, 185076–185078, 204474–204478, 204483, 214818, 236658, 238145; USNM 511230–511233, 534883, 538121–538122, 538124–538125, 538127, 539736, 539738, 545147). *Micronycteris hirsuta* (AMNH 94534, 94560, 139441–139442, 175604–175605, 175607, 175610, 175612, 175615, 176287, 176623, 179957, 179959, 182698, 217679–217680, 230114–230116, 255705, 267093–267096, 267857; USNM 337373, 517305, 539797). *Micronycteris megalotis* (AMNH 69154, 69164, 69194, 73497, 73500, 74476–74477, 91893, 92386, 94517, 97206, 97219, 98912, 183159, 207775–207777, 207779, 212255–212256, 216102, 230113, 230117, 243958, 246158, 256349, 256820, 256845, 260003, 266020, 267090–267092, 267411, 267862, 267864, 267090–267092). *Micronycteris minuta* (AMNH 71616, 71631, 92408–92411, 92689, 92693, 92695, 92846, 98916–98917, 175592–175593, 175595, 175597, 183169, 183295, 230119–230120, 233221, 237910, 244471, 267098, 267874). *Mimon bennettii* (AMNH 185862–185869; 185872, 256823, 256294, 265107, 265864, 267109–267110; USNM 316289). *Mimon crenulatum* (AMNH 64538, 64541, 78651–78652, 78655–78656, 79526, 79528, 92225, 92387–92388, 130695, 130724, 131085–131086, 175586, 207063, 233222, 236001, 256308, 267111–267115, 267437–267438, 267883–267884, 267888; USNM 335120, 516015, 521580). *Phylloderma stenops* (AMNH 126869, 205371–205372, 256299, 266077–266078, 267439–267441, 267890–267891; USNM 335142–335144, 336988–336989, 361532, 371547–371548, 373527, 388839–388841,

457937, 491318, 519694, 531030–531031, 548468, 562334, 579583). *Phyllostomus hastatus* (AMNH 42340, 95409, 96954, 96956, 96958, 169946, 183870, 202308, 209334, 230170–230171, 233176, 239876, 239878–239879, 243860, 243983, 266070, 266072–266076, 267128, 267433–267435, 267903, 267905; USNM 102911, 306560–306564, 549353). *Phyllostomus discolor* (AMNH 92398, 92400–92402, 149219–149221, 182713, 207804, 207806, 243743–243744, 243981, 254612–254613, 267124). *Phyllostomus elongatus* (AMNH 92120, 92417, 92419, 209331, 210676, 210679, 214317–214318, 230137–230138, 233226, 237927, 266055, 266063). *Tonatia brasiliense* (AMNH 267101–267104, 267426–267428; USNM 336990, 490096, 499293–499294, 562160, 566438). *Tonatia carrikeri* (AMNH 209322). *Tonatia evotis* (AMNH 267635). *Tonatia saurophila* (AMNH 139438, 266042–266049, 267099–267100, 267429–267431, 267910; USNM 554579, 581911). *Tonatia schulzi* (AMNH 267105–267106, 267420–267421). *Tonatia silvicola* (AMNH 61753, 69188, 78644, 78834–78835, 95440–95441, 96965, 96976, 97009, 97011–97013, 97340, 97350, 97353, 142906–142907, 182718, 237926, 262425, 267107–267108, 267924–267925; USNM 34509, 335107, 335110, 335113, 370084, 503848, 518862, 518864–518866, 539805, 549347, 574575, 579580). *Trachops cirrhosus* (AMNH 209352, 210683–210684, 233227, 235557, 236002, 255713, 256301, 266079–266089, 267129, 267442, 267927, 267929, 267932, 267934–267936; USNM 244254, 244260, 361533–361534, 371559, 460090, 513435, 526241, 549354, 562763–562764). *Trinycteris nicefori* (AMNH 78650, 149200, 175643–175645, 179984–179985, 184557–184559, 256822, 266015–266017, 266019, 267409–267410, 267446, 267876). *Vampyrum spectrum* (AMNH 7435–7436, 18707, 28993, 42895, 66815, 175717–175718, 184694, 202292, 256825, 261379, 267132, 267278, 267445; USNM 246253, 307233, 319373, 335159–335160, 335162–335163, 337312–337314, 346251, 346264–346265, 346267–346268, 393007, 562765–562766, 575471, 731786). **Stenodermatinae:** *Ametrida centurio* (AMNH 142612–142613, 142909, 172127, 187224–187225, 207967, 247645, 267274–267276, 267278–267279, 267375, 267973, 267975; USNM 370783–370786, 370795, 393758, 460135–460136, 494488, 494510, 494520, 531106–531108, 535108, 542285, 554827). *Ardops nichollsi* (AMNH 212557, 212896, 213925, 213952–213955, 217104, 238150–238151; USNM 110918, 113186, 113498–113499,

113501, 361905, 544871–544872, 580675–580676). *Ariteus flavescens* (AMNH 4121, 214944, 239109; USNM 53097, 96179–96181, 113926, 114042, 122658–122659, 252771, 534909–534911, 545167-545175, 545177–545184, 545203–545204, 546358). *Artibeus (Artibeus) amplus* (AMNH 185366). *Artibeus (Artibeus) fraterculus* (AMNH 47238, 47249). *Artibeus (Artibeus) hirsutus* (AMNH 188750). *Artibeus (Artibeus) jamaicensis* (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, 266340–266341, 266343–266344, 267202; USNM 538135–538136, 544816, 544818–544819, 544822, 544824–544827). *Artibeus (Artibeus) lituratus* (AMNH 180549, 210906, 266346, 267204, 267492, 268506, 268513). *Artibeus (Artibeus) obscurus* (AMNH 246641, 266278–266279, 266288, 268523). *Artibeus (Dermanura) anderseni* (AMNH 210841, 233759). *Artibeus (Dermanura) aztecus* (AMNH 175282, 190008). *Artibeus (Dermanura) cinereus* (AMNH 93500, 94179, 94181, 97075–97076, 212279, 212880–212881, 233782, 233784, 233777, 237964, 244084, 246627–246628, 246632, 248177, 256374, 266258–266263, 266265–266266, 266270, 266290–266291, 266302, 266305, 266307, 267197–267198, 267499; USNM 540677–540680, 549429, 549330, 549437–549438). *Artibeus (Dermanura) glaucus* (AMNH 246631). *Artibeus (Dermanura) gnomus* (AMNH 67650, 77531, 266293, 266301, 266310). *Artibeus (Dermanura) phaeotis* (AMNH 21083, 209590, 210825, 217410). *Artibeus (Dermanura) toltecus* (AMNH 190015). *Artibeus (Dermanura) watsoni* (AMNH 18760, 265122). *Artibeus (Koopmania) concolor* (AMNH 80340, 89945, 260014, 266267-266269, 267192–267195, 267477–267478, 267480–267485, 267488, 267502, 267981; USNM 405203, 405206, 549439–549441). *Centurio senex* (AMNH 99645, 175650–175651, 177419, 179989–179991, 180401, 183862, 208879, 214422, 243786–243788, 256330, 256846, 265125; USNM 22039/6322, 310237–310239, 310242, 310245, 335392, 346821–346822, 346827, 346832, 346840, 503837, 511740–511741, 511855–511856, 511859). *Chiroderma salvini* (AMNH 142484, 261667, 262537). *Chiroderma trinitatum* (AMNH 209521, 235607, 266255–266256, 267189). *Chiroderma villosum* (AMNH 37041, 209542–209544, 209547, 209552, 209554, 209558, 209560–209564, 209576, 210811, 233738, 243926, 243929, 245326–245327, 262526–262532, 262534, 262539, 267190–267191,

267474–267476, 268533–268534, 268536; USNM 522434–522435, 534314–534316, 574537). *Ectophylla alba* (FMNH 137219–137221, UMMZ 125633; USNM 315563, 319426, 324926, 335310, 335317–335325, 336259–336262, 563298, 579079). *Ectophylla macconelli* (AMNH 48270, 48274, 172126, 187223, 207068, 209577, 209579–209580, 214368, 215025, 233745–233749, 246226, 248886–248887, 262540–262541, 267281, 267556–267558, 267560–267564, 268539; USNM 315564, 361726, 460131–460132, 548426–549427, 574540). *Enchisthenes hartii* (AMNH 126239, 206872, 214367, 233598–233599, 233753, 233791–233800; USNM 310230, 310213–310217, 323538–323539, 370726–370727, 370729–370731, 483909–483910, 483919–483920, 483922, 494470, 507202, 539813, 562916–562917). *Phyllops falcatus* (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). *Platyrrhinus aurarius* (AMNH 261225, 261227–261228). *Platyrrhinus dorsalis* (AMNH 214355, 233187, 233640, 236105, 246610–246611, 246613). *Platyrrhinus helleri* (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). *Platyrrhinus infuscus* (AMNH 230647, 248882). *Platyrrhinus lineatus* (AMNH 37007, 210805, 255932, 260231). *Platyrrhinus ornatus* (AMNH 235560). *Pygoderma bilabiatum* (AMNH 234286, 234289–234301, 246401, 246405, 246408, 248334, 248336–248339, 261758, 261761–261762, 261764; USNM 14816/37502, 148161, 460507, 542744, 542745–542748). *Sphaeronycteris toxophyllum* (AMNH 21344–21345, 24379–24380, 76251, 92248, 194213, 209741, 235561, 261765, 262637, 265354; FMNH 122939; 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). *Stenoderma rufum* (AMNH

208982–208983; USNM 239110, 271210, 522706–522708, 549795). *Sturnira bogotensis* (AMNH 207851, 207853, 246570, 260870, 261537). *Sturnira erythromos* (AMNH 233529, 233597, 244948, 246572). *Sturnira lilium* (AMNH 185320–185321, 189881, 189893–189894, 189946, 203705, 204713, 204724, 209412, 210724, 214196, 233541–233542, 248108, 249091, 249096–249097, 266199, 266203–266207, 266210, 266215, 266226, 266228–266234, 266236, 267167, 267169; USNM 502244–502250, 502257–502259). *Sturnira ludovici* (AMNH 189779, 237364, 254636, 254638). *Sturnira nana* (AMNH 219172). *Sturnira tildae* (AMNH 248863, 266240, 266241, 266243, 266247, 267167). *Uroderma bilobatum* (AMNH 171294, 179994–179995, 209472, 209496, 217404, 217408, 217411, 233184–233185, 243770, 245322, 246350, 260193, 260196–260197, 260210, 261041, 266257, 267172–267178, 267183, 267465–267470, 268564–268565; USNM 312881, 370401, 522357–522358, 522361, 535093, 549406–549407, 549410, 549412). *Uroderma magnirostrum* (AMNH 209467, 210736–210737, 210740, 210749, 210768). *Vampyressa bidens* (AMNH 67997–67998, 71656, 76090, 208072, 214351, 233734–233737, 233785, 261625–261627, 261633, 261640; USNM 361713–361714, 408573, 408578, 496590, 530997, 554778, 562584–562585, 579598). *Vampyressa nymphaea* (AMNH 233189–233190, 235789–235790; USNM 304903, 305382, 305384, 309062, 309883–309889, 315555–315556, 318130, 379076, 483686–483687, 483693–483696, 520005–520006, 520009–520011, 579076). *Vampyressa pusilla* (AMNH 31501, 67986–67987, 71675, 71680, 141996–141997, 233191–233193, 238219, 256827, 262559, 266311, 267471–267472, 267185; USNM 370525, 372143, 408571, 440660–440661, 440668, 483729–483730, 483734–483736, 496566, 496584, 496586–496587, 503630, 503633–503635, 534302–534303, 535095, 574639). *Vampyrodes caraccioli* (AMNH 29431, 175642, 186381, 209518, 230649–230651, 230653–230655, 239254, 256828; USNM 6327, 309711, 393019–393020, 393022, 447008, 447010, 447012–447017 496565, 519716–519717, 519719, 519721, 539811, 567158, 574638, 579658).

## APPENDIX 2: DATA MATRIX

This data matrix includes all characters used in all analyses discussed in the text. All taxa are arranged alphabetically, but the familial and subfamilial names are not shown. This matrix is

available in electronic format on the World Wide Web at ftp://ftp.amnh.org/pub/mammalogy

*Mormoops*
00121 00000 00400 0---- -0--- --0-3 -0-00 --011 000{01}- 00002 --000 002-0 00000 00000 10000 11-00 00000 1010? ????? ????? ????? ?0000 200-- 00010 001-- --?00 00000 10000 00000 00000

*Pteronotus*
000{024}0 00000 01200 0---- -0--- --1-3 -0-00 0-0{02}0 {01}000- 00002 --000 00100 00000 00000 00000 11001 00000 00100 00?00 ??-00 ?111- 00000 200-- 3-010 001-- --?00 0000{01} 10??? ????? ?????

*Noctilio*
00000 02000 12400 0---- -0--- --0-3 -0-00 0-020 1000- 00000 --010 100-0 00000 00000 00011 000?0 ???20 00000 00?00 ??-00 ?001- 0001- 100-- 2-000 000-- --?00 00000 {01}0000 00000 00000

*Brachyphylla*
00201 00000 01402 11011 00-02 --001 -0000 0-010 0000- 00000 --000 000-1 100-0 00200 000?0 0???? ???50 02021 12000 00-?0 00000 1001- 100-- 00010 01-00 0001? 21100 20000 00010 00010

*Carollia*
10202 00000 0{01}412 10000 11-02 --001 -0100 0-001 0100- 00000 --000 000-1 100-0 00000 00000 01211 01150 11000 01000 00-10 01000 20000 100-- 00010 01-00 000?0 21111 2{12}000 00010 00000

*Rhinophylla*
10201 0000{01} 02412 20000 10-02 --000 00100 0-0?? ?100- 0000{04} --000 000-1 100-0 00??? 111?? ????? ???40 1122? ????? ????? ????? ?0000 100-- 00010 000-- --??? 21110 20000 00010 0000?

*Desmodus*
01011 00001 12402 10011 00-02 --100 00000 0-001 0000- 001-1 --003 100-1 101-1 11??? -0-01 01101 01110 02020 12011 00-00 0001- 01-1- 120-- 00000 1---- --0?1 00001 20000 00000 0001?

*Diaemus*
01011 00001 12402 10011 00-02 --100 00000 0-001 0000- 001-1 --003 100-1 101-1 11??? -00?? ????? ???10 02202 ????? ????? ????? ?1-1- 120-- 00000 1---- --??? ????1 20??? ????? ?????

*Diphylla*
10001 00001 02402 10011 00-02 --100 00000 0-001 0000- 00001 --003 100-1 101-0 11??? -0001 012?? ???10 0102? ????? ????? ????? ?1-1- 100-- 00000 1---- --??? ????1 10000 00000 00010

*Anoura*
10221 00001 0{12}402 10000 01022 --000

11-00 0-001 0{02}00- 00010 --11- 003-0 10000 00000 110?? ????1 ??00 010{02}0 23101 111?1 20100 31-00 10111 00001 01-00 0010? 21101 20000 00010 00000

*Choeroniscus*
10201 00000 0{01}{12}02 10000 01012 --000 11-00 0-0?? ?1-0- 10010 --11- 003-1 100-0 00000 111?? ????? ??00 01000 23100 111?1 2011- 31-00 10111 00001 01-10 1010? ????0 2{01}001 00011 0100?

*Choeronycteris*
10201 00000 01202 10000 01012 --000 11-00 0-0?? ?1-0- 10010 --11- 003-1 100-0 00000 11100 001?? ??00 01000 23100 111?1 2011- 31-00 10111 00001 01-10 101?? ????? 20001 00011 0100?

*Glossophaga*
10201 00000 00402 10000 01022 --000 11-00 0-001 0000- 00010 --000 003-0 10000 00000 11010 00101 11100 01000 23101 11001 21100 30000 10111 00001 01-11 12100 21101 20000 00010 0000?

*Hylonycteris*
10202 00000 01402 10000 01012 --000 11-00 0-0?? ?1-0- 00010 --11- 003-0 10000 00000 111?? ????? ??00 01000 23100 111?1 20100 31-00 10111 00011 01-10 101?? ????? 2???1 ??11 ?1?0?

*Leptonycteris*
10221 00001 014021 00000 1022- -0001 1-000 -0010 000-0 0010- -0000 03-01 01-01 00001 10000 01??? ??000 10202 31011 11?12 21003 00001 01110 00010 1-111 21?? 21101 20000 00010 10000

*Lichonycteris*
10202 00000 01402 10000 01012 --000 11-00 0-0?? ?1-0- 00010 --11- 003-1 101-0 10000 111?? ????? ??00 01000 23100 110?1 21100 31-00 10111 00011 01-10 1010? ????? 20??? ????? ?????

*Lionycteris*
00220 00000 01602 10000 11022 --000 10000 0-0?? ?100- 00000 --000 003-0 10000 00000 110?? ????? ??00 01000 23100 110?0 10000 10000 11100 02010 01-02 020?? ????1 ?0000 00010 1010?

*Lonchophylla*
10201 00000 0{02}602 10000 11022 --000 10000 0-0?? ?1-0- 00000 --000 003-0 10000 00000 110?? ????1 ??00 01000 23100 110?0 10000 10000 11100 01010 01-02 020?? 21101 20000 00010 10100

*Monophyllus*
10200 00000 00402 10000 01022 --000 11-00 0-0?? ?000- 00010 --000 003-0 20000 00000 100?? ????? ??00 01000 23101 110?1 21100 30000 10111 00001 01-11 121?? 21101 20000 00010 1000?

*Musonycteris*
????1 00000 00202 ??000 01012 --000 11-?0
0-0?? ?1-0- 10010 --11- 003-1 100-0 00000
111?? ????? ??00 01?0? ????? ????? ?????
????? ????? ????? ????? ????? ????? ??001
00011 0100?

*Platalina*
10201 00000 00602 10000 00-22 --000 10000
0-0?? ?1-0- 00000 --000 003-1 100-0 00000
111?? ????? ??00 01000 23100 110?0 10000
10000 11100 02000 01-02 020?? ????? ?????
????? ?????

*Scleronycteris*
????1 00000 01?02 ??000 ????2 --000 11-?0
0-0?? ?1-0- 00010 --11- 003-1 100-0 00000
111?? ????? ??00 01?0? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ?????
?????

*Erophylla*
00201 00000 01402 11010 00-02 --000 11-00
0-0?? ?000- 00000 --000 000-1 100-0 00211
110?? ???01 11151 21001 11000 00-?0 0111-
10000 10112 00000 01-02 001?? ????? 10???
????? ?????

*Phyllonycteris*
002{01}1 00000 02402 11010 00-02 --000
11-00 0-0?? ?100- 00000 --000 000-1 100-0
00211 110?? ????? ??51 02001 12000 00-10
0111- 10000 10112 00000 01-02 011?? 2110?
10000 00010 0001?

*Chrotopterus*
10231 00000 12002 0-000 21100 1-000 00001
0-0?? ?000- 00000 --012 00120 01010 00000
000?0 0???? ??40 1030? ????? ????? ?????
?0000 000-- 00010 01-00 00?0? ????? ?0010
01000 10010

*Glyphonycteris*
????2 00000 02402 10000 10-02 --000 00000
0-0?? ?000- 00000 --000 003-0 00010 00000
000?? ????? ??40 0100? ????? ????? ?????
?0000 100-- 02010 01-00 00??? ????? ?????
????? ?????

*Lampronycteris*
????0 00000 12402 10000 10-01 -0000 00000
0-0?? ?000- 00000 --000 002-0 00010 00000
000?? ????? ??10 0000? ????? ????? ?????
?0000 100-- 00010 01-00 00??? ????1 ?????
????? ?????

*Lonchorhina*
11221 00000 {01}{02}{45}12 10000 21100
0-000 00000 0-0?? ?010- 00000 --000 00110
00010 00000 000?0 0???1 ??00 0011? ?????
????? ????? ?0000 100-- 00010 001-- --???
????? 00000 00000 10010

*Macrophyllum*
10221 00001 00112 10000 21000 0-001 -0100
0-0?? ?000- 00000 --000 00110 00010 00000
000?0 0???1 ??50 0001? ????? ????? ?????

?0000 100-- 00010 001-- --??1 ????1 0?000
00010 0001?

*Macrotus*
10201 00000 12402 10000 01001 -0000 00001
11001 1000- 00000 --000 003-0 00010 00000
10000 01?11 00140 21012 01011 00-?0 00000
20000 100-- 00010 01-00 000?1 1000? 00000
00000 00010

*Micronycteris hirsuta*
11201 00000 12402 10000 12001 -2000 00001
100?? ?000- 00000 --000 002-0 00010 00000
100?0 0???1 ??41 2020? ????? ????? ?????
?0000 100-- 00010 01-00 00?0? 1000? 10???
????? ?????

*Micronycteris megalotis*
11201 00000 12402 10000 10-01 -1000 00001
100?? ?000- 00000 --000 003-0 00010 00000
100?0 0???1 ??41 2000? ????? ????? ?????
?0000 100-- 00010 01-00 00?01 10001 10???
????? ?????

*Micronycteris minuta*
????1 00000 12402 10000 10-01 -1000 00001
110?? ?010- 00000 --000 002-0 00010 00000
100?? ????? ??41 1100? ????? ????? ?????
?0000 100-- 00010 01-10 00??? ????1 10000
00000 1001?

*Mimon bennettii*
10201 00000 00012 10000 20-01 -0000 00000
0-0?? ?000- 00000 --010 000-0 00010 00000
000?0 0???? ??40 1000? ????? ????? ?????
?0000 100-- 00010 01-00 00??? ????? ?0???
????? ?????

*Mimon crenulatum*
10201 01001 00012 10000 20-00 0-001 -0000
0-0?? ?000- 00000 --010 000-0 00010 00000
000?0 0???? ??50 0000? ????? ????? ?????
?0000 100-- 00010 01-10 00??? ????1 00010
00000 1001?

*Phylloderma*
00211 00000 02402 10000 20-02 --001 -0000
0-0?? ?000- 00000 --000 002-0 00010 00000
000?? ????? ??40 0120? ????? ????? ?????
?0000 100-- 00010 01-00 00??? 21001 20???
????? ?????

*Phyllostomus*
0021{01} 00000 02{01}12 10000 20-00 0-001
-0000 0-0?? ?000- 00000 --000 000-000010
00000 00000 11210 00000 00202 01011 00-10
00000 20000 000-- 00010 01-00 00000 21001
{02}0000 00000 10010

*Tonatia*
11201 00000 {01}2{04}02 0-000 210{02}2
--001 -0001 0-0?? ?0{01}0- 00000 --010 002-0
00010 00000 000?0 0???1 ??41 {12}030?
????? ????? ????? ?0000 100-- 00010 01-00
00?01 ????1 00000 00000 10010

*Trachops*
10201 00000 02102 0-000 21002 --001 -0001

0-0?? ?000- 00000 --000 00110 01010 00000
000?0 0???1 ???40 1100? ????? ????? ?????
?0000 100-- 00010 01-00 00??0 10001 00000
01000 10010

*Trinycteris*
????2 02000 02402 10000 10-02 --000 00000
0-0?? ?000- 00000 --000 002-0 00010 00000
100?0 0???1 ???00 01002 01001 00-?0 00000
20000 100-- 00010 01-00 00001 ????? 10???
????? ?????

*Vampyrum*
10201 00000 12002 0-000 21100 1-000 00001
0-0?? ?000- 00000 --002 002-0 01010 00000
100?? ????? ???40 1032? ????? ????? ?????
?0000 000-- 00010 000-- --??? ????1 00000
00000 0001?

*Ametrida*
11202 00111 02011 20000 20-00 0-001 -0120
0-0?? ?00-- 01003 1-001 000-1 000-0 00200
000?? ????? ???00 0122? ????? ????? ?????
?0002 200-- 1-000 01-10 10??? 2221? 11000
10010 0000?

*Ardops*
00212 00101 02012 20000 20-01 -3001 -0120
0-0?? ?0030 00003 00001 010-1 000-0 00210
000?? ????? ???50 0122? ????? ????? ?????
?0002 200-- 1-000 01-10 10??? ????1 ?1000
10010 00000

*Ariteus*
11222 00101 02012 20000 20-01 -3001 -0120
0-0?? ?0030 00003 00001 010-1 001-0 00210
000?? ????? ???50 0122? ????? ????? ?????
?0002 200-- 1-000 01-10 10??? 2221? ?1000
10110 00000

*Artibeus* (*Artibeus*)
10221 1000{01} 02412 10000 20-00 0-001
-0110 0-001 0000- 00002 --001 010-1 00{01}-0
00200 000?1 0??00 00150 01222 01000 00-10
00001 20002 100-- 1-100 01-00 000{01}1
22211 {12}1010 00010 00001

*Artibeus* (*Dermanura*)
10221 1000{01} 02{024}12 10{02}00 20-00
0-001 -0110 0-0?? ?000- 00002 --001 010-1
001-0 {01}0{12}00 000?? ????? ???50 0122?
????? ????? ????? ?0002 100-- 1-100 01-00
00?{01}? ????1 {12}{01}000 00010 00001

*Artibeus* (*Koopmania*)
????2 00000 02312 10000 20-00 0-001 -0110
0-0?? ?000- 00002 --001 000-1 000-0 00200
000?? ????? ???50 0122? ????? ????? ?????
?0002 100-- 1-100 01-00 00??? ????1 ?1???
????? ????1

*Centurio*
11202 00111 12011 3---- ----- --0-2 -0-20 0-1??
?0021 00003 00001 000-1 001-0 10200 00010
011?? ???00 2122? ????? ????? ????? ?011- 200--
1-000 01-10 10?1? 2221? 10000 10010 00000

*Chiroderma*

10222 1{01}000 02{01}12 10{02}00 20-00
0-001 -0110 0-0?? ?000- 00000 --00{01} 000-1
10{01}-0 {01}0211 110?1 0???0 ???50
{01}122? ????? ????? ????? ?0002 100-- 1-100
01-00 00?1? ????1 20010 00010 00000

*Ectophylla alba*
10201 -0--0 02012 10100 20-00 0-001 -0110
0-0?? ?000- 00000 --000 000-1 101-0 10211
111?? ????? ???50 1122? ????? ????? ?????
?0002 000-- 1-000 01-00 00??? 2221? ?0???
????? ?????

*Ectophylla macconellii*
10222 00000 02012 10100 20-00 0-011 -0110
0-0?? ?000- 00000 --000 000-1 101-0 00211
111?? ????? ???50 1122? ????? ????? ?????
?0000 000-- 1-100 01-00 00??? ????1 10000
00010 00000

*Enchisthenes*
10221 10001 02412 10000 20-02 --001 -0110
0-0?? ?000- 00000 --001 000-1 000-0 00200
000?? ????? ???60 0122? ????? ????? ?????
?0002 100-- 1-100 01-00 00??? 22211 21000
00010 00000

*Phyllops*
11222 00111 02012 20000 20-01 -0001 -0120
0-0?? ?0031 00003 00001 010-1 000-0 00200
000?? ????? ???40 21222 01000 00-?0 00001
20002 200-- 1-000 01-10 100?? ????? ?1???
????? ?????

*Platyrrhinus*
10221 11001 02{01}12 10{02}00 20-00 0-001
-0110 0-0?? ?000- 00000 --001 010-1100-0
00{12}10 100?? ????? ???50 {01}1222 01001
00-?0 00001 20001 000-- 1-000 01-10 000{01}?
22211 {12}0100 00010 00000

*Pygoderma*
10202 00111 01012 10000 20-01 -0001 -0120
0-0?? ?001- 00003 01001 010-1 001-0 10200
000?? ????? ???40 0122? ????? ????? ?????
?0002 200-- 1-000 01-10 10??? ????? ?1000
10110 00000

*Sphaeronycteris*
10202 00111 02011 3-000 10-02 --022 -0-20
0-1?? ?0021 01003 1-001 000-1 000-0 00200
000?? ????? ???50 0122? ????? ????? ?????
?0102 200-- 1-000 01-10 10??? ????1 ?0???
????? ?????

*Stenoderma*
10222 00111 02012 20000 20-00 0-001 -0120
0-0?? ?0030 00003 01001 000-1 000-0 00210
000?? ????? ???50 0122? ????? ????? ?????
?0002 200-- 1-000 01-10 10??? ????? 11000
10110 00000

*Sturnira*
00202 00001 0{012}{04}12 10000 10-02 --001
-0110 0-001 0000- 00000 --0{01}0 000-1 100-0
{01}0{02}{01}{01} 000?0 0??10 00140 02020

00?00 ??-10 ?001- 20001 100-- 00010 01-00
00?00 22211 {12}0010 00010 00010
*Uroderma*
10221 11000 02012 10200 20-00 0-001 -0110
0-0?? ?000- 00002 --001 020-1 000-0 00210
100?0 0???? ???50 01222 01000 00-?0 00001
20001 100-- 1-100 01-10 1001? 22211 20100
00010 00000
*Vampyressa bidens*
10222 11000 02012 10200 20-00 0-001 -0110
0-0?? ?000- 00002 --010 000-1 101-0 00211
111?? ????? ???50 0122? ????? ????? ?????
?0001 100-- 1-100 01-00 00??? ????? ?????
????? ?????
*Vampyressa nymphaea*
????2 11000 02012 10200 20-00 0-001 -0110

0-0?? ?000- 00002 --000 000-1 101-0 10211
111?? ????? ???50 0122? ????? ????? ?????
?0001 100-- 1-100 01-00 00?1? ????? 20000
00010 00000
*Vampyressa pusilla*
11222 10000 02012 10200 20-00 0-011 -0110
0-0?? ?000- 00002 --000 000-1 101-0 10211
111?? ????? ???40 11222 01001 00-?0 00001
20000 100-- 1-100 01-00 0001? 22211 10???
????? ?????
*Vampyrodes*
11221 11001 02412 10200 20-00 0-001 -0110
0-0?? ?000- 00000 --001 020-1 101-0 00100
000?? ????? ???50 0122? ????? ????? ?????
?0001 000-- 1-100 01-10 00?1? 22211 10100
00010 00000

## APPENDIX 3: DISCRETE-STATE CHARACTERS NOT INCLUDED IN THIS STUDY

In the course of this study we reviewed numerous characters that do not appear in any form in our data set. These characters have not been used for a variety of reasons, which are noted below. Previously described characters that we omitted include the following:

(1) Characters described by previous authors as autapomorphies (or which would appear as autapomorphies in our analysis due to the level of taxonomic sampling): Gimenez (1993): character 3.3.3.7.; Marques-Aguiar (1994): character 11; Owen (1991): character 1; Van Den Bussche (1991, 1992): characters 29, 31, 34, 35, 39, 42, 44, 48, 55, 56; Simmons (1996): characters 3, 15, 20.

(2) Characters in which the derived condition occurs in all members of the ingroup or all taxa in our analysis: Straney (1980): character E1, K27; Hood and Smith (1982): characters 2, 4.

(3) Characters in which the derived condition only occurs in outgroup taxa: Van Den Bussche (1991, 1992): characters 40, 41, 45.

(4) Characters defined by previous authors that vary continuously within Phyllostomidae, or based on descriptions that suggest continuous variation: Straney (1980): characters D3 ⁻5 (see McDaniel, 1976), D6–12, H6, H7–8, H15, H16, J1, J2, J7, J8, K1, K2, K14–16, K18, K30; Owen (1987): characters 5, 7, 15, 19, 20, 22; Gimenez (1993): characters 3.3.2.4, 3.3.2.6, 3.3.3.1,

3.3.3.4, 3.3.3.6, 3.3.4.3, 3.3.4.4, 3.3.4.6, 3.3.4.12, 3.3.5.2, 3.3.5.4, 3.3.5.5, 3.3.5.7, 3.3.5.15; Lim (1993): character 8; Marques-Aguiar (1994): characters 8, 12, 14, 15, 19, 20, 25, 29, 30, 31; Gimenez et al. (1996): characters 1, 5, 7–9.

(5) Discrete-state characters appropriate at lower taxonomic levels than those investigated here (variable within most genera): Straney (1980): characters K4, K5, K17; Owen (1987): characters 12, 13, 16, 17; Marques-Aguiar (1994): characters 1, 2, 3, 5, 6, 13, 16–18, 22, 23, 27, 28. Simmons (1996): characters 2, 12, 13, 16, 17, 19, 21, 22.

(6) Characters that are variable within species: Straney (1980): characters E15–16 (see Griffiths, 1982: 26–27), E23 (see Griffiths, 1982: 26–27), H4, H5, J4, J5; Owen (1987): characters 8, 11, 18.

(7) Characters for which our observations differed from those of previous authors, and we were unable to observe or confirm the conditions reported by others: Straney (1980): characters, G4, G5, G21–23, H1, H2, H9, H11–14, J3, K28, K29; Gimenez (1993): characters 3.3.3.2, 3.3.4.1, 3.3.4.5, 3.3.4.13, 3.3.5.6, 3.3.5.10.

(8) Characters which we were unable to survey due to limited specimen availability: Straney (1980): characters K7, K9.

(9) Characters for which the variation reported may be due to sampling juveniles: Straney (1980): characters E2–8, H3.

## APPENDIX 4: TAXONOMIC DIAGNOSES

The following diagnoses apply to monophyletic groups described in the text and numbered in figure 66 and the genera *Lampronycteris*, *Glyphonycteris*, *Macrotus*, *Micronycteris*, *Phylloderma*, *Phyllostomus*, and *Trinycteris* and the two subgenera of *Mimon*. Both ACCTRAN and DELTRAN optimizations are given for each node (see Materials and Methods for a description of optimization procedures). Diagnoses are formatted as follows: (character number; consistency index)

character description, state number → state number. For example, ''(30; 0.333) chin morphology, 0 → 3'' indicates a change from state 0 to 3 for character 30. Unequivocal transformations (those occurring in all reconstructions) are indicated by a double arrow ''⇒,'' equivocal transformations (occurring in only some reconstructions) by a single arrow ''→.'' Please refer to individual character descriptions for character state information.

**Phyllostomidae:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 0 → 1; (15; 1.000) Number of lateral vibrissae, 0 ⇒ 2; (16; 0.500) Vibrissal papillae structure, 0 ⇒ 1; (30; 0.333) Chin morphology, 3 → 0; (40; 0.333) Vomeronasal cartilage shape, 0 → 1; (59; 1.000) p3 displacement, 0 → 1; (60; 0.167) W-shaped ectoloph presence on M1–M2, 0 ⇒ 1; (61; 0.333) M1 hypocone presence, 0 ⇒ 1; (78; 0.500) Caput mediale of m. triceps brachii insertion, 0 ⇒ 1; (80; 0.250) M. palmaris longus insertion on digit III, 0 → 1; (82; 0.333) M. palmaris longus insertion on digit V, 0 → 1; (83; 0.500) M. flexor digitorum profundus insertion on digit IV, 0 → 1; (84; 0.278) Longest metacarpal, 0 → 1; (87; 0.200) Calcar length, 0 ⇒ 1; (89; 0.333) Tail length, 0 → 2; (91; 0.667) M. sternohyoideus medial fibers origin, 0 ⇒ 1; (92; 0.600) M. sternohyoideus lateral fibers origin, 0 ⇒ 2; (122; 0.250) Horny papillae size, 0 → 1; (135; 0.400) Accessory olfactory bulb presence, 0 ⇒ 1; (136; 0.533) Inferior colliculi coverage, 1 → 2; (149; 0.250) Restriction site 54, 0 ⇒ 1. DELTRAN: (5; 0.214) Dorsal fur banding pattern, 0 → 1; (15; 1.000) Number of lateral vibrissae, 0 ⇒ 2; (16; 0.500) Vibrissal papillae structure, 0 ⇒ 1; (40; 0.333) Vomeronasal cartilage shape, 0 → 1; (60; 0.167) W-shaped ectoloph presence on M1–M2, 0 ⇒ 1; (61; 0.333) M1 hypocone presence, 0 ⇒ 1; (78; 0.500) Caput mediale of m. triceps brachii insertion, 0 ⇒ 1; (80; 0.250) M. palmaris longus insertion on digit III, 0 → 1; (83; 0.500) M. flexor digitorum profundus insertion on digit IV, 0 → 1; (87; 0.200) Calcar length, 0 ⇒ 1; (91; 0.667) M. sternohyoideus medial fibers origin, 0 ⇒ 1; (92; 0.600) M. sternohyoideus lateral fibers origin, 0 ⇒ 2; (135; 0.400) Accessory olfactory bulb presence, 0 ⇒ 1; (149; 0.250) Restriction site 54, 0 ⇒ 1.

**Desmodontinae:** ACCTRAN: (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (20; 0.500) Truncated spear, 0 → 1; (28; 0.500) Dorsal skin ridge on snout, 0 ⇒ 1; (50; 0.500) I1 occlusal margin shape, 0 ⇒ 1; (55; 0.800) Incisor occlusion, 0 ⇒ 3; (56; 0.500) P3 presence, 0 → 1; (63; 0.273) M3 presence, 0 ⇒ 1; (66; 0.400) m3 presence, 0 ⇒ 1; (67; 1.000) m1 shearing ridge, 0 ⇒ 1; (75; 0.250) Number of m. occiptopollicalus muscle bellies, 0 → 1; (94; 0.333) M. ceratohyoideus insertion on ceratohyoid, 0 → 1; (95; 0.167) M. cer-

atohyoideus insertion on stylohyoid, 0 → 1; (107; 0.500) Medial circumvallate papillae presence, 0 ⇒ 1; (109; 0.250) Lateral circumvallate papillae presence, 0 → 1; (121; 1.000) Horny papillae arrangement, 0 ⇒ 1; (130; 0.250) Male accessory morphology, 0 → 1. DELTRAN: (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (20; 0.500) Truncated spear, 0 → 1; (28; 0.500) Dorsal skin ridge on snout, 0 ⇒ 1; (50; 0.500) I1 occlusal margin shape, 0 ⇒ 1; (55; 0.800) Incisor occlusion, 0 ⇒ 3; (56; 0.500) P3 presence, 0 → 1; (63; 0.273) M3 presence, 0 ⇒ 1; (66; 0.400) m3 presence, 0 ⇒ 1; (67; 1.000) m1 shearing ridge, 0 ⇒ 1; (75; 0.250) Number of m. occiptopollicalus muscle bellies, 0 → 1; (84; 0.278) Longest metacarpal, 0 → 1; (89; 0.333) Tail length, 0 → 2; (107; 0.500) Medial circumvallate papillae presence, 0 ⇒ 1; (109; 0.250) Lateral circumvallate papillae presence, 0 → 1; (121; 1.000) Horny papillae arrangement, 0 ⇒ 1.

**Node 1:** ACCTRAN: (2; 0.100) Bulb on hair shaft base, 0 ⇒ 1; (4; 0.400) Hair scale margin shape, 0 ⇒ 1; (11; 0.429) Superciliary vibrissae presence, 0 ⇒ 1; (48; 1.000) I2 presence, 0 ⇒ 1; (65; 1.000) m2 presence, 0 ⇒ 1; (87; 0.200) Calcar length, 1 ⇒ 2; (112; 1.000) Lingual sulcus presence, 0 ⇒ 2. DELTRAN: (2; 0.100) Bulb on hair shaft base, 0 ⇒ 1; (4; 0.400) Hair scale margin shape, 0 ⇒ 1; (11; 0.429) Superciliary vibrissae presence, 0 ⇒ 1; (48; 1.000) I2 presence, 0 ⇒ 1; (65; 1.000) m2 presence, 0 ⇒ 1; (87; 0.200) Calcar length, 1 ⇒ 2; (112; 1.000) Lingual sulcus presence, 0 ⇒ 2; (136; 0.533) Inferior colliculi coverage, 1 → 2.

**Node 2:** ACCTRAN: (3; 1.000) Scale divergence from hair shaft, 0 ⇒ 2; (30; 0.333) Chin morphology, 0 → 1; (84; 0.278) Longest metacarpal, 1 → 5; (99; 0.500) Right and left m. geniohyoideus fusion, 0 → 1; (104; 0.250) M. colli profundus lateral slip presence, 1 ⇒ 0; (106; 1.000) M. cricopharyngeus slip number, 0 ⇒ 1; (119; 0.167) Basketlike papillae presence, 0 → 1; (131; 1.000) External uterine fusion, 0 ⇒ 2; (132; 0.667) Internal uterine fusion, 0 ⇒ 1; (133; 0.667) Attachment of oviduct to uterus, 0 ⇒ 1; (144; 0.333) Restriction site 47, 0 ⇒ 1. DELTRAN: (3; 1.000) Scale divergence from hair shaft, 0 ⇒ 2; (104; 0.250) M. colli profundus lateral slip presence, 1 ⇒ 0; (106; 1.000) M. cricopharyngeus slip number, 0 ⇒ 1; (122; 0.250) Large central horny papillae presence, 0 → 1; (131; 1.000) External uterine fusion, 0 ⇒ 2; (132; 0.667) Internal uterine fusion, 0 ⇒ 1; (133; 0.667) Attachment of oviduct to uterus, 0 ⇒ 1; (136; 0.533) Inferior colliculi coverage, 1 → 2; (144; 0.333) Restriction site 47, 0 ⇒ 1.

**Brachyphyllinae:** ACCTRAN: (12; 0.500) Genal vibrissae number, 2 ⇒ 1; (17; 0.500) Vibrissal
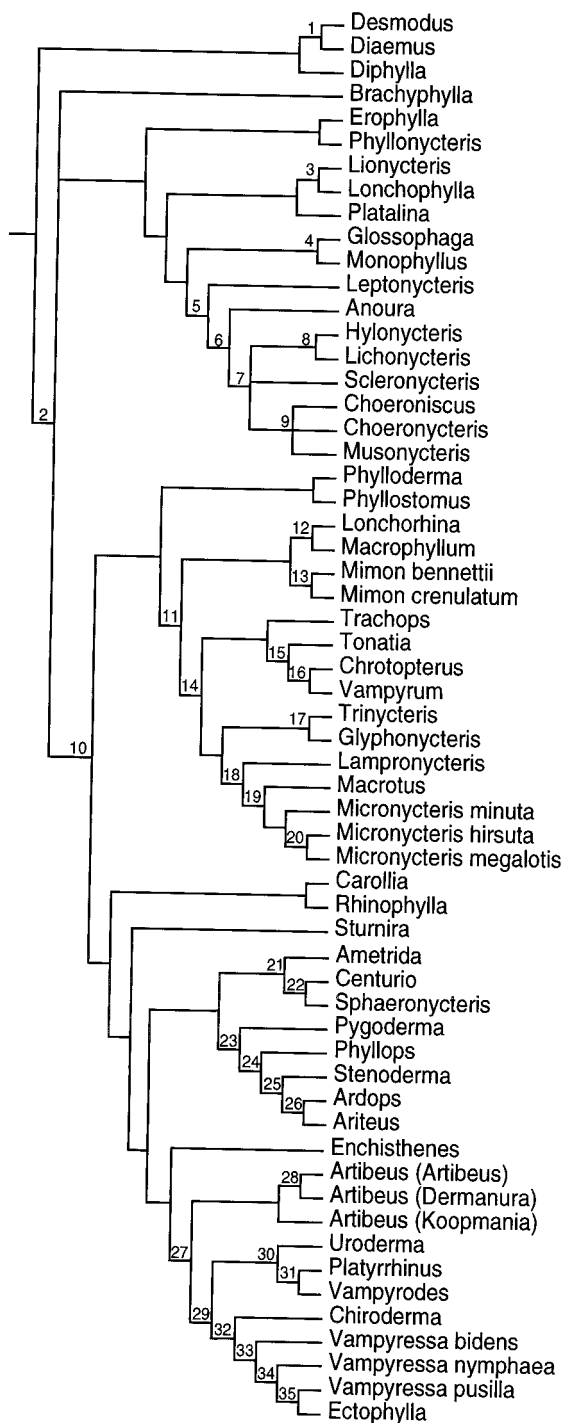
Fig. 66.   Strict consensus tree from our character congruence analysis with nodes numbered for reference to appendix 4, which presents apomorphies of the clades.

papillae in contact across dorsum of snout, 0 ⇒ 1; (20; 0.500) Truncated spear, 0 → 1; (39; 0.750) Vomeronasal tube development, 0 ⇒ 1; (40; 0.333) Vomeronasal cartilage shape, 1 ⇒ 0; (68; 0.714) m1 paraconid presence, 0 ⇒ 2; (87; 0.200) Calcar length, 1 ⇒ 2; (90; 0.500) M. mylohyoideus division, 0 ⇒ 1; (109, 0.250) Lateral circumvallate papillae presence, 0 → 1; (129; 0.800) Brunner's glands presence, 0 ⇒ 1; (135; 0.400) Accessory olfactory bulb presence, 1 ⇒ 0. DELTRAN: (12; 0.500) Genal vibrissae number, 2 ⇒ 1; (17; 0.500) Vibrissal papillae in contact across dorsum of snout, 0 ⇒ 1; (20; 0.500) Truncated spear, 0 → 1; (39; 0.750) Vomeronasal tube development, 0 ⇒ 1; (40; 0.333) Vomeronasal cartilage shape, 1 ⇒ 0; (68; 0.714) m1 paraconid presence, 0 ⇒ 2; (87; 0.200) Calcar length, 1 ⇒ 2; (89; 0.333) Tail length, 0 → 2; (90; 0.500) M. mylohyoideus division, 0 ⇒ 1; (109; 0.250) Lateral circumvallate papillae presence, 0 → 1; (119; 0.167) Basketlike papillae presence, 0 ⇒ 1; (129; 0.800) Brunner's glands presence, 0 ⇒ 1; (135; 0.400) Accessory olfactory bulb presence, 1 ⇒ 0.

**Hirsutaglossa:** ACCTRAN: (30; 0.333) Chin morphology, 1 → 0; (31; 1.000) Chin pad morphology, 0 ⇒ 1; (32; 0.500) Chin cleft presence, 0 → 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (72; 0.250) P4–M1 diastema, 0 ⇒ 1; (77; 0.500) M. spinodeltoideus origin, 1 → 0; (81; 1.000) M. palmaris longus insertion on digit IV, 0 ⇒ 1; (89; 0.333) Tail length, 2 → 0; (103; 0.333) M. sphincter colli profundus anterolateral slip presence, 0 → 1; (113; 1.000) Hairlike papillae presence, 0 ⇒ 1; (119; 0.167) Basketlike papillae presence, 1 → 0; (125.0.667) Anterior horny papillae number, 0 ⇒ 2; (128.0.500) Lingual artery number, 0 → 1. DELTRAN: (31; 1.000) Chin pad morphology, 0 ⇒ 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (72; 0.250) P4–M1 diastema, 0 ⇒ 1; (81; 1.000) M. palmaris longus insertion on digit IV, 0 ⇒ 1; (82; 0.333) M. palmaris longus insertion on digit V, 0 → 1; (113; 1.000) Hairlike papillae presence, 0 ⇒ 1; (125; 0.667) Anterior horny papillae number, 0 ⇒ 2.

**Phyllonycterinae:** ACCTRAN: (17; 0.500) Vibrissal papillae in contact across dorsum of snout, 0 ⇒ 1; (68; 0.714) m1 paraconid presence, 0 ⇒ 2; (69; 0.400) m1 metaconid presence, 0 ⇒ 1; (70; 0.667) m1 entoconid presence, 0 ⇒ 1; (85; 0.333) Digit III second phalanx length relative to first, 0 ⇒ 1; (90; 0.500) M. mylohyoideus division, 0 ⇒ 1; (102; 0.333) M. stylohyoideus presence, 0 ⇒ 1; (104; 0.250) M. sphincter colli profundus lateral slip presence, 0 ⇒ 1; (115; 1.000) Hairlike papillae shape, 0 → 2; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 1. DELTRAN: (17; 0.500) Vibrissal papillae in contact across dorsum of snout, 0 ⇒ 1; (32; 0.500) Chin cleft presence, 0 → 1; (68; 0.714) m1 paraconid presence, 0 ⇒ 2;

(69; 0.400) m1 metaconid presence, 0 ⇒ 1; (70; 0.667) m1 entoconid presence, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 0 → 5; (85; 0.333) Digit III second phalanx length relative to first, 0 ⇒ 1; (90; 0.500) M. mylohyoideus division, 0 ⇒ 1; (102; 0.333) M. stylohyoideus presence, 0 ⇒ 1; (103; 0.333) M. sphincter colli profundus anterolateral slip presence, 0 → 1; (104; 0.250) M. sphincter colli profundus lateral slip presence, 0 ⇒ 1; (115; 1.000) Hairlike papillae shape, 0 → 2; (128; 0.500) Lingual artery number, 0 → 1; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 1.

**Glossophaginae:** ACCTRAN: (1; 0.143) Pelage differentiation, 0 ⇒ 1; (12; 0.500) Genal vibrissae number, 2 ⇒ 0; (19; 0.500) Spear length, 1 ⇒ 0; (22; 0.286) Internarial region morphology, 0 → 1; (24; 1.000) Lateral horseshoe morphology, 0 ⇒ 2; (58; 0.273) p3 presence, 0 ⇒ 3; (60; 0.167) W-shaped ectoloph presence on M1-M2, 1 → 0; (84; 0.278) Longest metacarpal, 5 → 0; (91; 0.667) M. sternohyoideus medial fibers origin, 1 ⇒ 2; (92; 0.600) M. sternohyoideus lateral fibers origin, 2 ⇒ 3; (93; 1.000) M. sternohyoideus insertion, 0 ⇒ 1; (96; 1.000) M. hyoglossus origin, 0 ⇒ 1; (97; 1.000) M. geniohyoideus insertion, 0 ⇒ 1; (99; 0.500) Right and left m. geniohyoideus fusion, 1 → 0; (101; 1.000) M. genioglossus insertion, 0 → 1; (127; 0.667) Flanking horny papillae presence, 0 ⇒ 2; (146; 0.143) Restriction site 50, 0 → 1; (149; 0.250) Restriction site 54, 1 ⇒ 0. DELTRAN: (1; 0.143) Pelage differentiation, 0 ⇒ 1; (12; 0.500) Genal vibrissae number, 2 ⇒ 0; (19; 0.500) Spear length, 1 ⇒ 0; (24; 1.000) Lateral horseshoe morphology, 0 ⇒ 2; (58; 0.273) p3 presence, 0 ⇒ 3; (91; 0.667) M. sternohyoideus medial fibers origin, 1 ⇒ 2; (92; 0.600) M. sternohyoideus lateral fibers origin, 2 ⇒ 3; (93; 1.000) M. sternohyoideus insertion, 0 ⇒ 1; (96; 1.000) M. hyoglossus origin, 0 ⇒ 1; (97; 1.000) M. geniohyoideus insertion, 0 ⇒ 1; (127; 0.667) Flanking horny papillae presence, 0 ⇒ 2; (149; 0.250) Restriction site 54, 1 ⇒ 0.

**Lonchophyllini:** ACCTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 6; (32; 0.500) Chin cleft presence, 1 → 0; (42; 0.400) Zygomatic arch completeness, 0 ⇒ 1; (103; 0.333) M. sphincter colli profundus anterolateral slip presence, 1 → 0; (112; 1.000) Lingual sulcus presence, 0 ⇒ 1; (114; 1.000) Hairlike papillae distribution, 1 ⇒ 0; (117; 0.667) Anteriorly directed patch of medial-posterior papillae presence, 0 ⇒ 2; (128; 0.500) Lingual artery number, 1 → 0; (148; 1.000) Restriction site 53, 0 → 1. DELTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 6; (42; 0.400) Zygomatic arch completeness, 0 ⇒ 1; (101; 1.000) M. genioglossus insertion, 0 → 1; (112; 1.000) Lingual sulcus presence, 0 ⇒ 1; (114; 1.000) Hairlike papillae distribution, 1 ⇒

0; (117; 0.667) Anteriorly directed patch of medial-posterior papillae presence, 0 ⇒ 2.

**Node 3:** ACCTRAN: (21; 0.286) Central rib length, 0 ⇒ 1; (119; 0.167) Basketlike papillae presence, 0 ⇒ 1. DELTRAN: (21; 0.286) Central rib length, 0 ⇒ 1; (22; 0.286) Internarial region morphology, 0 → 1; (60; 0.167) W-shaped ectoloph presence on M1-M2, 1 → 0; (119; 0.167) Basketlike papillae presence, 0 ⇒ 1; (146; 0.143) Restriction site 50, 0 → 1; (148; 1.000) Restriction site 53, 0 → 1.

**Glossophagini:** ACCTRAN: (49; 1.000) Size of I1 verus I2, 0 ⇒ 1; (95; 0.167) M. ceratohyoideus insertion, 0 ⇒ 1; (100; 1.000) M. styloglossus insertion, 0 ⇒ 1; (101; 1.000) M. genioglossus insertion, 1 → 2; (106; 1.000) M. cricopharyngeus slip number, 1 ⇒ 3; (115; 1.000) Hairlike papillae shape, 0 → 1; (120; 1.000) Horny papillae location, 0 ⇒ 1; (124; 0.167) Central horny papillae number, 0 ⇒ 1; (125; 0.667) Anterior horny papillae number, 2 ⇒ 1;(126; 0.250) Posterior horny papillae number, 0 ⇒ 1. DELTRAN: (22; 0.286) Internarial region morphology, 0 → 1; (32; 0.500) Chin cleft presence, 0 → 1; (49; 1.000) Size of I1 verus I2, 0 ⇒ 1; (60; 0.167) W-shaped ectoloph presence on M1-M2, 1 → 0; (77; 0.500) M. spinodeltoideus origin, 1 → 0; (95; 0.167) M. ceratohyoideus insertion, 0 ⇒ 1; (100; 1.000) M. styloglossus insertion, 0 ⇒ 1; (101; 1.000) M. genioglossus insertion, 0 → 2; (103; 0.333) M. sphincter colli profundus anterolateral slip presence, 0 → 1; (106; 1.000) M. cricopharyngeus slip number, 1 ⇒ 3; (115; 1.000) Hairlike papillae shape, 0 → 1; (120; 1.000) Horny papillae location, 0 ⇒ 1; (124; 0.167) Central horny papillae number, 0 ⇒ 1; (125; 0.667) Anterior horny papillae number, 2 ⇒ 1; (126; 0.250) Posterior horny papillae number, 0 ⇒ 1; (128; 0.500) Lingual artery number, 0 → 1.

**Node 4:** ACCTRAN: (74; 0.333) Distal tip of clavicle attachment, 0 → 1; (102; 0.333) M. stylohyoideus presence, 0 ⇒ 1. DELTRAN: (102; 0.333) M. stylohyoideus presence, 0 ⇒ 1.

**Node 5:** ACCTRAN: (4; 0.400) Hair scale margin shape, 0 → 2; (10; 0.364) Uropatagial fringe presence, 0 → 1; (12; 0.500) Genal vibrissae number, 0 ⇒ 1; (98; 0.500) M. geniohyoideus split insertion type, 0 ⇒ 1. DELTRAN: (12; 0.500) Genal vibrissae number, 0 ⇒ 1; (98; 0.500) M. geniohyoideus split insertion type, 0 ⇒ 1.

**Node 6:** ACCTRAN: (53; 1.000) i1 presence, 0 ⇒ 1; (54; 0.286) i2 presence, 0 ⇒ 1; (107; 0.500) Medial circumvallate papillae presence, 0 ⇒ 1; (125; 0.667) Anterior horny papillae number, 1 ⇒ 0; (127; 0.667) Flanking horny papillae presence, 2 ⇒ 0; (146; 0.143) Restriction site 50, 1 → 0. DELTRAN: (53; 1.000) I1 presence, 0 ⇒ 1; (54; 0.286) I2 presence, 0 ⇒ 1; (107; 0.500) Medial

circumvallate papillae presence, 0 ⇒ 1; (125; 0.667) Anterior horny papillae number, 1 ⇒ 0; (127; 0.667) Flanking horny papillae presence, 2 ⇒ 0.

**Node 7:** ACCTRAN: (4; 0.400) Hair scale margin shape, 2 → 0; (10; 0.364) Uropatagial fringe presence, 1 → 0; (24; 1.000) Lateral horseshoe morphology, 2 ⇒ 1; (42; 0.400) Zygomatic arch completeness, 0 ⇒ 1; (60; 0.167) W-shaped ectoloph presence on M1-M2, 0 ⇒ 1; (73; 0.250) M1-M2 diastema, 0 ⇒ 1; (95; 0.167) M. ceratohyoideus insertion on stylohyoid, 1 ⇒ 0; (135; 0.400) Accessory olfactory bulb presence, 1 → 0; (140; 1.000) Restriction site 36, 0 ⇒ 1; (145; 1.000) Restriction site 49, 0 ⇒ 1; (147; 1.000) Restriction site 52, 0 ⇒ 1. DELTRAN: (24; 1.000) Lateral horseshoe morphology, 2 ⇒ 1; (42; 0.400) Zygomatic arch completeness, 0 ⇒ 1; (60; 0.167) W-shaped ectoloph presence on M1-M2, 0 ⇒ 1; (73; 0.250) M1-M2 diastema, 0 ⇒ 1; (95; 0.167) M. ceratohyoideus insertion on stylohyoid, 1 ⇒ 0; (140; 1.000) Restriction site 36, 0 ⇒ 1; (145; 1.000) Restriction site 49, 0 ⇒ 1; (147; 1.000) Restriction site 52, 0 ⇒ 1.

**Node 8:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 2; (119; 0.167) Basketlike papillae presence, 0 ⇒ 1. DELTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 2; (119; 0.167) Basketlike papillae presence, 0 ⇒ 1.

**Node 9:** ACCTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 2; (46; 1.000) Pterygoid laminae inflation, 0 ⇒ 1; (104; 0.250) M. sphincter colli profundus lateral slip presence, 0 ⇒ 1. DELTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 2; (46; 1.000) Pterygoid laminae inflation, 0 ⇒ 1; (104; 0.250) M. sphincter colli profundus lateral slip presence, 0 ⇒ 1.

**Node 10:** ACCTRAN: (1; 0.143) Pelage differentiation, 0 → 1; (14; 0.333) Lateral vibrissal column presence, 0 → 1; (19; 0.500) Spear length, 1 ⇒ 0; (21; 0.286) Central rib length, 0 → 1; (64; 1.000) M3 ectoloph shape, 0 → 1; (78; 0.500) M. triceps brachii caput mediale insertion, 1 → 2; (79; 0.500) M. palmaris longus insertion on digit II, 0 ⇒ 1; (82; 0.333) M. palmaris longus insertion on digit V, 1 → 0; (84; 0.278) Longest metacarpal, 5 ⇒ 4; (91; 0.667) M. sternohyoideus medial fibers origin, 1 ⇒ 0; (92; 0.600) M. sternohyoideus lateral fibers origin, 2 ⇒ 1; (106; 1.000) M. cricopharyngeus slip number, 1 ⇒ 2. DELTRAN: (19; 0.500) Spear length, 1 ⇒ 0; (30; 0.333) Chin morphology, 0 → 1; (79; 0.500) M. palmaris longus insertion on digit II, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 0 ⇒ 4; (91; 0.667) M. sternohyoideus medial fibers origin, 1 ⇒ 0; (92; 0.600) M. sternohyoideus lateral fibers origin, 2 ⇒ 1; (99; 0.500) Right and left m. geniohyoideus fusion, 0 → 1; (106; 1.000) M. cricopharyngeus

slip number, 1 ⇒ 2; (119; 0.167) Basketlike papillae presence, 0 → 1.

**Phyllostominae:** ACCTRAN: (21; 0.286) Central rib length, 1 → 2; (41; 0.667) Nasopalatine duct presence, 0 → 1; (60; 0.167) W-shaped ectoloph presence on M1-M2, 1 ⇒ 0; (61; 0.333) M1 hypocone presence, 1 ⇒ 0; (89; 0.333) Tail length, 2 → 0; (90; 0.500) M. mylohyoideus division, 0 ⇒ 2; (94; 0.333) M. ceratohyoideus insertion on ceratohyoid, 0 → 1; (95; 0.167) M. ceratohyoideus insertion on stylohyoid, 0 → 1; (133; 0.667) Location of oviductal entrance to uterus, 1 ⇒ 0; (144; 0.333) Restriction site 47, 1 ⇒ 0; (146; 0.143) Restriction site 50, 0 ⇒ 1. DELTRAN: (21; 0.286) Central rib length, 0 → 2; (60; 0.167) W-shaped ectoloph presence on M1-M2, 1 ⇒ 0; (61; 0.333) M1 hypocone presence, 1 ⇒ 0; (64; 1.000) M3 ectoloph shape, 0 → 1; (90; 0.500) M. mylohyoideus division, 0 ⇒ 2; (95; 0.167) M. ceratohyoideus insertion on stylohyoid, 0 → 1; (133; 0.667) Location of oviductal entrance to uterus, 1 ⇒ 0; (144; 0.333) Restriction site 47, 1 ⇒ 0; (146; 0.143) Restriction site 50, 0 ⇒ 1.

**Node 11:** ACCTRAN: (130; 0.250) Male accessory gland morphology, 0 ⇒ 1; (131; 1.000) External uterine fusion, 2 → 1; (132; 0.667) Internal uterine fusion, 1 → 0; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 0. DELTRAN: (1; 0.143) Pelage differentiation, 0 → 1; (59; 1.000) p3 displacement, 0 → 1; (130; 0.250) Male accessory gland morphology, 0 ⇒ 1; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 0.

**Lonchorhinini:** ACCTRAN: (12; 0.500) Genal vibrissae number, 2 ⇒ 0; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (84; 0.278) Longest metacarpal, 4 → 5; (87; 0.200) Calcar length, 1 ⇒ 0; (123; 0.500) Size of horny papillae in cluster, 0 → 1. DELTRAN: (12; 0.500) Genal vibrissae number, 2 ⇒ 0; (14; 0.333) Lateral vibrissal column presence, 0 → 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (87; 0.200) Calcar length, 1 ⇒ 0.

**Node 12:** ACCTRAN: (4; 0.400) Hair scale margin shape, 0 ⇒ 2; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (58; 0.273) p3 presence, 0 ⇒ 1; (89; 0.333) Tail length, 0 → 1; (122; 0.250) Large central horny papillae presence, 1 ⇒ 0. DELTRAN: (4; 0.400) Hair scale margin shape, 0 ⇒ 2; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (58; 0.273) p3 presence, 0 ⇒ 1; (89; 0.333) Tail length, 0 ⇒ 1; (122; 0.250) Large central horny papillae presence, 1 ⇒ 0; (123; 0.500) Size of horny papillae in cluster, 0 → 1.

*Mimon:* ACCTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 0; (54; 0.286) i2 presence, 0 ⇒ 1; (139; 0.200) Restriction site 32, 0 → 1. DELTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ 0; (54; 0.286) i2 presence, 0 ⇒ 1.

*Mimon* (*Anthorhina*)**:** ACCTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 1; (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (124; 0.167) Central horny papillae number, 0 ⇒ 1. DELTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 1; (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 4 → 5; (124; 0.167) Central horny papillae number, 0 ⇒ 1; (139; 0.200) Restriction site 32, 0 → 1.

*Mimon* (*Mimon*)**:** ACCTRAN: (25; 0.222) Labial horseshoe morphology, 0 ⇒ 1; (30; 0.333) Chin morphology, 1 ⇒ 0; (84; 0.278) Longest metacarpal, 5 → 4; (86; 0.385), Digit IV second phalanx length relative to first, 0 ⇒ 1. DELTRAN: (25; 0.222) Labial horseshoe morphology, 0 ⇒ 1; (30; 0.333) Chin morphology, 1 ⇒ 0; (86; 0.385), Digit IV second phalanx length relative to first, 0 ⇒ 1.

**Node 14:** ACCTRAN: (14; 0.333) Lateral vibrissal column presence, 1 → 0; (26; 1.000) Morphology of thin free labial edge of horseshoe, 0 → 1; (58; 0.273) p3 presence, 0 ⇒ 2. DELTRAN: (58; 0.273) p3 presence, 0 ⇒ 2; (131; 1.000) External uterine fusion, 2 → 1; (132; 0.667) Internal uterine fusion, 1 → 0.

**Vampyrini:** ACCTRAN: (13; 0.667) Interramal vibrissae number, 4 → 0; (16; 0.500) Vibrissal papillae morphology, 1 ⇒ 0; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (35; 0.500) Pinna morphology, 0 ⇒ 1; (62; 0.500) Metastyle length on M1-M2, 0 → 1; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 1. DELTRAN: (16; 0.500) Vibrissal papillae morphology, 1 ⇒ 0; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (35; 0.500) Pinna morphology, 0 ⇒ 1; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 1.

**Node 15:** ACCTRAN: (11; 0.429) Superciliary vibrissae presence, 0 → 1; (54; 0.286) i2 presence, 0 → 1; (59; 1.000) p3 displacement, 1 → 2; (87; 0.200) Calcar length, 1 ⇒ 0; (88; 0.429) Plagiopatagium attachment location, 0 ⇒ 3. DELTRAN: (87; 0.200) Calcar length, 1 ⇒ 0; (88; 0.429) Plagiopatagium attachment location, 0 ⇒ 3.

**Node 16:** ACCTRAN: (23; 0.500) Sella presence, 0 ⇒ 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (30; 0.333) Chin morphology, 1 ⇒ 0; (55; 0.800) Incisor occlusion, 0 ⇒ 2; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0. DELTRAN: (11; 0.429) Superciliary vibrissae presence, 0 → 1; (13; 0.667) Interramal vibrissae number, 4 → 0; (23; 0.500) Sella presence, 0 ⇒ 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (26; 1.000) Morphology of thin free labial edge of horseshoe, 0 → 1; (30; 0.333) Chin morphology, 1 ⇒ 0; (55; 0.800) Incisor occlusion, 0 ⇒ 2; (62; 0.500) Metastyle length on

M1-M2, 0 → 1; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0.

**Micronycterini:** ACCTRAN: (21; 0.286) Central rib length, 2 ⇒ 1; (30; 0.333) Chin morphology, 1 ⇒ 0; (136; 0.533) Inferior colliculi coverage, 0 → 1. DELTRAN: (21; 0.286) Central rib length, 2 ⇒ 1; (30; 0.333) Chin morphology, 1 ⇒ 0.

**Node 17:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 2; (94; 0.333) M. ceratohyoideus insertion on ceratohyoid, 1 → 0. DELTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 2.

*Glyphonycteris***:** ACCTRAN: (58; 0.273) p3 presence, 2 ⇒ 3; (117; 0.667) Anteriorly directed patch of medial-posterior papillae presence, 0 ⇒ 2. DELTRAN: (58; 0.273) p3 presence, 2 ⇒ 3; (117; 0.667) Anteriorly directed patch of medial-posterior papillae presence, 0 ⇒ 2.

*Trinycteris***:** ACCTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 2; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 4 ⇒ 0. DELTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 2; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 4 ⇒ 0; (136; 0.533) Inferior colliculi coverage, 0 → 1.

**Node 18:** ACCTRAN: (11; 0.429) Superciliary vibrissae presence, 0 ⇒ 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 1. DELTRAN: (11; 0.429) Superciliary vibrissae presence, 0 ⇒ 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 1.

*Lampronycteris***:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 0; (84; 0.278) Longest metacarpal, 4 ⇒ 1; (87; 0.200) Calcar length, 1 ⇒ 0. DELTRAN: (5; 0.214) Dorsal fur banding pattern, 1 ⇒ 0; (84; 0.278) Longest metacarpal, 4 ⇒ 1; (87; 0.200) Calcar length, 1 ⇒ 0.

**Node 19:** ACCTRAN: (35; 0.500) Pinna morphology, 0 ⇒ 1; (36; 1.000) Interauricular band presence, 0 ⇒ 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 2. DELTRAN: (35; 0.500) Pinna morphology, 0 ⇒ 1; (36; 1.000) Interauricular band presence, 0 ⇒ 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 2.

*Macrotus***:** ACCTRAN: (21; 0.286) Central rib length, 1 ⇒ 0; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (58; 0.273) p3 presence, 2 ⇒ 3; (89; 0.333) Tail length, 0 ⇒ 1; (136; 0.533) Inferior colliculi coverage, 1 → 0; (146; 0.143) Restriction site 50, 1 ⇒ 0. DELTRAN: (21; 0.286) Central rib length, 1 ⇒ 0; (22; 0.286) Internarial region morphology, 0 ⇒ 1; (41; 0.667) Nasopalatine duct presence, 0 → 1; (58; 0.273) p3 presence, 2 ⇒ 3; (89; 0.333) Tail length, 0 ⇒ 1; (94; 0.333) M. ceratohyoideus insertion on ceratohyoid, 0 → 1; (146; 0.143) Restriction site 50, 1 ⇒ 0.

*Micronycteris***:** ACCTRAN: (2; 0.100) Bulb on hair shaft base, 0 → 1; (27; 1.000) Thickened labial horseshoe morphology, 0 ⇒ 1; (85; 0.333) Digit III second phalanx length relative to first, 0 ⇒ 1. DELTRAN: (27; 1.000) Thickened labial horseshoe morphology, 0 ⇒ 1; (85; 0.333) Digit III second phalanx length relative to first, 0 ⇒ 1; (136; 0.533) Inferior colliculi coverage, 0 → 1.

**Node 20:** ACCTRAN: (37; 1.000) Notch depth in interauricular band, 1 ⇒ 0; (87; 0.200) Calcar length, 1 ⇒ 0. DELTRAN: (2; 0.100) Bulb on hair shaft base, 0 → 1; (37; 1.000) Notch depth in interauricular band, 1 ⇒ 0; (87; 0.200) Calcar length, 1 ⇒ 0.

**Phyllostomini:** ACCTRAN: (1; 0.143) Pelage differentiation, 1 → 0; (4; 0.400) Hair scale margin shape, 0 ⇒ 1; (76; 0.500) M. occipitopollicalus ventral attachment number, 0 → 1; (80; 0.250) M. palmaris longus insertion on digit III, 1 → 0; (83; 0.500) M. flexor digitorum profundus insertion, 1 → 0; (88; 0.429) Plagiopatagium attachment location, 0 ⇒ 2. DELTRAN: (4; 0.400) Hair scale margin shape, 0 ⇒ 1; (88; 0.429) Plagiopatagium attachment location, 0 ⇒ 2.

*Phylloderma***:** ACCTRAN: (14; 0.333) Lateral vibrissal column presence, 1 → 0; (58; 0.273) p3 presence, 0 ⇒ 2. DELTRAN: (58; 0.273) p3 presence, 0 ⇒ 2.

*Phyllostomus***:** ACCTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ (01); (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (84; 0.278) Longest metacarpal, 4 ⇒ 0; (87; 0.200) Calcar length, 1 ⇒ 0; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0. DELTRAN: (13; 0.667) Interramal vibrissae number, 4 ⇒ (01); (14; 0.333) Lateral vibrissal column presence, 0 → 1; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (76; 0.500) M. occipitopollicalus ventral attachment number, 0 → 1; (78; 0.500) M. triceps brachii caput mediale insertion, 1 → 2; (80; 0.250) M. palmaris longus insertion on digit III, 1 → 0; (83; 0.500) M. flexor digitorum profundus insertion, 1 → 0; (84; 0.278) Longest metacarpal, 4 ⇒ 0; (87; 0.200) Calcar length, 1 ⇒ 0; (94; 0.333) M. ceratohyoideus insertion on ceratohyoid, 0 → 1; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0.

**Nullicauda:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 1 → 2; (33; 0.500) Central papilla presence on chin, 0 ⇒ 1; (134; 1.000) Location of oviductal entrance to uterus, 0 ⇒ 1; (149; 0.250) Restriction site 54, 1 → 0. DELTRAN: (14; 0.333) Lateral vibrissal column presence, 0 → 1; (21; 0.286) Central rib length, 0 → 1; (33; 0.500) Central papilla presence on chin, 0 ⇒ 1; (134; 1.000) Location of oviductal entrance to uterus, 0 ⇒ 1.

**Carolliinae:** ACCTRAN: (42; 0.400) Zygomatic arch completeness, 0 ⇒ 1; (82; 0.333) M.

palmaris longus insertion on digit V, $0 \rightarrow 1$; (86; 0.385) Digit IV second phalanx length relative to first, $0 \Rightarrow 1$; (102; 0.333) M. stylohyoideus presence, $0 \rightarrow 1$. DELTRAN: (1; 0.143) Pelage differentiation, $0 \rightarrow 1$; (42; 0.400) Zygomatic arch completeness, $0 \Rightarrow 1$; (86; 0.385) Digit IV second phalanx length relative to first, $0 \Rightarrow 1$; (149; 0.250) Restriction site 54, $1 \rightarrow 0$.

**Stenodermatinae:** ACCTRAN: (10; 0.364) Uropatagial fringe presence, $0 \Rightarrow 1$; (34; 1.000) Internal labial papillae distribution, $0 \Rightarrow 1$; (68; 0.714) m1 paraconid presence, $0 \rightarrow 2$; (74; 0.333) Distal tip of clavicle attachment, $0 \rightarrow 1$; (78; 0.500) M. triceps brachii caput mediale insertion, $2 \rightarrow 1$; (80; 0.250) M. palmaris longus insertion on digit III, $1 \Rightarrow 0$; (105; 1.000) Passage direction of m. sphincter colli profundus lateral slip, $0 \rightarrow 1$; (110; 0.333) Lateral circumvallate papillae location, $0 \rightarrow 1$; (132; 0.667) Internal uterine fusion, $1 \Rightarrow 2$; (133; 0.667) Location of oviductal entrance to uterus, $1 \Rightarrow 2$. DELTRAN: (10; 0.364) Uropatagial fringe presence, $0 \Rightarrow 1$; (34; 1.000) Internal labial papillae presence, $0 \Rightarrow 1$; (80; 0.250) M. palmaris longus insertion on digit III, $1 \Rightarrow 0$; (89; 0.333) Tail length, $0 \rightarrow 2$; (132; 0.667) Internal uterine fusion, $1 \Rightarrow 2$; (133; 0.667) Location of oviductal entrance to uterus, $1 \Rightarrow 2$.

**Stenodermatini:** ACCTRAN: (21; 0.286) Central rib length, $1 \rightarrow 2$; (55; 0.800) Incisor occlusion, $0 \Rightarrow 1$; (61; 0.333) M1 hypocone presence, $1 \rightarrow 0$; (79; 0.500) M. palmaris longus insertion on digit II, $1 \rightarrow 0$; (88; 0.429) Plagiopatagium attachment location, $0 \Rightarrow 2$; (90; 0.500) M. mylohyoideus division, $0 \Rightarrow 2$; (110; 0.333) Lateral circumvallate papillae location, $1 \rightarrow 2$; (116; 1.000) Medial-posterior mechanical papillae inclination, $0 \Rightarrow 1$; (119; 0.167) Basketlike papillae presence, $1 \Rightarrow 0$; (129; 0.800) Brunner's glands presence, $0 \Rightarrow 1$; (130; 0.250) Male accessory gland morphology, $0 \rightarrow 1$; (137; 0.571) Sex chromosomes, $0 \Rightarrow 1$. DELTRAN: (1; 0.143) Pelage differentiation, $0 \rightarrow 1$; (21; 0.286) Central rib length, $1 \rightarrow 2$; (55; 0.800) Incisor occlusion, $0 \Rightarrow 1$; (61; 0.333) M1 hypocone presence, $1 \Rightarrow 0$; (68; 0.714) m1 paraconid presence, $0 \rightarrow 2$; (88; 0.429) Plagiopatagium attachment location, $0 \Rightarrow 2$; (90; 0.500) M. mylohyoideus division, $0 \Rightarrow 2$; (105; 1.000) $0 \rightarrow 1$; (110; 0.333) Lateral circumvallate papillae location, $0 \rightarrow 2$; (116; 1.000) Medial-posterior mechanical papillae inclination, $0 \Rightarrow 1$; (119; 0.167) Basketlike papillae presence, $1 \Rightarrow 0$; (129; 0.800) Brunner's glands presence, $0 \Rightarrow 1$; (137; 0.571) Sex chromosomes, $0 \Rightarrow 1$; (149; 0.250) Restriction site 54, $1 \rightarrow 0$.

**Stenodermatina:** ACCTRAN: (8; 1.000) White shoulder spot presence, $0 \Rightarrow 1$; (9; 0.500) White neck spot presence, $0 \Rightarrow 1$; (13; 0.667) Interramal vibrissae number, $4 \Rightarrow 0$; (16; 0.500) Vi-

brissal papillae morphology, $1 \rightarrow 2$; (34; 1.000) Internal labial papillae distribution, $1 \Rightarrow 2$; (44; 1.000) Posterior hard palate length, $0 \rightarrow 1$; (50; 0.500) I1 occlusal margin morphology, $0 \Rightarrow 3$; (111; 0.333) Papillae distribution on pharyngeal tongue, $1 \Rightarrow 2$; (124; 0.167) Central horny papillae number, $0 \Rightarrow 1$; (126; 0.250) Posterior horny papillae presence, $0 \Rightarrow 1$; (136; 0.533) Inferior colliculi coverage, $2 \Rightarrow 1$; (141; 1.000) Restriction site 38, $0 \Rightarrow 1$. DELTRAN: (5; 0.214) Dorsal fur banding pattern, $1 \rightarrow 2$; (8; 1.000) White shoulder spot presence, $0 \Rightarrow 1$; (9; 0.500) White neck spot presence, $0 \Rightarrow 1$; (13; 0.667) Interramal vibrissae number, $4 \Rightarrow 0$; (34; 1.000) Internal labial papillae distribution, $1 \Rightarrow 2$; (50; 0.500) I1 occlusal margin morphology, $0 \Rightarrow 3$; (111; 0.333) Papillae distribution on pharyngeal tongue, $1 \Rightarrow 2$; (124; 0.167) Central horny papillae number, $0 \Rightarrow 1$; (126; 0.250) Posterior horny papillae presence, $0 \Rightarrow 1$; (136; 0.533) Inferior colliculi coverage, $2 \Rightarrow 1$; (141; 1.000) Restriction site 38, $0 \Rightarrow 1$.

**Node 21:** ACCTRAN: (2; 0.100) Bulb on hair shaft, $0 \rightarrow 1$; (15; 1.000) Number lateral vibrissae, $2 \Rightarrow 1$; (44; 1.000) Posterior hard palate length, $1 \rightarrow 2$; (47; 0.500) Rostral morphology, $0 \rightarrow 1$; (51; 0.500) Morphology of main cusp of pointed upper incisor, $0 \rightarrow 1$; (84; 0.278) Longest metacarpal, $4 \Rightarrow 0$. DELTRAN: (15; 1.000) Number lateral vibrissae, $2 \Rightarrow 1$; (84; 0.278) Longest metacarpal, $4 \Rightarrow 0$.

**Node 22:** ACCTRAN: (16; 0.500) Vibrissal papillae morphology, $2 \rightarrow 3$; (21; 0.286) Central rib length, $2 \rightarrow 1$; (29; 0.667) Presence of outgrowth posterior to spear, $0 \rightarrow 2$; (30; 0.333) Chin morphology, $1 \Rightarrow 2$; (38; 1.000) Facial hood presence, $0 \Rightarrow 1$; (108; 1.000) Medial circumvallate papillae fusion, $0 \Rightarrow 1$; (137; 0.571) Sex chromosomes, $1 \Rightarrow 0$. DELTRAN: (16; 0.500) Vibrissal papillae morphology, $1 \rightarrow 3$; (30; 0.333) Chin morphology, $1 \Rightarrow 2$; (38; 1.000) Facial hood presence, $0 \Rightarrow 1$; (44; 1.000) Posterior hard palate length, $0 \rightarrow 2$; (108; 1.000) Medial circumvallate papillae fusion, $0 \Rightarrow 1$; (137; 0.571) Sex chromosomes, $1 \Rightarrow 0$.

**Node 23:** ACCTRAN: (25; 0.222) Labial horseshoe morphology, $2 \Rightarrow 1$; (57; 0.400) P4 accessory cusp presence, $0 \Rightarrow 1$; (143; 0.500) Restriction site 46, $0 \Rightarrow 1$. DELTRAN: (25; 0.222) Labial horseshoe morphology, $2 \Rightarrow 1$; (57; 0.400) P4 accessory cusp presence, $0 \Rightarrow 1$; (143; 0.500) Restriction site 46, $0 \Rightarrow 1$.

**Node 24:** ACCTRAN: (4; 0.400) Hair scale margin shape, $0 \Rightarrow 2$; (44; 1.000) Posterior hard palate length, $1 \rightarrow 3$. DELTRAN: (4; 0.400) Hair scale margin shape, $0 \Rightarrow 2$; (16; 0.500) Vibrissal papillae morphology, $1 \rightarrow 2$; (44; 1.000) Posterior hard palate length, $0 \rightarrow 3$.

**Node 25:** ACCTRAN: (27; 1.000) Thickened labial horseshoe morphology, $0 \rightarrow 3$; (45; 1.000)

Emarginate hard palate shape, 1 ⇒ 0; (69; 0.400) m1 metaconid presence, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 4 ⇒ 5. DELTRAN: (45; 1.000) Emarginate hard palate shape, 1 ⇒ 0; (69; 0.400) m1 metaconid presence, 0 ⇒ 1; (84; 0.278) Longest metacarpal, 4 ⇒ 5.

**Node 26:** ACCTRAN: (9; 0.500) White neck spot presence, 1 ⇒ 0. DELTRAN: (9; 0.500) White neck spot presence, 1 ⇒ 0; (27; 1.000) Thickened labial horseshoe morphology, 0 → 3.

**Ectophyllina:** ACCTRAN: (4; 0.400) Hair scale margin shape, 0 ⇒ 2; (5; 0.214) Dorsal fur banding pattern, 2 → 1; (6; 0.333) Facial stripes presence, 0 ⇒ 1; (75; 0.250) Number of m. occiptopollicalus muscle bellies, 0 → 1; (84; 0.278) Longest metacarpal, 4 → 5; (118; 0.333) Long-tipped bifid papillae presence, 0 ⇒ 1. DELTRAN: (4; 0.400) Hair scale margin shape, 0 ⇒ 2; (6; 0.333) Facial stripes presence, 0 ⇒ 1; (118; 0.333) Long-tipped bifid papillae presence, 0 ⇒ 1.

**Node 27:** ACCTRAN: (10; 0.364) Uropatagial fringe presence, 1 ⇒ 0; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (50; 0.500) I1 occlusal margin morphology, 0 → 2. DELTRAN: (10; 0.364) Uropatagial fringe presence,1 ⇒ 0; (25; 0.222) Labial horseshoe morphology, 2 ⇒ 0; (84; 0.278) Longest metacarpal, 4 → 5.

*Artibeus:* ACCTRAN: (150; 1.000) *Eco*RI defined satellite DNA repeat, 0 ⇒ 1. DELTRAN: (50; 0.500) I1 occlusal margin morphology, 0 → 2, (150. 1.000) *Eco*RI defined satellite DNA repeat, 0 ⇒ 1.

**Node 28:** ACCTRAN: (57; 0.400) P4 accessory cusp presence, 0 ⇒ 1; (63; 0.273) M3 presence, 0 → 1. DELTRAN: (57; 0.400) P4 accessory cusp presence, 0 ⇒ 1.

**Node 29:** ACCTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 1; (13; 0.667) Interramal vibrissae number, 4 ⇒ 0; (18; 1.000) Noseleaf color, 0 ⇒ 2; (61; 0.333) M1 hypocone presence, 0 → 1; (69; 0.400) m1 metaconid presence, 0 ⇒ 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (95; 0.167) M. ceratohyoideus insertion on stylohyoid, 0 → 1; (110; 0.333) Lateral circumvallate papillae location, 2 → 1; (137; 0.571) Sex chromosomes, 1 ⇒ 0. DELTRAN: (7; 0.500) Dorsal stripe presence, 0 ⇒ 1; (13; 0.667) Interramal vibrissae number, 4 ⇒ 0; (18; 1.000) Noseleaf color, 0 ⇒ 2; (69; 0.400) m1 metaconid presence, 0 ⇒ 1; (71; 0.125) P3–P4 diastema, 0 ⇒ 1; (137; 0.571) Sex chromosomes, 1 ⇒ 0.

**Node 30:** ACCTRAN: (57; 0.400) P4 accessory cusp presence, 0 ⇒ 2; (75; 0.250) Number of m. occipitopollicalus muscle bellies, 1 → 0;

(124; 0.167) Large central horny papillae number, 0 ⇒ 1; (138; 1.000) Restriction site 28, 0 ⇒ 1. DELTRAN: (57; 0.400) P4 accessory cusp presence, 0 ⇒ 2; (110; 0.333) Lateral circumvallate papillae location, 2 → 1; (124; 0.167) Large central horny papillae number, 0 ⇒ 1; (138; 1.000) Restriction site 28, 0 ⇒ 1.

**Node 31:** ACCTRAN: (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (50; 0.500) I1 occlusal margin morphology, 2 → 0; (68; 0.714) m1 paraconid presence, 2 → 1; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0; (136; 0.533) Inferior colliculi coverage, 2 → 1. DELTRAN: (10; 0.364) Uropatagial fringe presence, 0 ⇒ 1; (61; 0.333) M1 hypocone presence, 0 → 1; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0.

**Node 32:** ACCTRAN: (5; 0.214) Dorsal fur banding pattern, 1 → 2; (55; 0.800) Incisor occlusion, 1 → 0; (63; 0.273) Presence of M3, 0 → 1; (70; 0.667) m1 entoconid presence, 0 ⇒ 1; (72; 0.250) P4–M1 diastema, 0 ⇒ 1. DELTRAN: (5; 0.214) Dorsal fur banding pattern, 1 → 2; (61; 0.333) M1 hypocone presence, 0 → 1; (70; 0.667) m1 entoconid presence, 0 ⇒ 1; (72; 0.250) P4–M1 diastema, 0 ⇒ 1.

**Node 33:** ACCTRAN: (73; 0.250) M1-M2 diastema, 0 ⇒ 1. DELTRAN: (50; 0.500) I1 occlusal margin morphology, 0 → 2; (55; 0.800) Incisor occlusion, 1 → 0; (63; 0.273) M3 presence, 0 → 1; (73, 0.250) M1-M2 diastema, 0 ⇒ 1; (110; 0.333) Lateral circumvallate papillae location, 2 → 1.

**Node 34:** ACCTRAN: (66; 0.400) m3 presence, 0 ⇒ 1. DELTRAN: (66; 0.400) m3 presence, 0 ⇒ 1.

**Node 35:** ACCTRAN: (7; 0.500) Dorsal stripe presence, 1 ⇒ 0; (29; 0.667) Presence of outgrowth posterior to spear, 0 → 1; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 1; (110; 0.333) Lateral circumvallate papillae location, 1 ⇒ 0; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 1. DELTRAN: (7; 0.500) Dorsal stripe presence, 1 ⇒ 0; (86; 0.385) Digit IV second phalanx length relative to first, 0 ⇒ 1; (110; 0.333) Lateral circumvallate papillae location, 1 ⇒ 0; (136; 0.533) Inferior colliculi coverage, 2 ⇒ 1.

*Ectophylla:* ACCTRAN: (6; 0.333) Facial stripes presence, 1 → 0; (18; 1.000) Noseleaf color, 2 → 1; (50; 0.500) I1 occlusal margin morphology, 2 ⇒ 0; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0. DELTRAN: (18; 1.000) Noseleaf color, 2 → 1; (50; 0.500) I1 occlusal margin morphology, 2 ⇒ 0; (111; 0.333) Papillae distribution on pharyngeal tongue, 1 ⇒ 0.