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PHYLOGENETIC RELATIONSHIPS OF MORMOOPID BATS (CHIROPTERA: MORMOOPIDAE) BASED ON MORPHOLOGICAL DATA

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ABSTRACT

Mormoopidae is a small family of Neotropical microchiropteran bats that includes two genera (*Mormoops* and *Pteronotus*) and ten species, two of which are known only from fossils. Mormoopidae is typically classified as a member of Noctilionoidea, a group that minimally includes two other Neotropical families (Phyllostomidae and Noctilionidae) and may also include Mystacinidae, a taxon endemic to New Zealand and Australia. Phylogenetic relationships of extant mormoopid species and one extinct taxon, *Pteronotus pristinus*, were investigated in a series of parsimony analyses of 209 morphological characters including features of the skull, dentition, vomeronasal organ complex and brain, trachea and hyoid apparatus, tongue, face, ears, pelage, patagia, postcranial skeleton, postcranial myology, reproductive tract, and digestive tract. Three extant phyllostomid species, two noctilionids, two mystacinids, and one emballonurid species were included as outgroups to test monophyly of Mormoopidae and to provide a context for determining the sister group of the family. Results of parsimony analyses under a variety of different assumption sets indicate that Mormoopidae is monophyletic, and that *Pteronotus* and *Mormoops* are monophyletic sister taxa. Within the genus *Pteronotus*, several clades were repeatedly recovered: (1) *P. davyi* + *P. gymnonotus* (= subgenus *Pteronotus*); (2) *P. macleayi* + *P. quadridens*; (3) *P. personatus* + *P. macleayi* + *P. quadridens* (= subgenus *Chilonycteris*); (4) *P. parnellii* + *P. pristinus* + *P. personatus* + *P. macleayi* + *P. quadridens*; and (5) *P. parnellii* + *P. pristinus* (= subgenus *Phyllodia*). These results support monophyly of all subgenera of *Pteronotus* previously recognized, and additionally indicate that the subgenera *Pteronotus* and *Chilonycteris* are sister taxa. Comprehensive diagnoses for each species and clade of Mormoopidae are provided based on character optimizations and ancillary morphometric data from the literature.

Results of our parsimony analyses also have implications for understanding higher-level phylogeny of noctilionoid bats. Monophyly of each of the traditionally recognized families (i.e., Noctilionidae, Mystacinidae, Mormoopidae, and Phyllostomidae) was strongly supported. In congruence with recent analyses of mitochondrial gene-sequence data and DNA hybridization experiments, we found strong support for inclusion of Mystacinidae in Noctilionoidea. Using an emballonurid species to root the tree, we found the following interfamilial relationships of noctilionoids: (Noctilionidae (Mystacinidae (Phyllostomidae, Mormoopidae))). Lists of morphological synapomorphies of each of these groups are provided based on character optimizations.

INTRODUCTION

Mormoopidae is a small family of Neotropical microchiropteran bats that currently includes two genera (*Mormoops* and *Pteronotus*) and eight extant species; two additional species are known only from Quaternary fossils (Smith, 1972; Silva-Taboada, 1974, 1979; Koopman, 1993, 1994). Commonly known as mustached, ghost-faced, or naked-backed bats, these taxa are characterized by the presence of flaplike outgrowths below the lower lip and funnel-shaped ears. Mormoopids are small to medium in size (e.g., forearm length 35–66 mm) and are thought to be exclusively insectivorous (Koopman, 1984, 1994). Members of the family presently range from the southwestern United States to southern Brazil, and also occur in the Greater Antilles, Lesser Antilles, Dutch West Indes, and Trinidad and Tobago (Koopman, 1993, 1994). They live in a wide variety of habitats ranging from humid tropical forest to semiarid and arid subtropical forest and scrubland (Handley, 1976; Emmons, 1997; Reid, 1997; Smith, 1972). The most recent revision of Mormoopidae was that of Smith (1972), which has formed the basis for most modern treatments of the family.

The history of classification and nomenclature of mormoopids is complex and often confusing. Smith (1972) provided a comprehensive systematic literature review for the family, which we will not reproduce here. A few critical points from the pre-1970 literature, together with more recent taxonomic changes and phylogenetic inferences, are summarized below.

HISTORICAL BACKGROUND

CLASSIFICATION

The taxonomic history of Mormoopidae began with Leach (1821a, 1821b), who described *Mormoops* and *Aello. Pteronotus* and *Chilonycteris* were subsequently described by Gray (1838, 1839), and *Lobostoma* was named by Gundlach (1840). Gray (1843) named a sixth genus, *Phyllodia,* followed almost 60 years later by Gill's (1901) proposition of *Dermonotus* as a replacement name for *Pteronotus.* Various authors have proposed different synonomies for these taxa over the last 150 years, and misplaced holotypes, overlooked names, and arguments over nomenclatural priority have served to further complicate matters (see review in Smith, 1972). For most of the 20th century, classifications of Mormoopidae were based on that of Miller (1907), who recognized three genera (*Chilonycteris, Pteronotus,* and *Mormoops*), which he placed in the subfamily Chilonycterinae in the family Phyllostomidae. Dalquest and Werner (1954) recommended elevation of the group to family rank as Chilonycteridae, but this suggestion was overlooked or ignored by most authors prior to Smith's (1972) revision. Smith (1972) agreed that this group deserved familial status, but argued that the correct name for this taxon is Mormoopidae. Most subsequent authors have followed this recommendation. A lone dissenter was Hall (1981), who continued to recognize Chilonycterinae as a subfamily of Phyllostomidae based on taxonomic history and his perception that the ''grade of differentiation'' of this group was similar to that of ''some other groups of mammals currently treated as subfamilies.'' These arguments did not convince the rest of the systematic community, and the group has been listed under Mormoopidae in most classifications published since 1972 (e.g., Corbet and Hill, 1980; Koopman, 1984, 1993, 1994; McKenna and Bell, 1997; Simmons, 1998; Simmons and Geisler, 1998).

Smith (1972) recognized two genera, three subgenera, and eight extant species within Mormoopidae. *Mormoops* was shown to include two species, *M. blainvillii* and *M. megalophylla* (Smith, 1972). Smith (1972) divided *Pteronotus* into three subgenera: *Phyllodia* (including only *Pteronotus parnellii*), *Chilonycteris* (including *Pteronotus macleayii, P. fuliginosus,* and *P. personatus*), and *Pteronotus* (including *P. davyi* and *P. suapurensis*). Interestingly, Smith's (1972) classification did not entirely match his phylogenetic tree (fig. 1), which depicted *Pteronotus personatus* as more closely related to *P. davyi* and *P. suapurensis* than to *P. macleayii* and *P. fuliginosus.* However, Smith's (1972) revision was completed in a precladistic context, so this discrepancy was not widely recognized. Subsequent subgeneric classifications (e.g., Corbet and Hill, 1980; Herd, 1983; Koopman, 1994) retained Smith's (1972) subgeneric usage.

Although Smith's (1972) classification of Mormoopidae survived more-or-less intact into the 1990s, several significant nomenclatural changes have occurred since that publication. Silva-Taboada (1976) showed that *Lobostoma quadridens* Gundlach, 1840 is a senior synonym of *Chilonycteris fuliginosus* Gray, 1843, so *Pteronotus quadridens* is now recognized as the correct name for this species. Similarly, Smith (1977) subsequently demonstrated that *Chilonycteris gymnonotus* Wagner, 1843, is a senior synonym of *Dermonotus suapurensis* J. A. Allen, 1904, so *Pteronotus gymnonotus* is now recognized as the correct name for this species (see Carter and Dolan [1978] for discussion of authorship of *gymnonotus*). In addition, two fossil mormoopid species, *Mormoops magna* and *Pteronotus pristinus,* were described from Cuban cave deposits by Silva-Taboada (1974). Partial or complete synonomies for all currently recognized species and subspecies of mormoopids can be found in Smith (1972, 1977), Silva-Taboada (1976, 1979), Herd (1983), Adams (1989), Rodríguez-Durán and Kunz (1992), Koopman (1993), and Rezsutek and Cameron (1993).

PHYLOGENETIC RELATIONSHIPS

The first explicit phylogenetic tree of Mormoopidae was that of Smith (1972; fig. 1). Although Smith later became well known for his applications of cladistic methodology to bat systematics (e.g., Smith, 1976, 1980; Smith and Madkour, 1980; Hood and Smith, 1982, 1983), his tree of mormoopid relationships was developed in a precladistic context using methods of numerical taxonomy (Smith, 1972). This phenetic tree assumed monophyly of the family, a hypothesis that he supported based on morphological com-

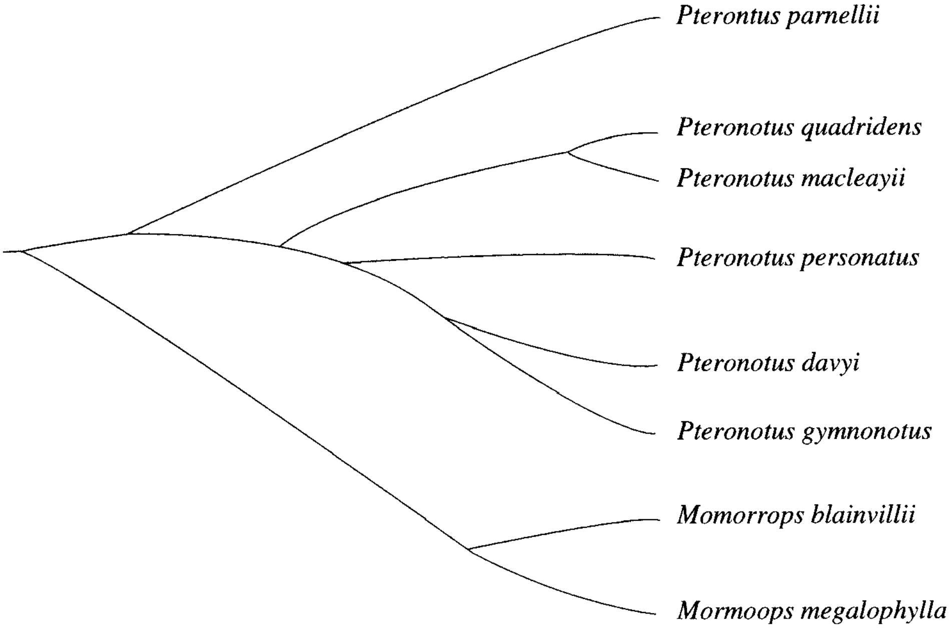

Fig. 1. Smith's (1972) phylogenetic tree of mormoopid species, with the taxonomy changed to reflect modern usage (i.e., *P. quadridens* = *P. fuliginosus*, *P. gymnonotus* = P. *suapurensis*). This tree, which was developed in a pre-cladistic context using methods of numerical taxonomy, was derived from analysis of 22 skull measurements and 20 qualitative multistate characters of the dentition and external morphology. The horizontal and vertical spacing of various branches was intended to depict degrees of similarity and differences among taxa. Redrawn from Smith (1972: fig. 14).

parisons to members of other chiropteran groups. In large part due to the thoroughness of Smith's (1972) study, this tree was very influential in shaping subsequent classifications of mormoopids.

Karyotypic studies including mormoopid species were completed in the late 1970s and early 1980s (e.g., Patton and Baker, 1978; Baker and Bickham, 1980; Sites et al., 1981). All species of *Pteronotus* and *Mormoops* were found to have the same gross karyotype (2N = 38, FN = 60), and banding comparisons indicated that they share a unique fission of chromosome 6/7 that occurs in no other bat family (Patton and Baker, 1978; Baker and Bickham, 1980; Sites et al., 1981). All extant species of *Pteronotus* share an identical, unique G-band karyotype, thus supporting monophyly of the genus (Sites et al., 1981). Monophyly of *Mormoops* was also supported by banding studies, and only a single difference in banding pattern was found between the karyotypes of *Mormoops* and *Pteronotus* (Sites et al., 1981). A sister-group relationship between Mormoopidae and Noctilionidae was proposed based on five inferred Robertsonian fusion events shared by these taxa (fusion of chromosomes 21/14, 17/9, 13/8, 22/3, and 18/2; Patton and Baker, 1978). All of these results were congruent with Smith's (1972) phylogenetic hypothesis.

Limited immunological studies conducted around the same time by Honeycutt (1981) produced divergent results. Analysis of albumin immunological distance data for a set of taxa including *Mormoops megalophylla, Pteronotus parnellii, Noctilio leporinus,* a mixed sample of several phyllostomid species, and a mixed sample of pteropodids (used to root the tree) resulted in a tree in which Mormoopidae was paraphyletic with respect to Phyllostomidae. However, poor sampling within Mormoopidae and inconsistencies in the data led Honeycutt (1981) to exercise caution in interpreting his results, which he regarded as inconclusive.

In one of the first papers to explicitly address the problem of combining disparate data sets in phylogenetic studies, Arnold et al. (1982) reviewed available morphological, immunological, allozyme, and karyotypic data relevant to mormoopid relationships. Phylogenetic trees for each data set were derived by hand by applying parsimony criteria to the discrete data sets (morphology, karyotypes, and allozymes) and distance methods to the immunological data (Arnold et el., 1982). The karyotype tree presented by Arnold et al. (1982: fig. 3) was based on data from Patton and Baker (1978) and Baker and Bickham (1980), which supported monophyly of a Mormoopidae + Noctilionidae clade, Mormoopidae, and *Pteronotus.*[1] The immunological tree was taken from Honeycutt (1981), which indicated paraphyly of Mormoopidae with respect to Phyllostomidae, with Noctilionidae as the sister group to these taxa. The morphology tree, which was based on 16 morphological characters derived from Smith (1972), supported monophyly of Mormoopidae, *Mormoops, Pteronotus,* and a clade consisting of *P. personatus, P. quadridens, P. macleayii,* and *P. davyi* (Arnold et al., 1982: fig. 2). Mormoopidae, Noctilionidae, and Phyllostomidae together formed a monophyletic clade Phyllostomoidea (= Noctilionoidea) in the morphology tree, which was rooted using emballonurids (Arnold et al., 1982: fig. 2). Finally, Arnold et al. (1982) presented a new data set derived from allozyme studies of 16 populations of mormoopids and 4 populations of noctilionids. A cladogram derived from these data supported monophyly of *Mormoops, Pteronotus,* and a clade consisting of *P. personatus, P. quadridens, P. macleayii,* and *P. davyi* (Arnold et al., 1982: fig. 1).

Arnold et al. (1982) concluded their paper by presenting a summary ‘‘composite cladogram’’ that was constructed using principles of taxonomic congruence and majority rule consensus. The incompatible immunological data were discounted for a variety of methodological reasons, and all nodes in the composite cladogram were ultimately found to be supported by between one and three of the four data sets (fig. 2). Within Mormoopidae, the relationships depicted were completely compatible with Smith’s (1972) tree (fig. 1). However, the Arnold et al. (1982) tree did not include all mormoopid species (*Pteronotus gymnonotus* was excluded), and relationships among species of *Pteronotus* were poorly resolved.

No new comprehensive phylogeny of Mormoopidae has been published since 1982. However, several studies have addressed the relationships of mormoopids to other families. Pierson (1986) and Pierson et al. (1986) proposed a phylogeny of bats based on a study of transferrin immunological distance data. They found that Mormoopidae, Noctilionidae, and Mystacinidae formed a clade, with Phyllostomidae as a very close relative to this group. More than a decade later, Kirsch et al. (1998) found very strong support for monophyly of a Mystacinidae + Noctilionidae + Mormoopidae + Phyllostomidae clade in a study of DNA hybridization data. Within this group, monophyly of a clade comprising Mormoopidae + Phyllostomidae was also very strongly supported, although only one mormoopid (*Pteronotus parnellii*) was included in the analysis. Relationships of this clade to Noctilionidae and Mystacinidae remained poorly resolved (Kirsch et al., 1998).

Simmons (1998) and Simmons and Geisler (1998) found support for somewhat different relationships in a series of analyses of higher-level bat relationships based on morphological data. Simmons (1998) and Simmons and Geisler (1998) found strong support for Noctilionoidea as traditionally recognized (Mormoopidae + Phyllostomidae + Noctilionidae). Within this group, weak support was found for a sister-group relationship between Mormoopidae and Noctilionidae in both analyses. In each case, *Mystacina* was tentatively placed as the most basal branch of the sister clade to Noctilionoidea. However, support for this placement was weak, and the authors noted that several other positions for Mystacinidae were only slightly less parsimonious given their data.

DNA sequence data are as yet unavailable for most mormoopids, but two studies have addressed relationships of mormoopids in the context of projects designed to resolve the

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[1] Arnold et al. (1982) completed their study before publication of Sites et al. (1981), so they were not aware of the karyotypic evidence for monophyly of *Mormoops.*

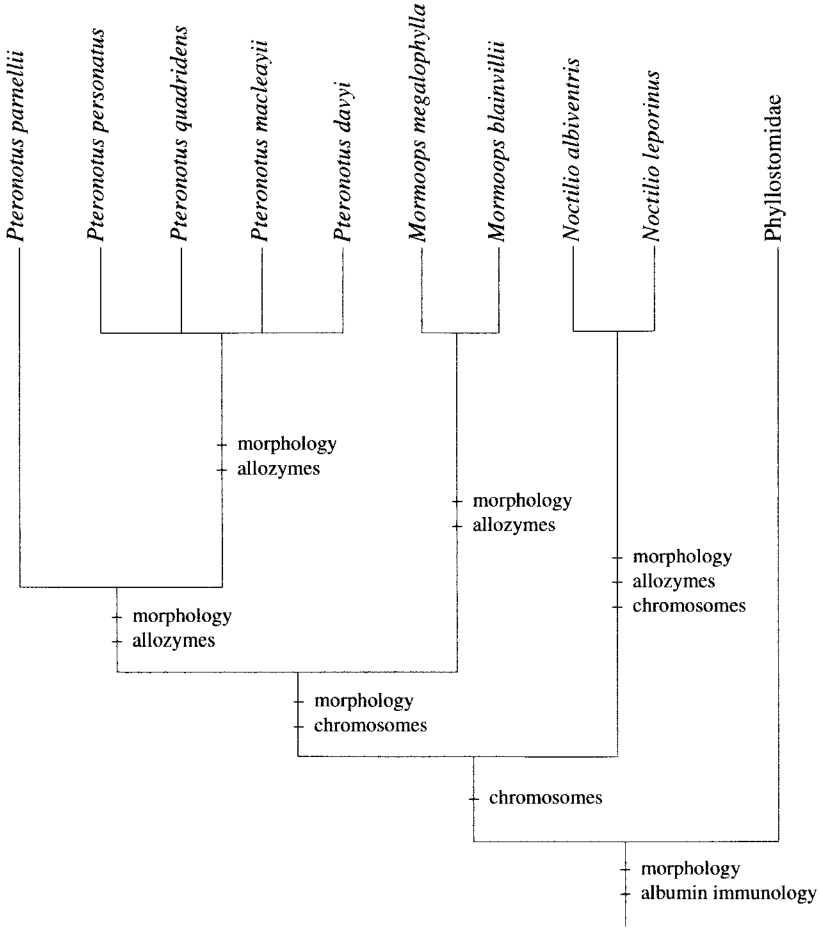

Fig. 2. Arnold et al.'s (1982) "composite cladogram" of relationships among noctilionoid species. This phylogeny was derived from taxonomic-congruence comparisons of trees derived from four data sets: albumin immunology, chromosomes, allozymes, and morphology. Data sets supporting each clade are indicated on the tree. Redrawn from Arnold et al. (1982: fig. 5).

phylogenetic position of *Mystacina* relative to other bat families. Kennedy et al. (1999) used mitochondrial cytochrome-b gene sequences to investigate relationships among 34 species including *Mormoops megalophylla, Pteronotus parnellii,* and *P. davyi.* The most surprising result of this study was the finding that Mormoopidae is not monophyletic; *Noctilio* was placed as the sister group of *Pteronotus* in all analyses, with *Mormoops* falling outside that clade (Kennedy et al., 1999). Support for this arrangement was very high in bootstrap and decay analyses of a weighted data set (codon positions weighted 5:16:1, transversions/transitions 2:1), while support for mormoopid monophyly was essentially nonexistent. Kennedy et al. (1999) additionally found strong support for placement of *Mystacina* within Noctilionoidea, although the exact position of this taxon relative to Phyllostomidae, *Noctilio,* and mormoopids varied under different analysis parameters.

Results of another study of mitochondrial gene sequences produced somewhat different results. Van Den Bussche and Hoofer (2000) analyzed DNA sequence data from three adjacent mitochondrial genes (12S rRNA, t-RNA^{Val}, and 16S rRNA) sampled in 11 noctilionoids and 17 outgroup species. Results of unweighted parsimony analyses supported monophyly of Noctilionoidea including *Mystacina,* and monophyly of each of families within this group. Mormoopidae and Phyllostomidae were found to be sister taxa, echoing the results of Kirsch et al. (1998). Mystacinidae was placed as the sister group to the Mormoopidae + Phyllostomidae clade. Mormoopidae, represented by *Mormoops megalophylla* and *Pteronotus parnellii,* was found to be monophyletic in 71–88% of bootstrap replicates (higher values were obtained using successive approximations weighting).

MORMOOPID SPECIES: A SYNOPSIS

The principal reference on morphology and distribution of mormoopid species is Smith (1972), but this resource is over 25 years old and it lacks any substantive consideration of ecology or the fossil record. To help fill these gaps, we provide below a brief synopsis of each mormoopid species including information on presently recognized subspecies, geographic range, fossil record, habitat preferences, roosting habits, and dietary habits. Literature citations are provided to facilitate access to the primary literature. For identification purposes, readers should consult keys to genera and extant species of mormoopids published in Smith (1972), Hall (1981), Herd (1983), Eisenberg (1989), and Rodríguez-Durán and Kunz (1992). Another helpful resource is Koopman (1994), which includes measurements and some diagnostic features of each extant species. Useful summaries of morphological and ecological data for various species were provided by Bateman and Vaughan (1974), Silva-Taboada (1976, 1979), Herd (1983), Adams (1989), Eisenberg (1989), Rodríguez-Durán and Kunz (1992), Rezsutek and Cameron (1993), Emmons (1997), and Reid (1997). Maps showing the geographic ranges of extant populations can be found in Hall (1981), Koopman (1982), Herd (1983), Adams (1989), Eisenberg (1989), Rodríguez-Durán and Kunz (1992), Rezsutek and Cameron (1993), Lancaster and Kalko (1996), and Reid (1997). Information on Quaternary fossils can be found in Koopman (1951, 1955, 1958, 1989), Ray et al. (1963), Silva Taboada (1974), Wilkins (1983), Steadman et al. (1984), Eshelman and Morgan (1985), Morgan and Woods (1986), and Morgan (1989, 1991). Tertiary mormoopid fossils are as yet unknown (Czaplewski, 1997; McKenna and Bell, 1997).

Mormoops blainvillii **Leach, 1821** (Antillean ghost-faced bat) is a medium-small species (forearm length = 43–50 mm; condylobasal length = 12–14 mm; 6–11 g) presently restricted to the Greater Antillean islands of Cuba, Jamaica, Hispaniola, Puerto Rico, and adjacent small islands (Silva-Taboada, 1979; Koopman, 1993, 1994; Lancaster and Kalko, 1996; Emmons, 1997). No subspecies are currently recognized (Smith, 1972; Hall, 1981; Koopman, 1994). Fossils of *M. blainvillii* have been reported from caves in the Bahamas, Antigua and Barbuda in the northern Lesser Antilles, and La Gonave off the west coast of Hispaniola (Koopman, 1951, 1955, 1989; Steadman et al., 1984; Morgan and Woods, 1986; Morgan, 1989), indicating that the Late Quaternary range of this species was more extensive than it is at present.

Like other mormoopids, *M. blainvillii* roosts in hot, humid caves (i.e., those with temperatures 26–40°C; Goodwin, 1970; Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán, 1995, 1998; Lancaster and Kalko, 1996). Colonies may number over 40,000 individuals (Rodríguez-Durán and Lewis, 1987). Moths are by far the most common item in the diet, which also includes some beetles, flies, homopterans, and hemipterans (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán et al., 1993).

Mormoops megalophylla **Peters, 1864** (Peters' ghost-faced bat; Ghost-faced bat; Leaf-chinned bat) is a medium-large species (forearm length = 49–61 mm; condylobasal length = 12–14 mm; 12–20 g) that is broadly distributed in the Caribbean and Central and South America (Koopman, 1993, 1994; Emmons, 1997; Reid, 1997). Four subspecies are currently recognized (Smith, 1972; Rezsutek and Cameron, 1993; Koopman, 1994): *M. m. megalophylla* (Baja California, southern Arizona, and southern Texas south to Honduras); *M. m. tumidiceps* (northern Colombia, northern Venezuela, Margarita Island

and Trinidad); *M. m. intermedia* (Aruba, Curaçao, and Bonaire islands), and *M. m. carteri* (coastal Ecuador and northwestern Peru). Pleistocene fossils of *M. megalophylla* have been found in Florida, Mexico, Cuba, Hispaniola, Jamaica, the Bahamas (Andros), Aruba, Curaçao, Margarita Island, Trinidad, Tobago, and southeastern Brazil (Koopman, 1958, 1989; Ray et al., 1963; Silva-Taboada, 1974; Wilkins, 1983; Eshelman and Morgan, 1985; Morgan and Woods, 1986; Morgan, 1989, 1991; Arroyo-Cabrales and Alvarez, 1990; Arroyo-Cabrales, 1992; Czaplewski and Cartelle, 1998). The records from Florida, the Bahamas, the Greater Antilles, and eastern Brazil (which do not support extant populations) indicate that the range of *M. megalophylla* was once more extensive than it is today.

Mormoops megalophylla has been captured at sites from sea level to about 3000 m in habitats ranging from lowland rainforest to semiarid and arid scrub forest (Webb and Baker, 1962; Smith, 1972; Bateman and Vaughan, 1974; Albuja, 1982; Graham and Barkley, 1984; Sanchez-Herrera et al., 1986; Bonaccorso et al., 1992; Rezsutek and Cameron; 1993; Reid, 1997). This species varies from uncommon to locally common depending on locality (Reid, 1997), typically appearing to be most abundant in hot lowland areas in the northern parts of its range (Easterla, 1973) and moist forested areas in the tropics (Handley, 1976). Favored roosting sites include caves and abandoned mine shafts, where these bats occur in colonies that may include as many as 500,000 individuals (Barbour and Davis, 1969; Bateman and Vaughan, 1974; Graham and Barkley, 1984; Bonaccorso et al., 1992; Rezsutek and Cameron; 1993). The diet of *M. megalophylla* consists of moths, beetles, and flies; most prey items are relatively large, with body lengths of 5–6 mm (Easterla and Whitaker, 1972; Ceballos and Galindo, 1984).

***Mormoops magna* Silva-Taboada, 1974** is known only from a pair of fossil humeri collected from cave in Cuba (Silva-Taboada, 1974, 1979). These elements resemble those of *M. megalophylla* but are larger than other specimens from the same fossil layer that have been referred to *M. megalophylla* (Silva-Taboada, 1974, 1979).

***Pteronotus parnellii* Gray, 1843** (Parnell's mustached bat; Mustached bat) is a medium-sized species (forearm length = 48–66 mm; condylobasal length = 16–22 mm; 10–28 g) that is broadly distributed from the Greater Antilles and tropical Mexico to northeastern Brazil, although it does not occur west of the Andes in South America (Silva-Taboada, 1979; Koopman, 1993, 1994; Emmons, 1997; Reid, 1997). Nine subspecies are currently recognized (Smith, 1972; Linares and Ojasti, 1974; Herd, 1983; Koopman, 1994): *P. p. parnellii* (= *boothi*; Cuba and Jamaica); *P. p. pusillus* (Hispaniola); *P. p. gonavensis* (Gonave Island off the east coast of Hispaniola); *P. p. portoricensis* (Puerto Rico); *P. p. mexicanus* (Mexico from Sonora and Tamaulipas to Oaxaca and Veracruz); *P. p. mesoamericanus* (western coast of Central America from Chiapas to western Panama; eastern coast of Central America from Veracruz and Yucatan to Honduras); *P. p. rubiginosus* (Honduras to Panama, Trinidad and Tobago, southern Venezuela to Surinam, eastern Peru, and northeastern Brazil); *P. p. fuscus* (northeastern Colombia and northern Venezuela except for the Paraguana peninsula); and *P. p. paraguensis* (Paraguana peninusla of northern Venezuela). *P. parnellii* has recently been found on the island of St. Vincent in the Lesser Antilles, but the subspecific status of this population has not yet been assessed (Vaughan and Hill, 1996). The fossil record of *P. parnellii* within its current range includes late Pleistocene fossils from Puerto Rico and subfossil remains from Mexico, Cuba, Jamaica, and eastern Brazil (Martin, 1972; Silva-Taboada, 1979; Herd, 1983; Koopman, 1989; Morgan, 1989; Czaplewski and Cartelle, 1998). Extinct populations are known from a number of Caribbean islands including Isla de Pinos, New Providence in the Bahamas, La Gonave, Antigua, Grand Cayman, and Tobago (Koopman, 1955, 1989; Silva-Taboada, 1979; Steadman et al., 1984; Eshelman and Morgan, 1985; Morgan and Woods, 1986; Morgan, 1989). These records indicate that the Late Quaternary range of *P. parnellii* was somewhat more extensive than it is today.

Pteronotus parnellii has been captured at sites from sea level to about 3000 m in habitats ranging from lowland rainforest to semiarid and arid scrub forest (Smith, 1972; Bowles et al., 1979; Silva-Taboada, 1979; Herd, 1983; Eisenberg, 1989; Reid, 1997). It is a relatively common bat throughout much of its range and is abundant at some localities, particularly in moist forests (Smith, 1972; Handley, 1976; Silva-Taboada, 1979; Herd, 1983; Reid, 1997). Preferred roosting sites include hot, humid caves and mines (Goodwin, 1970; Bowles et al., 1979; Silva-Taboada, 1979; Vizotto et al., 1980; Herd, 1983; Bonaccorso et al., 1992; Rodríguez-Durán, 1998), but *P. parnellii* also occurs in rainforest regions that have no such refugia (Simmons and Voss, 1998). In these areas, this species may occupy cavelike hollows in large trees.

The diet of *P. parnellii* consists principally of moths, beetles, orthopterans, and flies, with relative proportions of each varying among populations and seasons (Bateman and Vaughan, 1974; Howell and Burch, 1974; Silva-Taboada, 1979; Whitaker and Findley, 1980; Herd, 1983). Other insects occasionally taken include odonatans and hymenopterans (Silva-Taboada, 1979). Seeds were found in the feces of four individuals (Whitaker and Findley, 1980), but it is not known if fruit is intentionally ingested by this species. *P. parnellii* is unique among mormoopids in using long CF (constant frequency) echolocation calls and Doppler compensation (Novick, 1963, 1965, 1977; Novick and Vaisnys, 1964; Schnitzler, 1970a, 1970b, 1987; Fenton, 1980, 1982, 1984, 1994, 1995; Schnitzler and Henson, 1980; Simmons, 1980; Simmons and Stein, 1980; Neuweiler, 1984, 1989, 1990; Neuweiler and Fenton, 1988; Schnitzler and Kalko, 1998; Kalko and Schnitzler, 1998). All prey is apparently captured on the wing and there is no evidence that feeding roosts are ever used (Bateman and Vaughan, 1974; Herd, 1983).

***Pteronotus quadridens* Gundlach, 1840** (Sooty mustached bat) is the smallest species of *Pteronotus* (forearm length = 35–40 mm; condylobasal length = 12–14 mm; 3–6 g; Silva-Taboada, 1979; Koopman, 1994). The geographic range of this species is presently restricted to several islands in the Greater Antilles (Koopman, 1993, 1994). Two subspecies are currently recognized (Smith, 1972; Silva-Taboada, 1979; Rodríguez-Durán and Kunz, 1992; Koopman, 1994): *P. q. quadridens* (Cuba) and *P. q. fuliginosus* (= *inflata*; Jamaica, Hispaniola, and Puerto Rico). The fossil record of *P. quadridens* includes late Pleistocene and Holocene material from several caves in Cuba (Silva-Taboada, 1974, 1979; Woloszyn and Silva-Taboada, 1977) and the Bahamas (Andros and New Providence; Morgan, 1989). The latter populations are now extinct.

Pteronotus quadridens is one of the most abundant bats in Cuba and Puerto Rico, where it roosts principally in hot, humid caves (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán and Kunz, 1992; Rodríguez-Durán, 1995, 1998). Colony size may exceed 140,000 individuals (Rodríguez-Durán and Lewis, 1987).

Pteronotus quadridens feeds on flying insects that are captured primarily in the forest understory (Rodríguez-Durán and Kunz, 1992). Dietary analyses based on stomach contents and fecal samples indicate that a wide variety of prey are taken by these bats, including beetles, moths, flies, orthopterans, homopterans, hymenopterans, dyctiopterans, dermapterans, hemipterans, and heteropterans (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán et al., 1993). Remains from as many as seven different families of insects have been found in samples from a single individual *P. quadridens*, suggesting that these bats may be opportunistic feeders (Silva-Taboada, 1979; Rodríguez-Durán and Kunz, 1992). Small amounts of pollen have also been found in some stomach and fecal samples (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987), but this is thought to be a result of feeding of pollen-covered insects rather than intentional feeding directly on flower products (Rodríguez-Durán and Kunz, 1992).

***Pteronotus macleayi* Gray 1839** (Macleay's mustached bat) is another small-sized species (forearm length = 41–46 mm; condylobasal length = 14–16 mm; 4–8 g) that is presently confined to Cuba and Jamaica (Silva-Taboada, 1979; Koopman, 1993, 1994). Two subspecies are currently recognized (Smith, 1972; Koopman, 1994): *P. m. macleayi* (Cuba) and *P. m. griseus* (Jamaica). Fossils of this species are known from the late Quaternary of the Bahamas (New Providence), which indicates that the range of *P. macleayi* once extended farther north than it does today (Morgan, 1989).

Like other mormoopids, *P. macleayi* usually roosts in hot, humid caves (Goodwin, 1970; Smith, 1972, Silva-Taboada, 1979). Analyses of stomach contents indicate that this species preys only on flying insects, including flies, beetles, orthopterans, and homopterans (Silva-Taboada, 1979). Unlike other mormoopids, *P. macleayi* apparently does not eat moths (Silva-Taboada, 1979).

Pteronotus personatus **Wagner, 1843** (Wagner's mustached bat; Mustached bat) is a medium-sized species (forearm length = 40–49 mm; condylobasal length = 13–16 mm; 5–11 g) that is broadly distributed in mainland Central and South America (Bowles et al., 1979; Koopman, 1993, 1994; Emmons, 1997; Reid, 1997). Two subspecies are currently recognized (Smith, 1972; Brosset and Charles-Dominique, 1990; Koopman, 1994): *P. p. psilotis* (Sonora and Tamaulipas to Honduras) and *P. p. personatus* (Nicaragua south to French Guiana and eastern Peru, from there east to northeastern Brazil). Quaternary fossils of *P. personatus* have been found in Tobago, where this species is now extinct (Eshelman and Morgan, 1985).

Pteronotus personatus has been captured at sites from sea level to about 1000 m in habitats that range from rainforest to dry deciduous forest (Smith, 1972; Handley, 1976; Bowles et al., 1979; Brosset and Charles-Dominique, 1990; Reid, 1997). This species is relatively uncommon to locally common in Central America, and is less common south of Honduras (Reid, 1997). The preferred roosting site is hot, humid caves, where colonies may exceed 15,000 individuals (Dalquest and Hall, 1949; Smith, 1972; Bateman and Vaughan, 1974; Bowles et al., 1979; Vizotto et al., 1980; Bonaccorso et al., 1992).

Pteronotus davyi **Gray, 1838** (Davy's naked-backed bat; Lesser naked-backed bat; Little naked-backed bat; Trinidadian naked-backed bat) is a medium-small species (forearm length = 40–50 mm; condylobasal length = 13–16 mm; 5–11 g) that is broadly distributed in Central and South America and the Lesser Antilles (Jones, 1989; Koopman, 1993, 1994; Emmons, 1997; Reid, 1997). Three subspecies are currently recognized (Smith, 1972; Adams, 1989; Koopman, 1994): *P. d. fulvus* (Sonora and Nuevo Leon to Honduras), *P. d. davyi* (Nicaragua to coastal Venezuela and Trinidad, and north in the Lesser Antilles to Marie Galante [excluding St. Lucia, St. Vincent, Barbados, and the Grenadines]), and *P. d. incae* (northwestern Peru on both sides of the Andes). Although Vieira (1955), Mares et al. (1981), and Willig (1983, 1985) reported *P. davyi* from northeastern Brazil, these identifications were apparently based on the erroneous opinion that *P. davyi* is a senior synonym of *P. gymnonotus*; extant populations of true *P. davyi* remain unknown south of the Amazon River (Smith, 1977; Willig and Mares, 1989; Koopman, 1993; da Fonseca et al., 1996; Czaplewski and Cartelle, 1998). However, Pleistocene fossils of *P. davyi* have been found in Bahia in eastern Brazil (Czaplewski and Cartelle, 1998), suggesting that the range of this species was once much larger. Quaternary fossils of *P. davyi* have been found in Tobago, where this species is now extinct (Eshelman and Morgan, 1985).

Pteronotus davyi has been captured at sites from sea level to about 2300 m in habitats that range from rainforest to dry deciduous forest (Smith, 1972; Koopman, 1978, 1982; Adams, 1989; Reid, 1997). These bats may be locally common in dry and semideciduous lowland forest, but are less common in moist, evergreen forest (Handley, 1976; Reid, 1997). Hot, humid caves are the preferred roosting site, and colonies may include as many as 400,000–800,000 bats (Goodwin and Greenhall, 1961; Villa-R., 1967; Bateman and Vaughan, 1974; Birney et al., 1974; Bonaccorso et al., 1992). The diet of *P. davyi* consists of moths, some flies, and occasionally earwigs (forficulids; Villa-R, 1967; Howell and Burch, 1974; Adams, 1989). Prey is captured on the wing and there is no evidence that feeding roosts are ever used (Bateman and Vaughan, 1974).

Pteronotus gymnonotus **Wagner, 1843** (Big naked-backed bat; Greater naked-backed bat) is a medium-large species (forearm length = 49–56 mm; condylobasal length = 15–17 mm; 11–18 g) that ranges from Veracruz to French Guiana and central Brazil, although it does not occur west of the

Andes in South America (Koopman, 1993, 1994; Brosset et al., 1996; Emmons, 1997; Reid, 1997). No subspecies are currently recognized (Smith, 1972; Koopman, 1994). Quaternary fossils of *P. gymnonotus* have been found in Tobago, where this species is now extinct (Eshelman and Morgan, 1985).

Pteronotus gymnonotus has been captured at sites from sea level to about 3000 m in habitats that range from rainforest to dry semideciduous forest (Smith, 1972; Reid, 1997). This species is typically uncommon but may be locally abundant, particularly in dry, relatively open areas (Handley, 1966, 1976; Reid, 1997). *P. gymnonotus* apparently prefers to roost in caves, often with other mormoopids, and colonies may number in the thousands (Vizotto et al., 1980). Little is known about the diet of *P. gymnonotus,* but available data suggest that these bats consume mainly orthopterans, beetles, and moths (Howell and Burch; 1974; Whitaker and Findley, 1980).

***Pteronotus pristinus* Silva-Taboada, 1974** is a medium-sized species (greatest length of skull = 17–18 mm) known only from fossils collected from caves in Cuba (Silva-Taboada, 1974, 1979). Available material includes several complete skulls plus assorted postcranial elements (Silva-Taboada, 1974, 1979). Two mandibles from a fossil site in central Florida were referred to ''*Pteronotus* cf. *P. pristinus*'' by Morgan (1991). These specimens may represent *P. pristinus*; Morgan's (1991) identification was left as tentative only because he was unable to directly compare the Florida fossils with any of the Cuban material.

GOALS OF THE PRESENT STUDY

The present study was designed with four explicit goals: (1) to test the monophyly of the family Mormoopidae and provide a revised diagnosis of this group if monophyly can be demonstrated; (2) to identify the sister group of Mormoopidae; (3) to test previous hypotheses of interrelationships among mormoopid species (e.g., those of Smith [1972] and Arnold et al. [1982]) and provide revised diagnoses of all superspecific clades (e.g., genera and subgenera); and (4) to evaluate the affinities of the fossil species *Pteronotus pristinus* to extant taxa. We chose to focus on morphological data in this study because of our past experience with such data sets, and because of the promising patterns of character variation among mormoopids described by Smith (1972). Our objective was to produce a relatively well-resolved, well-supported phylogeny of Mormoopidae that could provide both a reference point for future phylogenetic analyses of molecular sequence data and serve as a basis for our ongoing work on morphological evolution, historical biogeography, and the evolution of echolocation call structure and foraging strategies.

MATERIALS AND METHODS

TAXONOMIC SAMPLING, OUTGROUPS, AND TREE ROOTING

Our taxonomic sample included all extant species presently recognized within Mormoopidae (see above). *Mormoops magna,* known only from fossil humeri, was judged too incomplete to be included in our study. *Pteronotus pristinus,* another fossil taxon, was included in some but not all analyses. A list of specimens examined is provided in appendix 1.

In gathering data for this study, we initially scored each currently recognized mormoopid subspecies as a separate taxon in order to facilitate preliminary tests of Smith's (1972) hypotheses of species limits. Examination of the resulting data matrix revealed many gaps (particularly in soft-tissue characters) but no substantive within-species character variation in mormoopids. We therefore pooled our observations by species for the ingroup mormoopid taxa, which simultaneously reduced redundancy and increased completeness within the data set. With respect to species limits within Mormoopidae, we concluded that available discrete character data are entirely consistent with Smith's (1972) taxonomic conclusions. Further species-level revisionary work on mormoopids will require morphometric and/or biochemical analyses far beyond the scope of the present study.

Only one outgroup is necessary to root a phylogenetic tree (Nixon and Carpenter, 1993), but at least two outgroups are usually included in cladistic analyses to establish character polarities and to permit testing of ingroup monophyly (Maddison et al., 1984). Ideally, outgroups should comprise the nearest sister-taxa to the ingroup because the probability of homoplasy increases with time since divergence from a common ancestor. As discussed in the Introduction, Mormoopidae is widely regarded as belonging to the monophyletic superfamily Noctilionoidea, where phylogenetic analyses have placed it either with Noctilionidae (e.g., Patton and Baker, 1978; Arnold et al., 1982; Simmons, 1998; Simmons and Geisler, 1998; Kennedy et al., 1999) or as the sister group of Phyllostomidae (Van Valen, 1979; Novacek, 1991; Kirsch et al., 1998; Van Den Bussche and Hoofer, 2000). Several authors have convincingly argued that another family, Mystacinidae, is also closely related to these taxa (Pierson, 1986; Pierson et al., 1986; Kirsch et al., 1998; Kennedy et al., 1999; Van Den Bussche and Hoofer, 2000).

Based on the studies cited above, we included representatives of three noctilionoid families in our study as putative outgroups: Phyllostomidae (represented by *Macrotus waterhousii*, *Macrotus californicus*, and *Artibeus jamaicensis*), Noctilionidae (*Noctilio leporinus*, *Noctilio albiventris*), and Mystacinidae (*Mystacina tuberculata* and *Mystacina robusta*). Because relationships among these families remain uncertain, we additionally included a member of the family Emballonuridae (*Saccopteryx bilineata*) as a more distal outgroup. Recent studies all agree that Emballonuridae falls outside the smallest clade containing the noctilionoid taxa listed above (e.g., Pierson, 1986; Pierson et al., 1986; Kirsch et al., 1998; Simmons, 1998; Simmons and Geisler, 1998; Van Den Bussche and Hoofer, 2000). Accordingly, we rooted our trees using *Saccopteryx bilineata,* and allowed the relative positions of the noctilionoid taxa (including mystacinids) to vary. Although we could not score every species for all of the characters in our data set, we chose to use species (rather than genera or families) as outgroup OTUs to facilitate future combination of our data with molecular data sets.

SOURCES OF DATA

Within the limits of specimen availability, we examined standard museum specimens (dried skins, skulls, skeletons, and fluid-preserved material) of all extant species included in our study (see appendix 1 for specimens examined). A single skull of the fossil species *Pteronotus pristinus* was also included in our study (fig. 3). We initially obtained morphological information from the literature (e.g., Smith, 1972; Hill and Daniel, 1985), but subsequently we scored most cranial, dental, skeletal, and external characters directly from specimens. We did not collect any new information on features of the vomeronasal complex and brain (characters 48–52), hyoid apparatus (characters 54–71), hair microstructure (characters 108–110), postcranial myology (characters 177–196), reproductive tract (characters 200–204), or digestive tract (characters 205–209). As described below under the character descriptions, these features were scored directly from literature accounts.

The following institutional abbreviations are used in the text, figures, and appendices:

AMNH, American Museum of Natural History, New York, New York, USA; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **MVZ,** Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; **ROM,** Royal Ontario Museum, Toronto, Canada; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

DEFINITION OF CHARACTERS AND ORDERING OF CHARACTER STATES

Most of the characters employed in the present study reflect features that vary among mormoopids and are thus potentially phylogenetically informative with respect to species-level relationships in the family. However, the goals of our study included testing mormoopid monophyly and identification of the sister group of Mormoopidae, so we also included characters representing putative synapomorphies of Mormoopidae. Other characters relevant to relationships among the outgroups were also included in our data set (even if they are invariant within Mor-

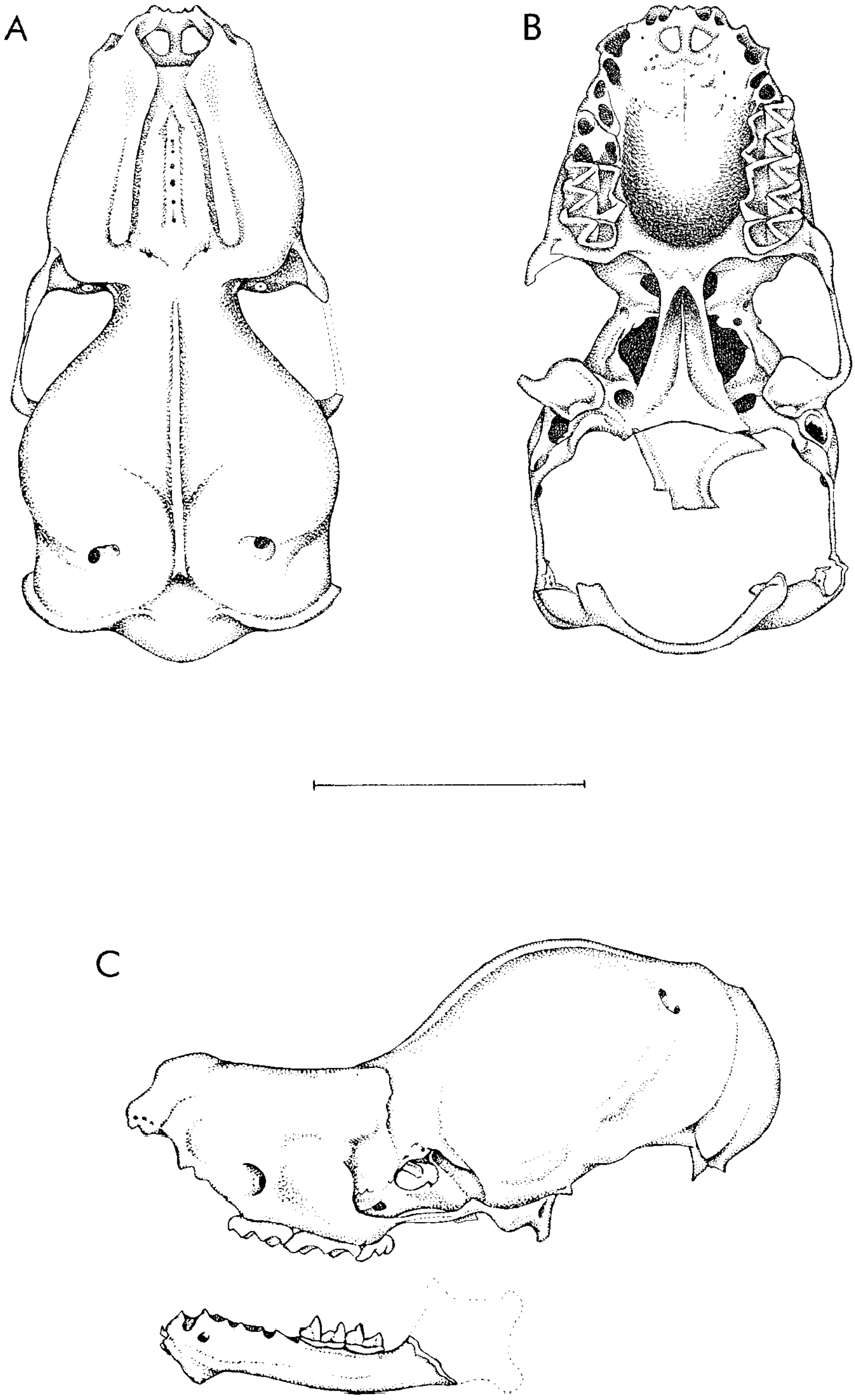

Fig. 3. Dorsal (**A**), ventral (**B**), and lateral (**C**) views of the skull of *Pteronotus pristinus* (ROM 59132), a fossil species known only from Cuba. Scale bar = 10 mm.

moopidae) so as to contribute structure to the basal part of the tree.

Our methods of character definition and description followed Simmons (1993, 1998) and Simmons and Geisler (1998). Unlike those studies, however, we chose to include putative autapomorphies (derived character states observed in only one terminal taxon) in our data set. In this we follow Omland (1997) and Livezey (1998), who have argued that such characters contribute to estimates of overall divergence. Formal scoring of such traits additionally facilitates development of taxonomic diagnoses for terminal taxa as well as future integration of data from species not included in the original study. The few instances of within-species polymorphism detected were treated by erecting alternative character states to describe polymorphic conditions.

Two categories of missing data are commonly recognized in phylogenetic analyses: (1) missing data that result from lack of specimens or appropriate observational data (e.g., soft-tissue characters that cannot be scored in fossil taxa or rare extant species), and (2) missing data that result from evolutionary modifications that may render characters inapplicable under some conditions (e.g., presence/absence of a hypocone on M3 cannot be scored in taxa that lack M3). We followed convention in scoring the former type of missing data as ‘‘?’’ and the latter as ‘‘–’’ in our data matrix.

Our final data set consisted of a total of 209 characters: 27 characters of the skull, 20 dental characters, 5 characters of the vomeronasal complex and brain, 19 characters of the trachea and hyoid apparatus, 5 characters of the tongue, 26 characters describing features of the face, ears, and vibrissae, 14 characters of the pelage and patagia, 60 characters of the postcranial skeleton, 21 characters of postcranial myology, 7 features of the reproductive tract, and 5 characters of the digestive system. Character-state data were recorded in a taxon-character matrix using MacClade version 3.0 (Maddison and Maddison, 1992) and were imported into other software for analysis. While most of our characters were binary (155 = 74%), our data set included a number of multistate characters (54 = 26%). A total of 34 of these multistate characters described progressive gradations in size, shape, degree of development, meristic counts, or color patterns, and these were treated as ordered characters in many of our analyses. The proscribed sequences of character-state transformation (and our justification for expecting changes to be restricted to these sequences) are discussed below under the relevant character descriptions.

POLARITY

Patterns of distribution of character states among multiple outgroups are often used to provide preliminary assessments of character polarity prior to phylogenetic analyses (e.g., Simmons and Geisler, 1998). Although the present study included multiple putative outgroups, only one taxon (*Saccopteryx bilineata*) was used to root the tree. Suggesting that character states seen in this species necessarily represent the primitive condition would be misleading, particularly since Emballonuridae is highly derived in some respects and the family has been distinct since at least the Middle Eocene (Simmons and Geisler, 1998). Accordingly, we do not provide a priori assessments of character polarity below. A posteriori conclusions concerning polarity of selected characters are discussed in the context of taxonomic diagnoses in the ‘‘Discussion and Conclusions’’ section below.

COMPLETENESS

Data completeness is a problem that perpetually plagues phylogenetic studies that include fossils and/or difficult-to-study soft-tissue characters. Completeness of a taxon may be defined as the percentage of characters for which it can be scored in a given analysis (Simmons, 1993; Simmons and Geisler, 1998). In the context of morphological data matrices, fossil taxa are typically much less complete than extant taxa, and rare taxa (which are often omitted from studies that require destructive sampling) are typically less complete than more common taxa. Data gaps resulting from these patterns may reduce both phylogenetic resolution and perceived level of clade support in phylogenetic analyses. However, the effects of these prob-

TABLE 1

Statistics on Character Codings for Mormoopid Data Set

Terminal taxon	Characters scored "0"–"6"[a]	Characters scored "-"	Characters scored "?"	Percent completeness[b]
Saccopteryx bilineata	183 (87.6%)	8 (3.8%)	18 (8.6%)	91.4%
Noctilio albiventris	173 (82.8%)	4 (1.9%)	32 (15.3%)	84.7%
Noctilio leporinus	195 (93.3%)	4 (1.9%)	10 (4.8%)	95.2%
Mystacina robusta	149 (71.3%)	4 (1.9%)	56 (26.8%)	73.2%
Mystacina tuberculata	126 (60.3%)	3 (1.4%)	80 (38.3%)	61.7%
Macrotus waterhousii	195 (93.3%)	1 (0.5%)	13 (6.2%)	93.8%
Macrotus californicus	184 (88.0%)	1 (0.5%)	24 (11.5%)	88.5%
Artibeus jamaicensis	193 (92.3%)	2 (1.0%)	14 (6.7%)	93.3%
Pteronotus parnellii	209 (100%)	0	0	100%
Pteronotus pristinus	33 (15.8%)	0	176 (84.2%)	15.8%
Pteronotus personatus	175 (83.7%)	2 (1.0%)	32 (15.3%)	84.7%
Pteronotus macleayii	179 (85.6%)	0	30 (14.4%)	85.6%
Pteronotus quadridens	177 (84.6%)	2 (1.0%)	30 (14.4%)	85.6%
Pteronotus davyi	178 (85.1%)	2 (1.0%)	29 (13.9%)	86.1%
Pteronotus gymnonotus	172 (82.3%)	0	37 (17.7%)	82.3%
Mormoops blainvillii	176 (84.2%)	1 (0.5%)	33 (15.8%)	84.2%
Mormoops megalophylla	189 (90.4%)	1 (0.5%)	19 (9.1%)	90.9%
Total	2886 (81.2%)	35 (1.0%)	633 (17.8%)	82.2%

[a] Percentages reflect the percent of the total characters (n = 209) used in the analysis.

[b] Completeness is defined as the percentage of characters for which a taxon can be scored based on available data; it was calculated by subtracting the percentage of characters scored "?" from 100%.

lems are frequently overestimated, and inclusion of fossil taxa and soft-tissue characters may have significant positive effects on the outcome of an analysis (see discussion in Simmons and Geisler [1998] and references cited therein). We therefore followed many recent authors in concluding that the potential benefits of including fossils and soft-tissue characters in phylogenetic studies far outweigh the analytical problems that they may introduce (Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992, 1994; Simmons, 1993; Simmons and Geisler, 1998). Simmons and Geisler (1998) argued that calculating the percent completeness of each taxon in a given data set can provide a useful basis for a posteriori consideration of the effects of completeness on the analysis. These data for our study are presented in table 1.

METHODS OF PHYLOGENETIC ANALYSIS

Phylogenetic analyses were conducted using the parsimony algorithm implemented in PAUP* version 4.0b3a (Swofford, 2000). The branch-and-bound option of PAUP was used to identify all equally parsimonious shortest trees and to calculate tree statistics. Near-most-parsimonious trees (one to five steps longer) were identified in subsequent branch-and-bound analyses, and a decay analysis was performed following the methods of Bremer (1988). A branch-and-bound bootstrap analysis with 10,000 replicates and a character jackknife analysis (50% character deletion, branch-and-bound, 10,000 replicates) were additionally used to evaluate relative support for various groupings.

Two analyses were conducted including different subsets of taxa: one including only extant species (excluding *Pteronotus pristinus*), and a second analysis including all taxa. To test the effects of ordering multistate characters on the resulting tree topology, we also conducted a separate analysis of the complete data set with all characters unordered. Additional analyses of our complete data set (with characters ordered) were also performed to find the shortest trees compatible with the phylogenies previously published by Smith (1972), Arnold et al. (1982), and Kennedy et al. (1999). Results and comparisons of these analyses are presented under "Results" below.

Character optimizations were calculated using both the ACTRAN (accelerated transformation optimization) and DELTRAN (delayed transformation optimization) as implemented in PAUP* version 4.0b3a (Swofford, 2000). Discussions of the similarities and differences between these methods can be found in Simmons (1993) and Simmons and Geisler (1998). MacClade version 3.0 (Maddison and Maddison, 1992) was used to visualize the results of character mapping.

CHARACTER DESCRIPTIONS

SKULL

Character 1: *Premaxilla fused to maxilla (0); or premaxilla articulates with maxilla via ligaments, premaxilla freely movable (1).* The nasal branch of the premaxilla is defined as that portion of the premaxilla that lies on the face adjacent to the narial opening. The nasal branch of the premaxilla is fused to the maxilla in all mormoopids and most of the outgroups (*Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata, Mystacina robusta, Noctilio leporinus, Noctilio albiventris*). In contrast, the premaxilla in *Saccopteryx bilineata* articulates with the maxilla via ligaments. This arrangement allows the premaxillae to move freely with respect to the rest of the facial skeleton.

Character 2: *Palatal branch of premaxilla well-developed, right and left premaxillae fused across midline of palate (0); or palatal branch absent, right and left premaxilla not in contact on palate (1).* The palatal branches of the premaxillae are defined as those portion of the premaxillae that contribute to the anterior palate. The palatal branches of the premaxilla are well-developed and the right and left premaxillae are fused across the midline of the palate in all mormoopids and most of the outgroups (*Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata, Mystacina robusta, Noctilio leporinus, Noctilio albiventris*). In contrast, the palatal branches of the premaxilla are absent in *Saccopteryx bilineata.* As a result, the right and left premaxillae do not contact one another in the palatal region. Although this character has the same distribution of states as character 1, these features are not necessarily linked in bats. Some taxa that have freely-movable premaxilla also have well-developed palatal processes that are fused across the midline (e.g., nycterids). Accordingly, we treated these as separate characters in our analysis.

Character 3: *Pair of incisive foramina present (0); or incisive foramina absent (1).* A pair of incisive foramina, bordered anteriorly, medially, and laterally by the premaxillae and posteriorly by the maxillae, is found in the anterior palate of most taxa including all species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in *Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata,* and *Mystacina robusta.* In contrast, the incisive foramina are absent in both species of *Noctilio,* which lack any perforations in the anterior palate. This character cannot be scored in *Saccopteryx bilineata,* which lacks a premaxillary contribution to the anterior palate (see character 2).

Character 4: *Hard palate extends posteriorly into interorbital region (0); or terminates at the level of the zygomatic roots (1).* The hard palate, which forms a bony separation between the oral and nasal passages, terminates posteriorly at the mesopterygoid fossae. The position of the posterior edge of the hard palate varies independently of the posterior extent of the molar toothrow, and is apparently linked to the structure of the nasal passages and soft tissues of the pharyngeal region. The hard palate extends posteriorly into the interorbital region in mormoopids and most of the outgroups (*Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata, Mystacina robusta, Noctilio leporinus, Noctilio albiventris*). In contrast, the hard palate terminates at the level of the zygomatic roots in *Saccopteryx bilineata.*

Character 5: *Rostrum not upturned, angle between long axis of anterior half of zygomatic arch and occlusal surface of molar toothrow less than 10° (0); or rostrum slightly upturned, angle 13–26° (1); or rostrum strongly upturned, angle 28–34° (2).* The long axis of the rostrum lies roughly parallel to the long axis of the zygomatic arch in many bats, resulting in a skull morphology that lacks any obvious "upturning" of the rostrum relative to the braincase. Measuring the degree of upturning of the rostrum is complicated by numerous factors, including modifications of the zygomatic arch (e.g., dorsoventral curvature) and modifications of the rostrum (e.g., foreshortening and dorsal curvature). In noctilionoids, the anterior half of the zygomatic arch usually appears straight in lateral view, and the occlusal surface of the first and second molar teeth (M1 and M2) describe a plane with which zygomatic arch orientation may be compared. The occlusal plane of molar teeth lies at an angle of 13–26° to the long axis of the anterior half of the zygomatic arch in all species of *Pteronotus,* giving these bats the appearance of having a slightly upturned rostrum (fig. 4). A more extreme condition is seen in both species of *Mormoops,* which have a strongly-upturned rostrum characterized by an angle of 28–34° between the zygomatic arch and molar occlusal plane (fig. 4). Among the outgroups, a slightly upturned rostrum (measured using the criteria described above) is seen in *Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata, Noctilio leporinus,* and *Noctilio albiventris.* Both species of *Mystacina* and *Saccopteryx bilineata* are characterized by a different condition in which the rostrum is not upturned, and the occlusal plane of molar teeth lies at an angle of less than 10° to the long axis of the anterior half of the zygomatic arch. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect the logical sequence of transformation from an unflexed rostrum (''0'') to a strongly upturned rostrum (''2'').

Character 6: *Nasals flat or convex (0); or nasals concave (1).* The nasal bones in most bats are either flat or convex upward when seen in lateral view. In contrast, all species of *Pteronotus* and *Mormoops* have nasals that are concave upward (fig. 4). The outgroups all have nasals that are flat or convex, suggesting that concave nasals represent a derived condition. This character appears to be correlated with presence of an upturned rostrum in mormoopids (see character 1), but these features are decoupled in the outgroups. *Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Noctilio leporinus,* and *Noctilio albiventris* each have a slightly upturned rostrum, but lack concave nasals. Accordingly, we chose to treat these as separate characters in our analysis.

Character 7: *Nasal foramina small or absent (0); or pair of large foramina present in posterior nasal region below forehead (1).* The nasal bones of most bats are imperforate or include only a few small foramina. This condition is seen in all mormoopids and most of the outgroups (*Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Mystacina tuberculata, Mystacina robusta, Saccopteryx bilineata*). In contrast, both species of *Noctilio* are characterized by presence of a pair of large foramina in the posterior portion of the nasals just below the forehead.

Character 8: *Maximum rostral breadth less than or equal to length of maxillary toothrow (0); or greater than length of maxillary toothrow (1).* The shape of the rostrum in dorsal view can be described by comparing maximum breadth of the rostrum (which usually occurs at the level of the last premolar or first molar) with the length of the maxillary toothrow. *Pteronotus parnellii, P. macleayii, P. quadridens, P. personatus, P. pristinus,* and both species of *Mormoops* have a rostral breadth that is less than or equal to the length of the maxillary toothrow. In contrast, *Pteronotus davyi* and *P. gymnonotus* have a rostral breadth that is greater than the length of the maxillary toothrow. Similar variation is seen among the outgroups. *Saccopteryx bilineata,* both species of *Mystacina,* and both species of *Macrotus* have a rostral breadth that is less than or equal to the length of the maxillary toothrow, while *Artibeus jamaicensis* and both species of *Noctilio* have a rostral breadth that is greater than the length of the maxillary toothrow.

Character 9: *Rostrum length less than one-half of total length of skull (0); or equal to or greater than one-half of length of skull (1).* The relative length of the rostrum in bats varies independently of rostral breadth. We defined rostral length as the distance between the anteriormost point on the skull (excluding teeth) and the interorbital constriction (the point of minimum skull breadth in the orbital region). Skull length was defined as the greatest length of the skull excluding teeth. *Pteronotus parnellii, P. pristinus, P. personatus, P. davyi, P. gymnonotus,* and

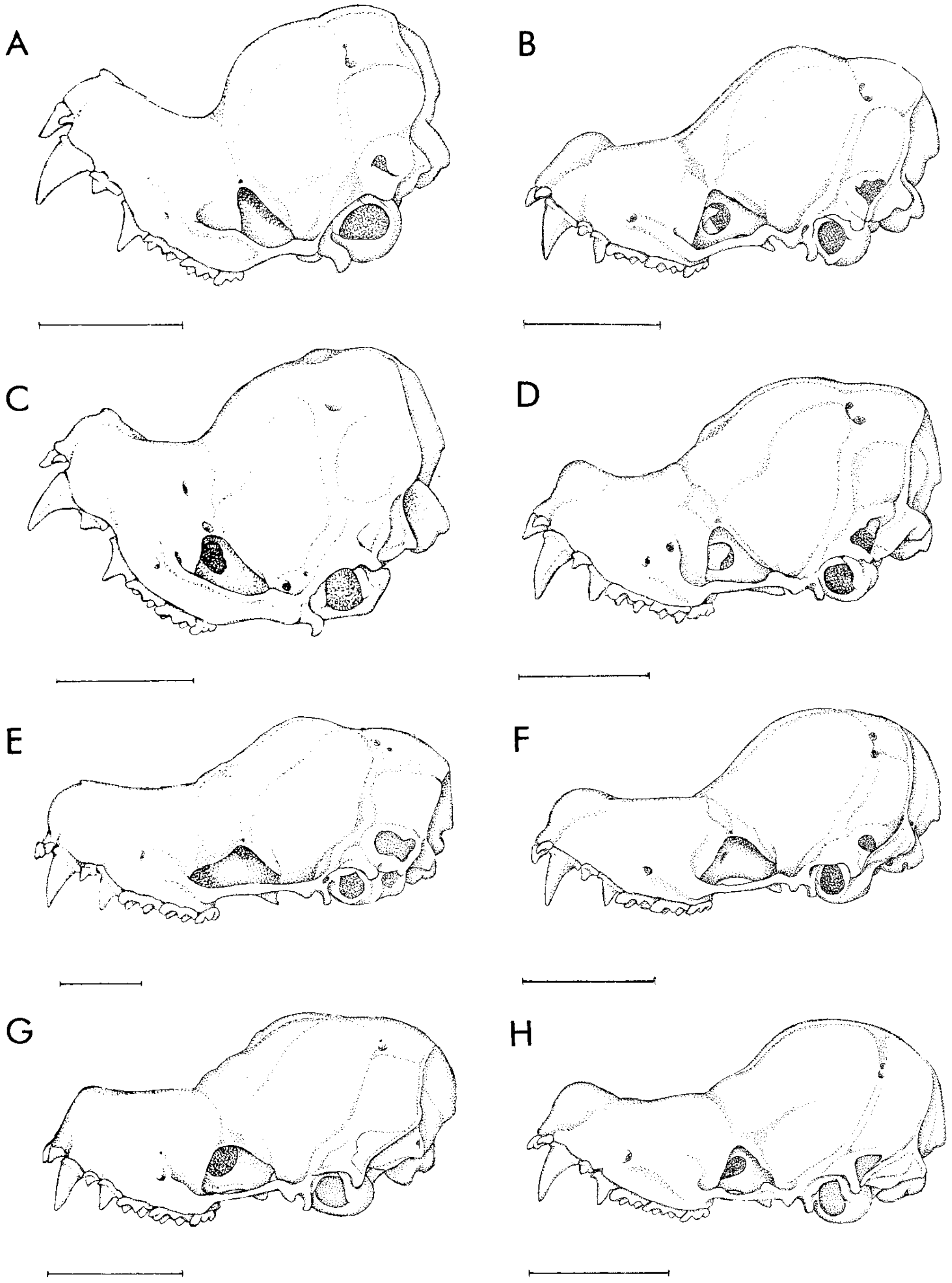

Fig. 4. Lateral views of the skulls of (**A**) *Mormoops blainvillii* (AMNH 45197), (**B**) *Pteronotus davyi* (AMNH 204965), (**C**) *Mormoops megalophylla* (AMNH 27300), (**D**) *Pteronotus gymnonotus* (AMNH 32092), (**E**) *Pteronotus parnellii* (AMNH 129749), (**F**) *Pteronotus macleayii* (AMNH 60899), (**G**) *Pteronotus personatus* (AMNH 32136), and (**H**) *Pteronotus quadridens* (AMNH 39357). Note the differences in degree of upturn of the rostrum relative to the braincase, and in the position of the infraorbital foramen and anterior rim of the orbit relative to the toothrow. Scale bars = 5 mm.

Fig. 5. Dorsal views of the skulls of (**A**) *Mormoops blainvillii* (AMNH 45197), (**B**) *Mormoops megalophylla* (AMNH 27300), (**C**) *Pteronotus davyi* (AMNH 204965), (**D**) *Pteronotus gymnonotus* (AMNH 32092), (**E**) *Pteronotus parnellii* (AMNH 129749), (**F**) *Pteronotus personatus* (AMNH 32136), (**G**) *Pteronotus macleayii* (AMNH 60899), and (**H**) *Pteronotus quadridens* (AMNH 39357). Note the differences in relative proportions of the skull (e.g., breadth of the rostrum, zygomatic arches, and mastoid region compared with skull length). Scale bars = 5 mm.

both species of *Mormoops* are characterized by having a rostral length that is less than one-half the length of the skull (fig. 5). In contrast, the rostrum is noticeably longer in *Pteronotus quadridens* and *P. macleayi*, where rostral length (as defined above) is equal to or greater than one-half of the total length of the skull (fig. 5). All of the outgroups have a rostrum length that is less than one-half of the length of the skull.

Character 10: *Infraorbital foramen not enlarged, diameter less than one-eighth the height of the rostrum (0); or enlarged, diameter one-quarter to one-half the height of the rostrum (1).* The infraorbital foramen, which is located in the maxilla, marks the anterior opening of the infraorbital canal. The size of the infraorbital foramen can be evaluated by comparing diameter of the foramen to the height of the rostrum above M1.

The infraorbital foramen is not enlarged (i.e., foramen diameter less than one-eighth the height of the rostrum) in all extant species of *Pteronotus* and *Mormoops* (fig. 4). In contrast, the infraorbital canal is enlarged and its diameter is approximately one-quarter to one-third the height of the rostrum in *Pteronotus pristinus* (fig. 3) Among the outgroups, the infraorbital foramen is not enlarged in *Artibeus jamaicensis, Macrotus waterhousii, Macrotus californicus, Noctilio leporinus, Noctilio albiventris,* and *Saccopteryx bilineata,* but this foramen is enlarged (one-half the height of the rostrum) in both species of *Mystacina.*

Character 11: *Infraorbital foramen located above posterior half of P4 (0); or above anterior half of M1 (1); or above posterior half of M1 (2); or anterior half of M2 (3).* The infraorbital foramen in *Pteronotus personatus* is located directly above (dorsal to) the anterior half of M2, roughly above the parastyle (fig. 4). In contrast, the infraorbital foramen is located above the posterior half of M1 (above the metacone) in *P. davyi* and *P. gymnonotus* (fig. 4). The infraorbital foramen is located above the anterior half of M1 (above the paracone) in *P. parnellii, P. macleayi, P. quadridens,* and *P. pristinus* (figs. 3, 4). Both species of *Mormoops* exhibit a fourth condition in which the infraorbital foramen occurs above the posterior half of P4 (fig. 4). Among the outgroups, both species of *Mystacina have* an infraorbital foramen that opens above the posterior half of M1. Both species of *Noctilio* and both species of *Macrotus* have the foramen above the anterior half of M1, and the infraorbital foramen opens above the posterior half of P4 in *Artibeus jamaicensis* and *Saccopteryx bilineata*. Transformations in this character were ordered 0 ↔ 1 ↔ 2 ↔ 3 to reflect our assumption that changes in the position of the infraorbital foramen relative to the toothrow occur in a progressive fashion.

Character 12: *Anterior rim of orbit terminates above P4 (0); or above M1 (1); or above anterior half of M2 (2); or above posterior half of M2 (3).* The anterior terminus of the orbit, which in most bats is marked by a sharply demarcated rim, may occur in different positions relative to the toothrow. This variation affects both the relative position of the eye, which typically occupies the anteriormost portion of the orbit, and the length of the infraorbital canal, which begins in the anterior orbit and terminates on the face at the infraorbital foramen (see character 11). The anterior rim of the orbit terminates above (dorsal to) the posterior half of M2 in all species of *Pteronotus* (fig. 4). In contrast, the anterior orbital rim terminates above M1 in both species of *Mormoops* (fig. 4). Among the outgroups, the anterior rim of the orbit terminates above P4 in *Saccopteryx bilineata,* above M1 in both species of *Noctilio,* above the anterior half of M2 in *Artibeus jamaicensis* and both species of *Macrotus,* and above the posterior half of M2 in both species of *Mystacina.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 ↔ 3 to reflect our assumption that changes in the position of the infraorbital foramen relative to the toothrow occur in a progressive fashion.

Character 13: *Postorbital process present (0); or absent (1).* The postorbital process is a laterally projecting process of the frontal that forms part of the posterodorsal rim of the orbit. A postorbital process is absent in all mormoopids (fig. 5) and most of the outgroups. In contrast, a well-developed, elongate postorbital process is present in *Saccopteryx bilineata.*

Character 14: *Zygomatic breadth greater than mastoid breadth (0); or less than mastoid breadth (1).* The maximum breadth of the skull in bats may occur in either the zygomatic region anterior to the braincase or in the mastoid region at the posterior end of the braincase. Zygomatic breadth (the maximum breadth of the skull measured across the zygomatic arches) is greater than mastoid breadth (maximum breadth of the skull measured across the mastoid region) in *Pteronotus parnellii, P. pristinus, P. davyi, P gymnonotus,* and both species of *Mormoops* (figs. 3, 5). In contrast, mastoid breadth is greater than zygomatic breadth in *Pteronotus personatus, P. quadridens,* and *P. macleayii.* Zygomatic breadth is greater than mastoid breadth in all of the outgroups.

Character 15: *Parietals not inflated (0); or inflated in area encasing cerebellum (1).* In most bats the parietal bones, which cover the brain in the region of the cerebellum, are not notably inflated with respect to the bones of the anterior braincase (i.e., the frontals). In contrast, the parietal bones are markedly inflated over the cerebellum in *Mormoops* (fig. 5). All species of *Pteronotus* lack inflated parietals (fig. 5), as do all of the outgroups.

Character 16: *Epitympanic recess shallow and broad (0); or deep, constricted in area (1).* The epitympanic recess in bats lies in the dorsolateral roof of the middle-ear space, where it houses the incus and the joint between the malleus and incus (Simmons and Geisler, 1998). The epitympanic recess is deep and constricted in area in all species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina.* In contrast, the epitympanic recess is shallow and broad in *Artibeus jamaicensis* and both species of *Macrotus.*

Character 17: *Fossa for m. stapedius indistinct (0); or deep, constricted in area, forms a crescent-shaped fissure (1).* The fossa for the origin of m. stapedius is located in the posterior roof of the middle-ear space (Simmons and Geisler, 1998). When well defined, it occupies a cavity dorsal to the crista parotica (Simmons and Geisler, 1998). The fossa for m. stapedius is indistinct in all species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in both species of *Mystacina.* In contrast, the fossa for the origin of m. stapedius is deep and constricted in area in *Saccopteryx bilineata,* both species of *Noctilio, Artibeus jamaicensis,* and both species of *Macrotus.* In these taxa, the fossa for m. stapedius forms a crescent-shaped fissure.

Character 18: *Fenestra cochleae small or of moderate size, maximum diameter <20% of the external width of the first half turn of the cochlea (0); or enlarged, maximum diameter >25% of the external width of the first half turn of the cochlea (1).* The fenestra cochleae (= fenestra rotundum) is a membrane-covered opening in the tympanic wall of the petrosal. It faces posteriorly or posterolaterally, and separates the scala tympani (at the base of the cochlear labyrinth) from the middle-ear cavity. The fenestra cochleae appears relative large in all species of *Pteronotus* and *Mormoops,* where it has a maximum diameter >25% of the external width of the first half turn of the cochlea. A similar condition is seen in most of the outgroups. In contrast, the fenestra cochleae is smaller (maximum diameter <20% of the external width of the first half turn) in *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 19: *Pars cochlearis of petrosal sutured to basisphenoid (0); or loosely attached to basisphenoid via ligaments and/or thin splints of bone (1).* The pars cochlearis of the petrosal (which in microchiropterans consists principally of the bone enclosing the enlarged cochlea) is loosely attached to the basisphenoid via ligaments and/or thin splints of bone in all species of *Mormoopids* and *Pteronotus.* A similar condition is seen in most of the outgroups. In contrast, the pars cochlearis of the petrosal is sutured to the basisphenoid in *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 20: *Cochlea phanerocochlear (0); or cryptocochlear (1).* Novacek (1985b, 1991) described variation in cochlear structure among bats and recognized two distinct patterns of petrosal ossification and adult cochlear morphology. The "phanerocochlear" state occurs when the petrosal wall is thin and poorly ossified, resulting in a condition where the cochlear labyrinth is clearly visible externally in the adult (Novacek, 1985b, 1991). In contrast, a "cryptocochlear" condition occurs when strong petrosal ossification produces a thicker encasement of bone around the cochlea, hiding the cochlear labyrinth from external view in adults (Novacek, 1985b, 1991). *Pteronotus parnellii* exhibits the cryptocochlear condition. In contrast, all other extant species of *Pteronotus* and both species of *Mormoops* have a phanerocochlear cochlea. Among the outgroups, the phanerocochlear condition occurs in *Saccopteryx bilineata, Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Mystacina.* Both species of *Noctilio* have a cryptocochlear cochlea. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 21: *Cochlea greatly enlarged (0); or moderately enlarged (1).* Numerous authors have discussed the degree of enlargement of the cochlea in microchiropteran bats, a feature that appears to be correlated with echolocation and foraging habits (Novacek, 1985a, 1987, 1991; Habersetzer and Storch, 1992; Simmons and Geisler, 1998). Habersetzer and Storch (1992) plotted cochlear width (measured from the end of the first half turn of the cochlea to the end of the second half turn) versus basicranial width, and found a small zone of overlap between nonecholocating megachiropterans and echolocating microchiropterans. Simmons and Geisler (1998) added additional data points to this plot, and formalized these data in phylogenetic character which they used in assessment of interfamilial relationships. Based on their data plot (Simmons and Geisler, 1998: fig. 29), they recognized three character states: (A) cochlea not enlarged (taxa that fall below the zone of overlap between Megachiroptera and Microchiroptera); (B) cochlea moderately enlarged (taxa that fall in the zone of overlap between Megachiroptera and Microchiroptera); and (C) cochlea greatly enlarged (taxa that fall above the zone of overlap between Megachiroptera and Microchiroptera). Extant bats in the ‘‘cochlea not enlarged’’ group do not use sophisticated echolocation. Some bats with a ‘‘moderately enlarged’’ cochlea do not use sophisticated echolocation (i.e., the megachiropterans), but others do (i.e., the microchiropterans). However, none of the latter group are typical aerial insectivores (Simmons and Geisler, 1998). Although some may combine aerial hawking with other foraging strategies, most apparently rely on passive acoustic cues and/or vision to detect invertebrate or small vertebrate prey that are captured by gleaning or landing on the prey, or they feed on fruit or nectar that is detected by vision or olfaction (Simmons and Geisler [1998] and references cited therein). In contrast, all bats with the ‘‘cochlea greatly enlarged’’ use sophisticated laryngeal echolocation, and most are expert aerial hawkers that obtain most or all of their food in this manner (Simmons and Geisler [1998] and references cited therein).

In the present study, we scored taxa using Simmons and Geisler’s (1998: fig. 29) methods and data, adding new observations only for the species not explicitly scored in that study. We found that all species of *Pteronotus* and *Mormoops* have a greatly enlarged cochlea. Among the outgroups, a similar condition is seen in *Saccopteryx bilineata,* both species of *Noctilio, Mystacina tuberculata,* and *Artibeus jamaicensis.* In contrast, *Mystacina robusta* and both species of *Macrotus* have a moderately enlarged cochlea.

Character 22: *Ectotympanic bulla extends medially across two-thirds or more of cochlea (0); or extends across one-half of cochlea (1); or extends across no more than one-third of cochlea (2).* The auditory bulla of bats is poorly developed, consisting of a single ectotympanic element that typically covers only part of the ventral exposure of the cochlea. The ectotympanic bulla extends medially across two-thirds or more of the cochlea in both species of *Mormoops* and all extant species of *Pteronotus,* with the exception of *P. parnellii.* In the latter species, the ectotympanic bulla extends across no more than one-third of the cochlea. Among the outgroups, the ectotympanic bulla extends medially across two-thirds or more of the cochlea in *Artibeus* jamaicensis, both species of *Macrotus,* and both species of *Mystacina.* In contrast, the ectotympanic bulla extends across one-half of the cochlea in *Saccopteryx bilineata* and both species of *Noctilio.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in relative coverage of the cochlea by the ectotympanic bulla occur in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored ‘‘?’’ for this character.

Character 23: *Tympanic annulus inclined, lies at angle of 35–55° relative to the basicranial plane (0); or semivertical, lies at angle of 75–90° relative to basicranial plane (1).* The tympanic annulus is that part of the ectotympanic that forms the ring that supports the tympanic membrane. In bats the annulus is typically composed of relatively dense bone (as opposed to the thinner medial portion of the ectotympanic, which forms the bulla), and it lies in a plane that defines the orientation of the tympanic membrane. The tympanic annulus is semivertical (plane of annulus lies at angle of 35–55° relative to the basicranial plane) in all extant species of *Pteronotus* and *Mormoops.* A similar condition is found among the outgroups in *Artibeus jamaicensis* and both species of *Macrotus.* In contrast, the tympanic annulus is inclined at an angle of 35–55° relative to the basicranial plane in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 24: *Basisphenoid with wide, shallow longitudinal furrows (0); or with narrow, deep furrows (1); or with deep pits (2).* In most noctilionoids the basisphenoid is trapezoid-shaped, wider anteriorly than posteriorly, and has two parallel furrows along its entire length. In part owing to the shape of the basisphenoid, the furrows are less well defined anteriorly than posteriorly. *Pteronotus macleayii, P. quadridens, P. personatus, P. davyi, P. gymnonotus,* and both species of *Mormoops* have basisphenoid furrows that are wide and shallow, covering the entire width of the basisphenoid. In contrast, *Pteronotus parnellii* and *P. pristinus* have narrow, deep furrows down the center of the basisphenoid. Both species of *Macrotus* have similar narrow and deep furrows, while *Artibeus jamaicensis,* both species of *Noctilio,* and both species of *Mystacina* have furrows that are wide and shallow. *Saccopteryx bilineata* exhibits an alternative condition in which the basisphenoid is dominated by a pair of large, deep pits.

Character 25: *Basioccipital not constricted (0); or constricted (1).* In bats the basioccipital forms the posterior floor of the braincase, typically extending anteriorly between the cochlea. In *Pteronotus parnellii,* the basioccipital is markedly constricted anteriorly so that the width of the anterior portion of this element is approximately one-third the width of the foramen magnum. In contrast, the basioccipital is not so constricted in *Mormoops* and the remaining species of *Pteronotus.* In these forms, the width of the anterior basioccipital is approximately one-half the width of the foramen magnum. The basioccipital is similarly unconstricted in both species of *Noctilio,* both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* The basioccipital is constricted in *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 26: *Angular process projects above the level of the occlusal plane (0); or at or below the level of the occlusal plane (1).* The angular process in bats extends from the posteroventral "corner" of the lower jaw. This process projects above the level of the occlusal plane of the molar toothrow in all species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Saccopteryx bilineata* and both species of *Noctilio.* In contrast, the angular process lies either at or entirely below the level of the occlusal plane in both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 27: *Coronoid process of lower jaw does not extend dorsally above level of condyloid process (0); or coronoid process one and one-half times the height of the condyloid process (1); or two times the height of the condyloid process (2).* The coronoid process of the lower jaw does not extend dorsally above the level of the condyloid process in any species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Saccopteryx bilineata* and both species of *Noctilio.* In contrast, the coronoid process extends above the level of the condyloid process in both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus.* The relative height of these processes (as measured from the lower border of the body of the mandible) varies considerably. The coronoid process is one and one-half times the height of the condyloid process in both species of *Mystacina* and *Artibeus jamaicensis,* while it is two times the height of the condyloid process in both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

DENTITION

Character 28: *Two pairs upper incisors (I1 and I2) present (0); or only one pair of upper incisors (I1) present, I2 absent (1).* Most bats have two pairs of upper incisor teeth. The inner incisors (which lie adjacent to each other and the midsagittal plane) are typically interpreted as homologous to I1 in other mammals; the outer incisors are thought to represent I2 (Thomas, 1908; Andersen, 1912; Slaughter, 1970). All members of *Pteronotus* and *Mormoops* have two pairs of upper incisors. Among the outgroups, both species of *Noctilio,* both species of *Macrotus,* and *Artibeus jamaicensis* also have two pairs of upper incisors. In contrast, both species of *Mystacina* have only one pair of lower incisors, which correspond in shape and position to I1 of other bats; I2 appears to be absent in this genus. *Saccopteryx bilineata* also has only a single pair of upper incisors, which we interpret as homologous to I1 based on comparisons with other emballonurids that retain two pairs of upper incisors (e.g., *Emballonura*).

Character 29: *Inner upper incisors (I1) taper to blunt point (0); or bilobed (1).* All extant species of *Pteronotus* and *Mormoops* have bilobed inner upper incisors (I1). Among the outgroups, both species of *Macrotus* also have similar bilobed inner upper incisors. In contrast, *Saccopteryx bilineata,* both species of *Noctilio,* both species of *Mystacina,* and *Artibeus jamaicensis* exhibit a different condition in which each inner upper incisor tapers to a blunt point. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 30: *Height of outer upper incisors (I2) less than one-half that of inner incisors (I1) (0); or I2 and I1 subequal in height (1).* The height of the outer upper incisors (I2) is less than one-half that of the inner incisors (I1) in all species of *Pteronotus* and *Mormoops* (fig. 4). This condition is also seen in both species of *Noctilio* and both species of *Macrotus.* In contrast, I2 and I1 are subequal in height in *Artibeus jamaicensis.* Taxa lacking I2 (*Saccopteryx bilineata* and both species of *Mystacina*; see character 28) could not be evaluated for this character, and so were scored ''–'' in our data set. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 31: *Lingual cingulae present on upper incisors (I1 and I2) (0); or absent (1).* Each upper incisor has a distinct lingual cingulum at its base in all extant species of *Pteronotus.* In contrast, lingual cingulae are absent from these teeth in both species of *Mormoops. Saccopteryx bilineata* similarly lacks a lingual cingulum on the upper incisors, but the remaining outgroups have a lingual cingulum on the base of each upper incisor. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 32: *Diastema absent between outer upper incisor (I2) and canine (0); or present (1).* There is no diastema between the outer upper incisor (I2) and canine tooth (C) in *Pteronotus parnellii.* In contrast, a distinct diastema is present between these teeth in *Pteronotus macleayii, P. quadridens, P. personatus, P. davyi, P. gymnonotus, P. pristinus,* and both species of *Mormoops.* Among the outgroups, *Artibeus jamaicensis* and both species of *Macrotus* and lack a diastema between I2 and C, while such a diastema is present in both species of *Noctilio. Saccopteryx bilineata* and both species of *Mystacina* have a diastema present anterior to the canine, but this taxon lacks I2 so the condition is not comparable to that seen in other taxa. Accordingly, we scored these species ''–'' for this character.

Character 33: *Three pairs of lower incisors (i1, i2, i3) present (0); or two pairs (i1 and i2) present (0); or only one pair (i1) present (1).* The maximum number of lower incisors found in any bat is three pairs. All members of *Pteronotus* and *Mormoops* have two pairs of lower incisors (fig. 6), which we presume to be homologous to i1 and i2 following Miller (1907). *Artibeus jamaicensis* and both species of *Macrotus* also have two pairs of lower incisors, again presumed to represent i1 and i2. In contrast, *Saccopteryx bilineata* retains three pairs of lower incisors. Both species of *Noctilio* and both species of *Mystacina* have only one pair of lower incisors that seem to correspond in shape and position to i1 of other bats; i2 and i3 appear to be absent in these forms (Miller, 1907). Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in the number of incisor teeth occurred in a progressive fashion.

Although the number of upper and lower incisors is correlated in many species (e.g., mormoopids), this is not true in all taxa. For example, *Saccopteryx bilineata* has three pairs of lower incisors but only one pair of upper incisors; both species of *Noctilio* have

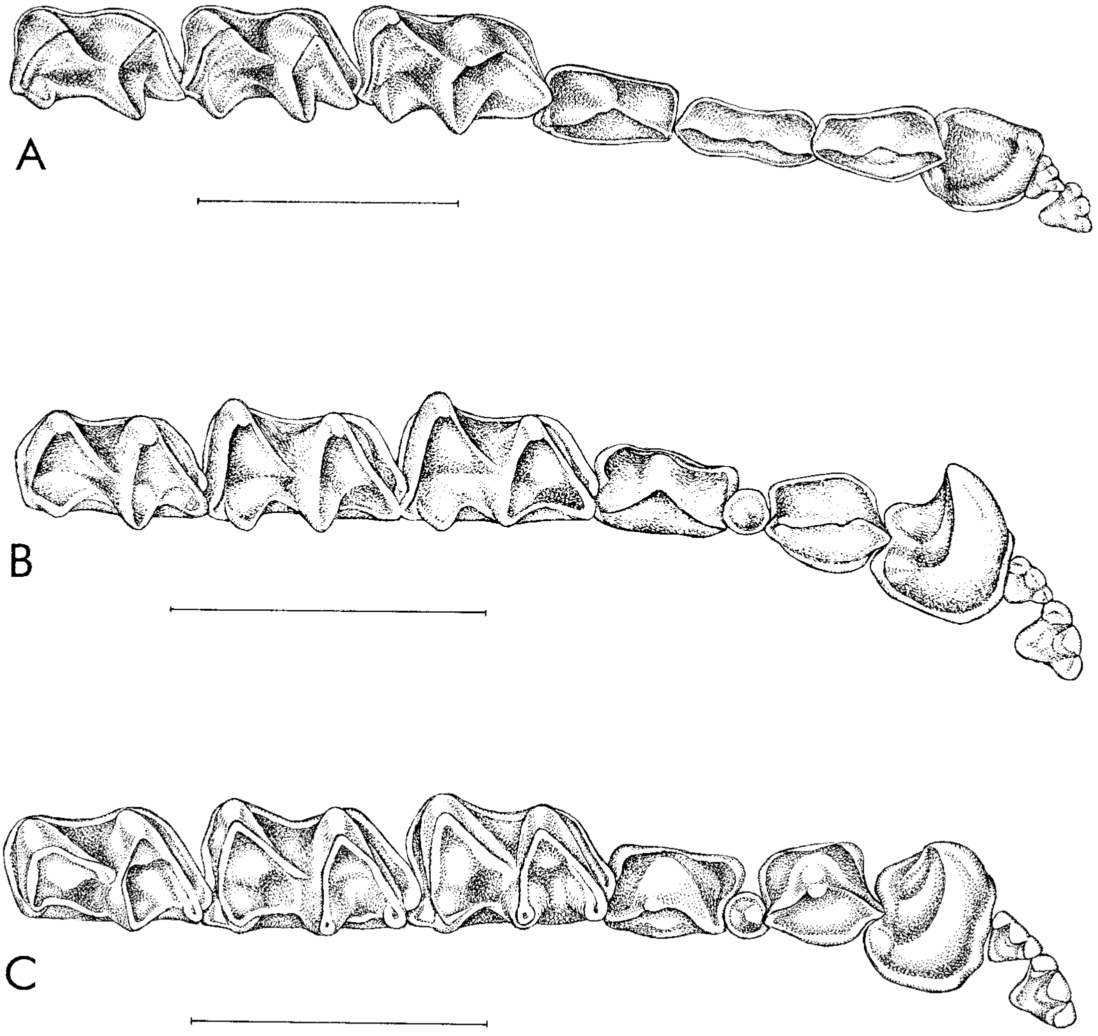

Fig. 6. Occlusal views of the left lower toothrow of (**A**) *Mormoops blainvillii* (AMNH 45197), (**B**) *Pteronotus quadridens* (AMNH 39357), and (**C**) *Pteronotus davyi* (AMNH 204965). Note the relative proportions of the premolars (p3 reduced in *Pteronotus* species) and the morphology of the talonid basin (nyctalodont in *Mormoops blainvillii* and *Pteronotus quadridens,* myotodont in *Pteronotus davyi*).

two pairs of upper incisors but only one pair of lower incisors. The number of upper versus lower incisors therefore appears to be decoupled among the taxa in our study. Accordingly, we have treated these as separate characters.

Character 34: *Inner lower incisors (i1) trilobed (0); or bilobed (1).* All extant species of *Pteronotus* and *Mormoops* have trilobed inner lower incisors (i1; fig. 6). Among the outgroups, *Saccopteryx bilineata,* both species of *Mystacina,* and *Noctilio albiventris* similarly have a trilobed i1. In contrast, i1 is bilobed in *Noctilio leporinus,* both species of *Macrotus,* and *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 35: *Second lower incisors (i2) trilobed (0); or bilobed (1).* The second lower incisors (i2) are trilobed in *Pteronotus macleayii, P. quadridens, P. personatus, P. davyi, P. gymnonotus,* and both species of *Mormoops* (fig. 6). In contrast, *Pteronotus par-*

nellii has bilobed outer lower incisors. Among the outgroups, *Saccopteryx bilineata* has trilobed outer lower incisors, while these teeth are bilobed in and both species of *Macrotus* and *Artibeus jamaicensis.* Both species of *Noctilio* and both species of *Mystacina* cannot be scored for this character because they lack i2 (see character 34 above); these taxa were scored ''–'' for this character in our analysis. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 36: *Upper first premolar (P1) present (0); or absent (1).* Much has been written regarding the homologies of the premolar cheekteeth in bats (e.g., Miller, 1907; Thomas, 1908; Andersen, 1912; Slaughter, 1970; Handley, 1959; Simmons and Handley, 1998). No bat has more than three upper premolars, and opinions have varied with respect to the identity of the missing tooth. We follow Thomas (1908), Andersen (1912), Handley (1959), and Simmons and Handley (1998) in recognizing the premolars in bats as P1, P3, and P4; the missing tooth is presumed to be P2. Changes in the composition of the premolar dentition were treated as binary characters (rather than as a single ordered multistate character, as we did with the incisor dentition) because the sequence of loss or gain of teeth at the P1/p1 and P3/p3 loci are not clear.

Two upper premolars are present in all species of *Pteronotus* and *Mormoops* (fig. 4). These apparently correspond to P3 and P4; P1 is absent in these taxa (Miller, 1907). P1 is similarly absent in both species of *Noctilio,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus* (Miller, 1907). In contrast, P1 is present in *Saccopteryx bilineata* (Simmons and Handley, 1998).

Character 37: *Upper third premolar (P3) present (0); or absent (1).* The upper third premolar (P3) is present in all species of *Pteronotus* and *Mormoops* (fig. 4). This tooth is also present in both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* In contrast, P3 is absent in *Saccopteryx bilineata* and both species of *Noctilio.*

Character 38: *Diastema absent between P3 and P4 (0); or present (1).* There is no diastema between P3 and P4 in any species of *Pteronotus* (fig. 4). In contrast, a distinct diastema is present between these teeth in both species of *Mormoops* (fig. 4). Among the outgroups, a diastema between P3 and P4 is lacking in *Artibeus jamaicensis* and both species *Mystacina,* while such a diastema is present in both species *Macrotus.* P3 is absent in *Saccopteryx bilineata* and both species of *Noctilio,* so these taxa were scored ''–'' for this character.

Character 39: *Crown height of P3 subequal to that of P4 (0); or height of P3 less than one-half height of P4 (1).* The relative crown height of P3 and P4 varies among bats. P4 is typically a large tooth with a crown height equal to or greater than that of the molars; P3 may be of similar size, or reduced relative to the other cheek teeth. The crown height of P3 is reduced to less than one-half the height of P4 in all extant species of *Pteronotus* and *Mormoops* (fig. 4). In contrast, crown height of P3 is subequal to that of P4 in both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* Both species of *Noctilio* and *Saccopteryx bilineata* cannot be scored for this character because they lack P3 (see character 38 above); these taxa were scored ''–'' for this character in our analysis. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 40: *First lower premolar (p1) present (0); or absent (1).* No bat has more than three lower premolars. As with the upper dentition, there has been considerable debate regarding the identity of these teeth. Many authors have identified the three bat premolars as p2, p3, and p4 (e.g., Miller, 1907; Slaughter, 1970), but the anteriormost tooth is more likely homologous with p1 of other mammals (Thomas, 1908; Handley, 1959). Three lower premolars (which we presume to be p1, p3, and p4) are present in all species of *Pteronotus* and *Mormoops* (fig. 6). *Saccopteryx bilineata* and both species of *Macrotus* also retain p1. In contrast, p1 is absent in both species of *Noctilio,* both species of *Mystacina,* and *Artibeus jamaicensis.*

Character 41: *Third lower premolar (p3) present (0); or absent (1).* The third lower premolar is present in all species of *Pteronotus* and *Mormoops* (fig. 6). Similarly, p3 is present in both species of *Noctilio,* both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* In contrast, p3 is absent in *Saccopteryx bilineata* (Simmons and Handley, 1998).

Character 42: *Lower p3 with one root (0); or with two roots (1).* The lower third premolar p3 is a single-rooted tooth in all species of *Pteronotus.* In contrast, this tooth has two roots in both species of *Mormoops.* Among the outgroups, p3 is single-rooted in both species of *Noctilio,* both species of *Mystacina robusta,* and *Artibeus jamaicensis,* but this tooth has two roots in both species of *Macrotus.* This character was scored ''–'' in *Saccopteryx bilineata,* which lacks p3 (see character 41).

Character 43: *Crown length of lower p3 and p4 subequal (0); or p3 reduced, crown length of p3 less than or equal to one-half the crown length of p4 (1).* Crown length of the lower p3 and p4 are approximately subequal in both species of *Mormoops.* In contrast, p3 is reduced to a peglike tooth whose crown length is less than or equal to one-half the crown length of p4 in all species of *Pteronotus* (fig. 6). Among the outgroups, p3 and p4 are subequal in both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus,* while p3 is reduced (crown length approximately one-half the length of p4) in both species *Noctilio.* This character was scored ''–'' in *Saccopteryx bilineata,* which lacks p3 (see character 41).

Character 44: *No cuspule present on premetacrista on M1 and M2 (0); or cuspule present (1).* The premetacrista is a crestlike ridge that connects the mesostyle and metacone on the upper molars A small cuspule is present on the labial premetacrista in *Pteronotus personatus.* In contrast, no cuspule is present in this position in *Mormoops* or any other species of *Pteronotus.* A cuspule is similarly lacking on the premetacrista in *Saccopteryx bilineata,* both species of *Noctilio,* both species of *Mystacina,* and both species of *Macrotus. Artibeus* cannot be scored for this character due to modification of the molar teeth for frugivory, so this taxon is scored ''–'' for this character.

Character 45: *Upper and lower third molars (M3 and m3) present (0); or absent (1).* The upper and lower third molars (M3 and m3) are present in all species of *Pteronotus* and *Mormoops* (figs. 4, 6). These teeth are also present in most of the outgroups. In contrast, M3 and m3 are both absent in *Artibeus jamaicensis.* Unlike the situation with the incisors and premolars, where evolution in the upper and lower dentitions appears decoupled, changes in the upper and lower molar dentition are correlated among our taxa. Accordingly, we treated absence of M3/m3 as a single character.

Character 46: *Lower first and second molars (m1 and m2) myotodont (0); or nyctalodont (1); or modified for fruit feeding, cusps and cristids not distinct (2).* As discussed by Simmons and Geisler (1998), morphology of the talonid of the lower first and second molars (m1 and m2) varies among bats. Most extant species have lower molar teeth in which the hypoconulid lies adjacent to the entoconid on the lingual edge of the tooth. Menu and Sigé (1971) distinguished two forms of the talonid that occur among these taxa: the postcristid (which originates from hypoconid) may either connect with the hypoconulid (a condition described as ''nyctalodonty'') or bypass the hypoconulid to connect with the entoconid (''myotodonty''). *Pteronotus parnellii, P. davyi, P. gymnonotus,* and *P. pristinus* have myotodont lower molars (fig. 6). In contrast, *P. macleayii, P. quadridens, P. personatus,* and both species of *Mormoops* have nyctalodont lower molars (fig. 6). Among the outgroups, *Saccopteryx bilineata* is nyctalodont, but both species of *Mystacina,* both species of *Noctilio,* and both species of *Macrotus* have myotodont lower molars. *Artibeus jamaicensis* has molar teeth that have been modified for frugivory in such a way that the cusps and cristids are no longer distinct.

Character 47: *Cristid obliqua on lower first and second molars (m1 and m2) extends from hypoconid to middle of posterior wall of protocristid (0); or extends from hypoconid to metaconid (1).* As noted by Czaplewski (1997), the cristid obliqua on the lower first and second molars (m1 and m2) extends from hypoconid to middle of posterior wall of protocristid in most bats. This condition occurs in all species of *Pteronotus* and *Mormoops* (fig. 6) and also characterizes *Saccopteryx bilineata,* both species of *Mystacina,* and both species of *Macrotus* among the outgroups. In contrast, the cristid obliqua extends from hypoconid to the metaconid on all of the lower molars in both species of *Noctilio.*

As noted under character 46, *Artibeus jamaicensis* has molar teeth that have been modified for frugivory in such a way that the cusps and cristids are no longer distinct. To avoid scoring this condition twice in our analysis, *Artibeus jamaicensis* was scored "–" for the present character.

VOMERONASAL COMPLEX AND BRAIN

Character 48: *Vomeronasal epithelial tube absent (0); or rudimentary, lacking a neuroepithelial medial lining (1); or well-developed, neuroepithelial medial lining present (2).* Wible and Bhatnagar (1996) investigated morphology of the vomeronasal system in 51 species of bats including seven of the taxa in our study. They found that the vomeronasal epithelial tube is well developed, with a neuroepithelial medial lining, in *Pteronotus parnellii.* The vomeronasal tube is rudimentary (lacking a neuroepithelial lining) in *Mormoops megalophylla,* and the tube is entirely absent in *Pteronotus personatus.* Among the outgroups, *Noctilio leporinus* and *Mystacina tuberculata* lack a vomeronasal epithelial tube, while this structure is well developed in *Macrotus californicus* and *Artibeus jamaicensis* (Wible and Bhatnagar, 1996). This character was ordered 0 ↔ 1 ↔ 2 in our analyses to reflect the logical sequence through which a well-developed vomeronasal epithelial tube ("2") is thought to be progressively lost ("0"), or vice versa. Data were not available for *Pteronotus macleayi, P. quadridens, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii, Saccopteryx bilineata, Noctilio albiventris, Mystacina robusta,* and *Macrotus waterhousii,* which were scored "?" for this character.

Character 49: *Vomeronasal cartilage curved in cross section ("J", "C", "U", or "O" shaped) (0); or bar-shaped in cross section (1); or cartilage absent (2).* The vomeronasal cartilage lies ventrolateral to the anterior nasal septum and supports the vomeronasal epithelial tube (Wible and Bhatnagar, 1996). *Mormoops megalophylla* has a vomeronasal cartilage that is curved in cross section. In contrast, *Pteronotus parnellii* and *P. personatus* have bar-shaped vomeronasal cartilage. *Noctilio leporinus* also has bar-shaped cartilage, while *Macrotus californicus* and *Artibeus jamaicensis* have a curved vomeronasal cartilage. *Mystacina tuberculata* lacks the vomeronasal cartilage entirely (Wible and Bhatnagar, 1996). Data were not available for *Pteronotus macleayi, P. quadridens, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii, Saccopteryx bilineata, Noctilio albiventris, Mystacina robusta,* and *Macrotus waterhousii,* which were scored "?" for this character.

Character 50: *Nasopalatine duct absent (0); or present (1).* The nasopalatine duct connects the nasal cavity to the oral cavity through the incisive foramen (Wible and Bhatnagar, 1996). This duct is absent in *Pteronotus parnellii,* but is present in *P. personatus* and *Mormoops megalophylla.* Among the outgroups, the nasopalatine duct is present in *Artibeus jamaicensis* but is absent in *Macrotus californicus, Noctilio leporinus,* and *Mystacina tuberculata.* Data were not available for *Pteronotus macleayi, P. quadridens, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii, Saccopteryx bilineata, Noctilio albiventris, Mystacina robusta,* and *Macrotus waterhousii,* which were scored "?" for this character.

Character 51: *Accessory olfactory bulb absent (0); or present (1).* The accessory olfactory bulb (AOB) is an anatomically distinct portion of the forebrain that receives sensory information from the vomeronasal nerve (Wible and Bhatnagar, 1996). Although presence of an AOB is correlated with degree of development of the vomeronasal epithelial tube (see character 14), we followed Wible and Bhatnagar (1996) in treating these as separate characters pending further research on the connections of these structures. An AOB is present in *Pteronotus parnellii,* but is absent in *P. personatus* and *Mormoops megalophylla* (Wible and Bhatnagar, 1996). Among the outgroups, an AOB is present in *Artibeus jamaicensis* but is absent in *Noctilio leporinus.* Data were not available for *Pteronotus macleayi, P. quadridens, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii, Saccopteryx bilineata,* *Noctilio albiventris, Mystacina robusta,* both species of *Macrotus,* and both species of *Mystacina,* which were scored ‘‘?’’ for this character.

Character 52: *Inferior colliculi fully exposed on dorsal surface of brain, not covered by cerebellar vermis or cerebral hemispheres (0); or inferior colliculi partially exposed, medial longitudinal fissure and medial portions of colliculi covered by rostral extension of cerebellar vermis (1); or inferior colliculi not exposed, completely covered by cerebellar vermis and cerebral hemispheres (2).* As discussed and illustrated by Wetterer et al. (2000), there is significant variation among noctilionoids in the degree of exposure of the inferior colliculi on the dorsal surface of the brain. The inferior colliculi are partially exposed on the dorsal surface of the brain in *Pteronotus parnellii, P. gymnonotus,* and *Mormoops megalophylla* (Schneider, 1957, 1972; Henson, 1970; Stephan, 1977). In these forms, a rostral extension of the cerebellar vermis covers the medial portion of each colliculus and the longitudinal fissure between them, but the lateral portion of each inferior colliculus is clearly visible along the edges of the cerebellar vermis. Among the outgroups, a similar condition is seen in *Noctilio leporinus* (Baron et al., 1996). In contrast, the inferior colliculi are entirely visible (no portion is covered by the cerebellum) in *Macrotus californicus* (McDaniel, 1976). A third condition is seen in *Artibeus jamaicensis,* in which the inferior colliculi are completely covered by the cerebellar vermis and cerebral hemispheres (McDaniel, 1976; Bhatnagar and Kallen, 1974). No portion of the inferior colliculi are visible on the brain surface in dorsal view. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect the hypothesis that covering or uncovering of the inferior colliculi by the cerebellum occurs in a progressive fashion. Data were not available for *Pteronotus macleayi, P. quadridens, P. personatus, P. davyi, P. pristinus, Mormoops blainvillii, Saccopteryx bilineata, Noctilio albiventris, Mystacina robusta,* and *Macrotus waterhousii,* which were scored ‘‘?’’ for this character.

TRACHEA AND HYOID APPARATUS

The bones, cartilages, and muscles of the hyoid apparatus of bats have been discussed extensively by Sprague (1943), Griffiths (1982, 1983, 1994), Griffiths and Smith (1991) and Griffiths et al. (1992). We follow Griffiths' terminology for osteological and myological features, which are identical to those used by Sprague (1943) with two exceptions: (1) the element termed the hypohyal by Sprague (1943) is identified as the ceratohyal by Griffiths (1982, 1983, 1994), and (2) the element termed the ceratohyal by Sprague (1943) is identified as the epihyal by Griffiths (1982, 1983, 1994).

Character 53: *Tracheal rings subequal in diameter throughout length of trachea (0); or first 5–8 rings enlarged to form tracheal expansion posterior to larynx (1).* In most mammals, including most bats, the cartilaginous rings that support the trachea are of more-or-less uniform diameter throughout the length of the postlaryngeal trachea (Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992; Simmons, 1998; Simmons and Geisler, 1998). However, some bats have ‘‘tracheal expansions’’ posterior to the larynx (Griffiths, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992; Simmons, 1998; Simmons and Geisler, 1998). These expansions consist of balloonlike spaces supported by tracheal rings that have a diameter greater than that of the ‘‘normal’’ tracheal rings composing the remainder of the trachea (Griffiths, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). All extant species of *Pteronotus* and *Mormoops* have a tracheal expansion that involves the first 5–8 tracheal rings (fig. 7). No tracheal expansion is seen in any of the outgroups (fig. 7). Data were not available for *Mystacina tuberculata* and *Pteronotus pristinus,* which were scored ‘‘?’’ for this character.

Character 54: *Basihyal with entoglossal process (0); or with entoglossal process (1).* The basihyal of many bats includes a medial entoglossal process that provides an attachment site for several hyoid muscles (Griffiths 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al. 1992). An entoglossal process is present in *Pteronotus personatus* and *P. parnellii* (Griffiths, 1982, 1983). Similarly, an entoglossal process is present on the basihyal in *Noctilio leporinus, Mystacina robusta, Macrotus waterhousii,* and *Artibeus jamaicensis* (Sprague, 1943; Griffiths, 1982,

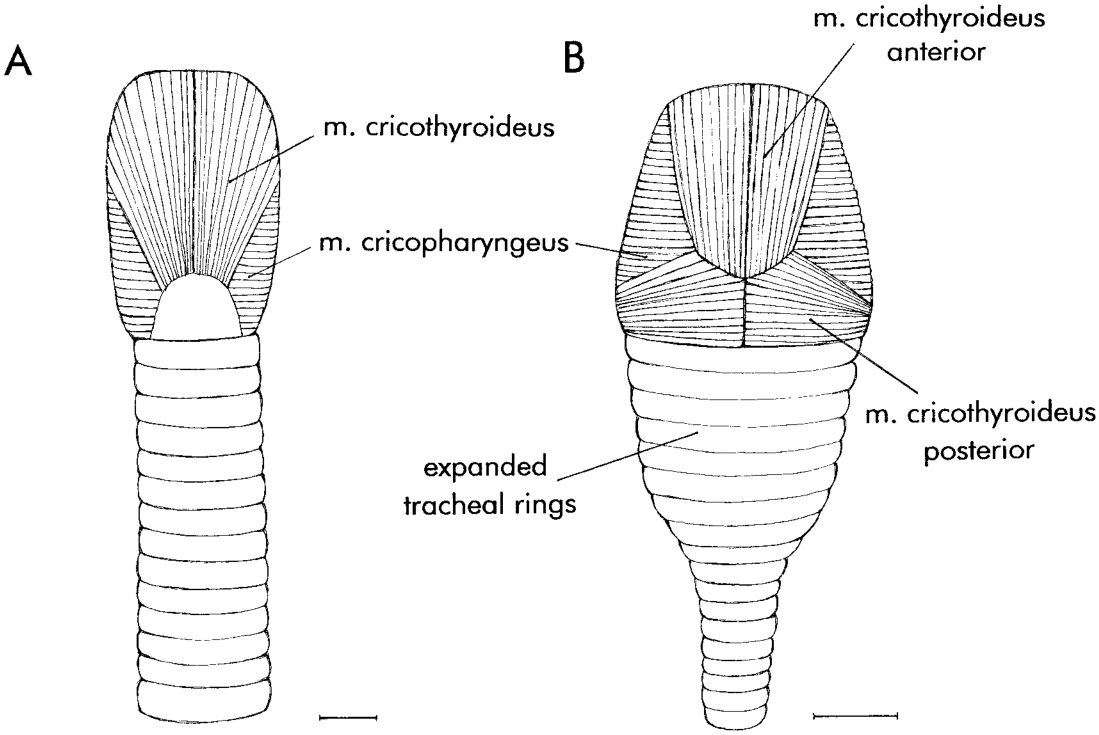

Fig. 7. Ventral views of the larynx and anterior trachea of (**A**) *Macrotus waterhousii* and (**B**) *Pteronotus davyi* (redrawn from Griffiths, 1978: figs. 2, 4). Note the expanded tracheal rings and division of m. cricothyroideus into two muscles in *P. davyi.* Scale bars = 1 mm.

personal commun.). In contrast, the basihyal element lacks an entoglossal process in *Saccopteryx bilineata* (Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 55: *Ceratohyal unreduced, approximately equal in length to epihyal (0); or ceratohyal reduced to half the length of epihyal (1); or ceratohyal reduced to tiny cartilaginous element (2).* In *Pteronotus personatus,* the ceratohyal and epihyal (sensu Griffiths) are rodlike elements that are approximately the same length (Griffiths, 1982, 1983). In contrast, the ceratohyal is reduced in length to a short, stubby element that is roughly half the length of epihyal in *Pteronotus parnellii* (Griffiths, 1983). Among the outgroups, *Saccopteryx bilineata, Mystacina robusta,* and *Macrotus waterhousii* have a ceratohyal that is roughly half the length of the epihyal (Griffiths, 1982, personal commun.). The ceratohyal is reduced to a tiny cartilaginous element in *Noctilio leporinus* (Sprague, 1943). Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that reduction or lengthening of the ceratohyal relative to the epihyal occurs in a progressive fashion. Data were not available for *Pteronotus macleayii, P. quadridens, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata, Macrotus californicus,* and *Artibeus jamaicensis,* which were scored "?" for this character.

Character 56: *M. mylohyoideus undivided sheet of muscle with no aponeurosis (0); or undivided but with anterior aponeurosis (1); or with a pronounced break, clearly divided into distinct anterior and posterior muscular parts by a fleshy aponeurosis (2).* M. mylohyoideus in bats originates from the medial surface of the mandible and inserts into the elements of the hyoid and/or other muscles of the hyoid region (Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). M. mylohyoideus consists of a undivided sheet of muscle with an aponeurotic anterior portion in *Pteronotus parnellii* (Sprague, 1943). Among the outgroups, *Saccopteryx bilineata, Noctilio leporinus,* and *Mystacina robusta* have an undivided m. mylohyoideus that lacks the anterior aponeurosis seen in *Pteronotus* (Sprague, 1943; Griffiths, personal commun.; Griffiths and Smith, 1991). In contrast, m. mylohyoideus exhibits a pronounced break and is clearly divided into distinct anterior and posterior parts by a fleshy aponeurosis in *Macrotus waterhousii* and *Artibeus jamaicensis* (Griffiths, 1982). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 57: *M. mylohyoideus inserts on basihyal, basihyal raphe, and thyrohyal (0); or on basihyal and basihyal raphe only (1).* M. mylohyoideus runs ventral to the midline strap muscles and inserts on the basihyal and basihyal raphe in *Pteronotus parnellii, Artibeus jamaicensis, Macrotus waterhousii, Mystacina robusta,* and *Noctilio leporinus* (Sprague, 1943; Griffiths, 1982, personal commun.). In contrast, m. mylohyoideus inserts on the basihyal raphe, basihyal, and also onto the thyrohyal in *Saccopteryx bilineata* (Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 58: *M. mandibulo-hyoideus absent (0); or present (1).* M. mandibulo-hyoideus, which represents the medial portion of the anterior digastric muscle, is absent in *Pteronotus parnellii, Artibeus jamaicensis, Macrotus waterhousii, Noctilio leporinus,* and *Saccopteryx bilineata* (Sprague, 1943; Griffiths, 1982, Griffiths and Smith, 1991). In contrast, a small m. mandibulo-hyoideus with a tendon is present in *Mystacina robusta* (Griffiths, personal commun.). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 59: *M. stylohyoideus present, passes superficial to digastric muscles (0); or superficial slip absent (1).* M. stylohyoideus in bats originates from the medial stylohyal and inserts into the anterior cornu of the hyoid (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). M. stylohyoideus is absent (or is reduced to a few fibers fused with m. stylopharyngeus, deep to the digastric muscles) in *Pteronotus parnellii, Artibeus jamaicensis, Macrotus waterhousii, Mystacina robusta,* and *Noctilio leporinus* (Sprague, 1943; Griffiths, 1982, 1983, personal commun.). In contrast, m. stylohyoideus is present as a distinct muscle that runs superficial to the digastric muscles in *Saccopteryx bilineata* (Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 60: *M. geniohyoideus originates by fleshy fibers directly from the bone of the mandible (0); or originates by long tendon from the mandible (1).* M. geniohyoideus originates from the inner surface of the anterior mandible and inserts into the tongue (Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). In *Pteronotus parnellii,* m. geniohyoideus originates by means of a long tendon from the mandible (Griffiths, personal commun.). A similar condition is seen in *Saccopteryx bilineata* (Griffiths and Smith, 1991). In contrast, m. geniohyoideus originates by fleshy fibers directly from the bone of the mandible in *Artibeus jamaicensis, Macrotus waterhousii, Mystacina robusta,* and *Noctilio leporinus* (Sprague, 1943; Griffiths, 1982, personal commun.). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus,* *Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 61: *Paired m. geniohyoideus muscles partially or completely fused across midline (0); or muscles not fused (1).* M. geniohyoideus is partially or completely fused with its counterpart across the midline in *Pteronotus parnellii* (Sprague, 1943). Among the outgroups, a similar condition is seen in *Artibeus jamaicensis* (Sprague, 1943). In contrast, the right and left m. geniohyoideus are not fused in *Noctilio leporinus* (Sprague, 1943). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Saccopteryx bilineata Noctilio albiventris, Mystacina tuberculata, M. robusta, Macrotus waterhousii,* and *M. californicus,* which were scored "?" for this character.

Character 62: *M. sternohyoideus origin includes entire anterodorsal surface of manubrium and medial tip of clavicle (0); or origin includes entire anterodorsal surface of manubrium but does not include clavicle (1); or origin restricted to medialmost surface manubrium in vicinity of anterior process (2).* M. sternohyoideus in bats extends between the sternum and the hyoid region (Sprague, 1943; Griffiths, 1978; 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). The origin of this muscle includes the entire anterodorsal surface of the manubrium and the medial tip of the clavicle in *Pteronotus parnellii* (Sprague, 1943). In contrast, the origin of m. sternohyoideus is restricted to the anterodorsal surface of the manubrium and the clavicular origin is lacking in *P. davyi* and *M. megalophylla* (Griffiths, 1978). Among the outgroups, the origin m. sternohyoideus includes the entire anterodorsal surface of the manubrium and the medial tip of the clavicle in *Macrotus waterhousii, Artibeus jamaicensis, Noctilio leporinus,* and *Saccopteryx bilineata* (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). *Mystacina robusta* exhibits a different condition in which the origin of this muscle is restricted to the medialmost surface of the manubrium in the vicinity of the anterior process (Griffiths, personal commun.). Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in the lateral extent of the origin of m. sternohyoideus occur in a progressive fashion. Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 63: *Midline hyoid strap musculature with m. geniohyoideus and m. hyoglossus directly attached to basihyal via fleshy fibers (0); or muscles attached indirectly to basihyal via basihyal tendon (1).* The midline hyoid strap musculature of bats includes m. geniohyoideus and m. hyoglossus (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). In many bats, these muscles are attached indirectly to the basihyal via the basihyal tendon, resulting in what has been described as a "free-floating" strap muscle condition (Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). This condition is seen in *Pteronotus parnellii, Artibeus jamaicensis, Macrotus waterhousii, Mystacina robusta,* and *Noctilio leporinus* (Sprague, 1943; Griffiths, 1978, 1982, personal commun.). In contrast, m. geniohyoideus and m. hyoglossus attach directly to the basihyal via fleshy fibers in *Saccopteryx bilineata* (Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 64: *M. styloglossus with one belly (0); or with two bellies separated by lateral portion of m. hyoglossus (1).* M. styloglossus in bats originates from the stylohyoid process and/or the adjacent surface of the skull and inserts into the tongue (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). In *Pteronotus parnellii* this muscle has two bellies that are separated by the lateral portion of m. hyoglossus (Griffiths, 1983). Among the outgroups, m. styloglossus has two bellies in *Mystacina robusta* (Griffiths, personal commun.), but only one belly in *Saccopteryx bilineata, Noctilio leporinus, Macrotus waterhousii,* and *Artibeus jamaicensis* (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 65: *Origin of m. ceratohyoideus includes ceratohyal (0); or origin does not include ceratohyal (1).* M. ceratohyoideus in bats originates from the anterior cornu of the hyoid and inserts on the thyrohyal (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). The origin of m. ceratohyoideus includes the epihyal element in all of the taxa in our study (Sprague, 1943; Griffiths, 1982, personal commun.; Griffiths and Smith, 1991). In *Pteronotus parnellii,* an adjacent portion of this muscle originates from the ceratohyal (Griffiths, 1978). Among the outgroups, a similar origin occurs in *Saccopteryx bilineata, Noctilio leporinus,* and *Artibeus jamaicensis* (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). In contrast, m. ceratohyoideus does not have a ceratohyal origin in *Macrotus waterhousii* and *Mystacina robusta* (Griffiths, 1982, personal commun.). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 66: *Origin of m. ceratohyoideus does not include stylohyal (0); or origin does include stylohyal (1).* M ceratohyoideus lacks a stylohyal origin in *Pteronotus parnellii, Saccopteryx bilineata, Noctilio leporinus, Mystacina robusta,* and *Artibeus jamaicensis* (Sprague, 1943; Griffiths, 1978, 1982, personal commun.; Griffiths and Smith, 1991). In contrast, the origin of m. ceratohyoideus does include the stylohyal element in *Macrotus waterhousii* (Griffiths, 1982). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 67: *M. sternothyroideus originates from clavicle (0); or from manubrium of sternum (1).* M. sternothyroideus in bats originates from the sternal region and inserts onto the thyroid cartilage (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). M. sternothyroideus originates from the medial tip of the clavicle (not from any part of the sternum) in *Pteronotus parnellii* (Sprague, 1943; Griffiths, 1978). A similar condition is seen in *Artibeus jamaicensis, Macrotus waterhousii, Noctilio leporinus,* and *Saccopteryx bilineata* (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). In contrast, m. sternothyroideus originates from the lateral manubrium (not the clavicle) in *Mystacina robusta* (Griffiths, personal commun.). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 68: *M. omohyoideus originates from clavicle (0); or originates from scapula (1); or muscle absent (2)* M. omohyoideus connects the shoulder girdle with the hyoid apparatus. In bats, the origin of this muscle may be from either the scapula or the clavicle (Sprague, 1943; Griffiths, 1982, 1983, 1994; Griffiths and Smith, 1991; Griffiths et al., 1992). M. omohyoideus is present and originates from the scapula in *Pteronotus parnellii* (Sprague, 1943). Among the outgroups, m. omohyoideus similarly originates from the scapula in *Noctilio leporinus* and *Artibeus jamaicensis* (Sprague, 1943). In contrast, this muscle originates from the clavicle in *Saccopteryx bilineata* (Griffiths and Smith, 1991). M. omohyoideus is absent in *Mystacina robusta* (Griffiths, personal commun.). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata, Macrotus* *californicus,* and *M. waterhousii,* which were scored "?" for this character.

Character 69: *M. sphincter colli profundus present (0); or absent (1).* M. sphincter colli profundus in bats 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). M. sphincter colli profundus is absent in *Pteronotus parnellii* (Sprague, 1943). In contrast, this muscle is present in *Macrotus waterhousii, Artibeus jamaicensis,* and *Noctilio leporinus*(Sprague, 1943; Griffiths, 1982). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. davyi, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata, M. robusta, Saccopteryx bilineata,* and *Macrotus californicus,* which were scored "?" for this character.

Character 70: *M. cricopharyngeus consists of a single large slip (0); or three or more slips (1).* M. cricopharyngeus in bats originates from the cricoid cartilage and inserts into the dorsal wall of the pharynx (Griffiths, 1978; Griffiths and Smith, 1991). M. cricopharyngeus consists of a single large slip in *Pteronotus parnellii, P. davyi,* and *Mormoops megalophylla* (Griffiths, 1978). A similar condition is seen among the outgroups in *Noctilio leporinus* and *Saccopteryx bilineata,* but m. cricopharyngeus consists of three or more slips in *Macrotus waterhousii* and *Artibeus jamaicensis* (Sprague, 1943; Griffiths, 1978, 1982; Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops megalophylla, M. blainvillii, Noctilio albiventris, Mystacina tuberculata, M. robusta,* and *Macrotus californicus,* which were scored "?" for this character.

Character 71: *M. cricothyroideus consists of a single undivided muscle sheet (0); or two muscles present, m. cricothyroideus anterior and m. cricothyroideus posterior (1).* M. cricothyroideus in most mammals consists of single muscle sheet that originates from the cricoid cartilage of the larynx and inserts on the thyroid cartilage (Griffiths, 1978). In contrast, two cricothyroid muscles are present on each side of the larynx in *Pteronotus parnellii, P. davyi,* and *Mormoops megalophylla* (fig. 7). In these bats, cricothyroideus anterior originates from the wide, calcified anterior portion of the cartilage and inserts on the ventrolateral thyroid cartilage; m. cricothyroideus posterior originates from the soft, uncalcified lateral walls of the cricoid cartilage and inserts on the medial surface of the thyroid cornu (Griffiths, 1978). Both muscles are innervated my branches of n. laryngeus cranialis, the nerve which innervates the single m. cricothyroideus found in other mammals (Griffiths, 1978). In contrast to the mormoopid condition, *Saccopteryx bilineata, Macrotus waterhousii,* and *Artibeus jamaicensis* have a m. cricothyroideus that consists of a single, undivided sheet of muscle on each side of the larynx (fig. 7; Griffiths, 1978; Griffiths and Smith, 1991). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, M. blainvillii, Noctilio albiventris, Mystacina tuberculata, M. robusta,* and *Macrotus californicus,* which were scored "?" for this character.

TONGUE

Character 72: *Horny papillae of different sizes, largest near midline (0); or all horny papillae of uniform size (1).* Terminology for describing structure and distribution of tongue papillae is complex and often confusing. We follow Park and Hall (1951), Greenbaum and Phillips (1974), Griffiths (1982), Gimenez (1993), Gimenez et al. (1996), and Wetterer et al. (2000) in recognizing groups of presumably homologous tongue papillae based on morphology of individual papillae and position of papillae on the tongue. "Horny papillae" describes a cluster of enlarged, bifid papillae located at the midline near the tip of the tongue (Park and Hall, 1951). The horny papillae are all of roughly uniform size in all extant species of *Pteronotus.* In contrast, the horny papillae are of different sizes in both species of *Mormoops.* In these species, the posteromedial horny papillae are much larger than others in the cluster. Among the outgroups, a similar condition is seen in *Mystacina tuberculata, Artibeus* *jamaicensis,* and both species of *Macrotus.* In contrast, the horny papillae are of uniform size in *Saccopteryx bilineata* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

Character 73: *Lateral circumvallate papillae absent (0); or present (1).* Paired circumvallate papillae (one lateral and one medial) are located near the proximal base of the tongue in many bats (Park and Hall, 1951; Greenbaum and Phillips, 1974; Griffiths, 1982; Gimenez, 1993; Gimenez et al, 1996; Wetterer et al., 2000). Lateral vallate papillae are present in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, they are also present in *Mystacina tuberculata, Artibeus jamaicensis,* and both species of *Macrotus.* In contrast, lateral vallate papillae are absent in *Saccopteryx bilineata* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

Character 74: *Distal tips of medial-posterior mechanical papillae directed toward midline of tongue (0); or directed toward pharyngeal region (1); or directed toward anterior tip of tongue (2); or papillae basin-shaped with no clear inclination (3).* The medial-posterior mechanical papillae are those papillae located anterior to the circumvallate papillae in roughly the middle one-third of the tongue (Gimenez, 1993; Wetterer et al., 2000). Most medial-posterior mechanical papillae are thick, fleshy, and terminate in one or more rounded points (Wetterer et al., 2000). The distal tips of the medial posterior mechanical papillae are directed toward the pharyngeal region in both species of *Mormoops.* In contrast, these papillae are somewhat basin-shaped and show no clear inclination in any direction in extant species of *Pteronotus.* Among the outgroups, the tips of the medial-posterior mechanical papillae are directed toward the pharyngeal region in *Mystacina tuberculata* and both species of *Macrotus,* and in the opposite direction (toward the tip of the tongue) in *Artibeus jamaicensis* (Wetterer et al., 2000). A fourth condition, in which the medial posterior mechanical papillae are directed medially toward the midline of the tongue, is seen in *Saccopteryx bilineata* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

Character 75: *Basketlike medial-posterior mechanical papillae present (0); or absent (1).* "Basketlike papillae" are medial-posterior mechanical papillae that have central concavities and fleshy, cylindrical bases (Park and Hall, 1951; Wetterer et al., 2000). The rim of each basketlike papilla is uneven and may be adorned with from 1 to 10 pointed projections that form a fringe along the basket edge (Park and Hall, 1951; Wetterer et al., 2000). Basketlike papillae are present in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, they are also present in *Saccopteryx bilineata, Mystacina tuberculata,* and both species of *Macrotus.* In contrast, basketlike papillae are absent in both species of *Noctilio* and *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

Character 76: *Pharyngeal region of tongue totally bare, papillae absent along lateral edges (0); or with medial bare patch, papillae present along lateral edges (1).* The pharyngeal region of the tongue is defined as that part of the tongue that lies proximal to the circumvallate papillae (Sontag, 1925). The pharyngeal region of the tongue is completely bare of papillae in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Saccopteryx bilineata.* In contrast, only the medial portion of the pharyngeal region of the tongue is bare in both species of *Noctilio, Mystacina tuberculata,* both species of *Macrotus, Artibeus jamaicensis,* and both species of *Noctilio.* In these forms, mechanical papillae are present along the lateral edges of the tongue in the pharyngeal region. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

FACE, EARS, AND VIBRISSAE

Character 77: *Internal labial papillae absent (0); or present (1).* Internal labial papillae are small, fleshy projections that occur in patches inside the lips and cheeks of some bats (Silva-Taboada and Pine, 1969; Wetterer et al., 2000). Internal labial papillae are absent in all extant species of *Pteronotus* and *Mormoops*. A similar condition is seen among in *Saccopteryx bilineata, Mystacina tuberculata,* both species of *Noctilio,* and both species of *Macrotus.* In contrast, internal labial papillae are present along the lingual edge of the lower lip in *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" in our analysis.

Character 78: *Cheek pouches absent (0); or present (1).* Cheek pouches are epithelium-lined pockets in the cheeks that open inside the mouth. These are absent in most bats, including all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, cheek pouches are absent in *Saccopteryx bilineata,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus,* but are present in both species of *Noctilio.* The cheek pouches in *Noctilio* are formed by posterolateral expansion of m. buccinator, with the resulting pocket extending posteriorly to cover a large section of m. masseter (Murray and Strickler, 1975). These pouches are apparently used primarily for food storage during foraging (Murray and Strickler, 1975). Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 79: *Lower lip and chin without multiple dermal papillae (0); or with multiple dermal papillae (1).* Multiple dermal papillae are present on the lower lip and chin in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, similar multiple papillae are present in *Artibeus jamaicensis.* Multiple papillae are absent in both species of *Macrotus,* both species of *Noctilio,* both species of *Mystacina,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 80: *Lower lip of small or moderate size, dorsoventral height less than height of nostrils (0); or lip large and platelike, dorsoventral height equal or greater than the nostrils (1).* Both species of *Mormoops* have a lower lip of moderate size, characterized by dorsoventral height less than the height of the nostril. In contrast, all extant species of *Pteronotus* have a large, platelike lower lip that has a height equal to or greater than height of the nostrils. The outgroups all have a small or moderate lower lip whose dorsoventral height is less than the height of the nostrils. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 81: *Lower lip without small horseshoe-shaped pad at midline (0); or pad present (1).* The lower lip of both species of *Mormoops* is characterized by a horseshoe-shaped dermal pad that is centered above the chin and extends perpendicular to the nostrils when the mouth is closed. This horseshoe-shaped pad is tiny; that is, the height of the pad is approximately one-fourth the width of the lower lip. A similar horseshoe-shaped lip pad is absent in extant members of the genus *Pteronotus* and all of the outgroups. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 82: *No transverse flap below lower lip (0); or one transverse flap present below lower lip (1); or two transverse rows of flaps present (2).* Most bats do not have transverse flaps below the lower lip. In contrast, extant species of *Pteronotus* and *Mormoops* have one or more transverse flaps of skin that project from the lower lip. Extant species of *Pteronotus* have a single transverse flap on the lower lip, while both species of *Mormoops* have two rows of transverse flaps. Among the outgroups, both species of *Noctilio* have two rows of transverse flaps below the lower lip. *Saccopteryx bilineata,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus* lack flaps transverse flaps entirely. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 83: *Anterior edge of labio-nasal region protrudes anteriorly beyond edge of lower lip, muzzle appears pointed (0); or edge does not protrude anteriorly, muzzle appears blunt (1).* The anterior edge of the labio-nasal region does not protrude anteriorly beyond the edge of the lower lip in any extant species of *Pteronotus* or *Mormoops.* As a result, the muzzle in these taxa appears to be relatively blunt (i.e., not pointed). A similar condition is seen among the outgroups in *Artibeus jamaicensis* and both species of *Macrotus.* In contrast, the anterior edge of the labio-nasal region does protrude anteriorly beyond edge of lower lip in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina,* giving the muzzle a pointed appearance. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 84: *Nostrils tubelike, openings face slightly laterally and are not adjacent (0); or nostrils open directly adjacent to each other and face anteriorly (1).* The nostrils open adjacent to each other and face anteriorly in all extant species of *Pteronotus.* In contrast, both species of *Mormoops* have tubelike nostrils that open slightly laterally. *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina* also have tubelike nostrils, while both species of *Macrotus* and *Artibeus jamaicensis* have nostrils that are adjacent and open anteriorly. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 85: *Narial pad with v-shaped notch present between nostrils (0); or narial pad with narrow, papillated vertical ridge between nostrils (1); or narial pad with wide, smooth-sided vertical ridge between nostrils (2); or narial pad flat, with no notch or ridge between nostrils (3).*

The narial pad in bats is highly variable in form and ornamentation. There is no notch or ridge between the nostrils on the narial pad in *Pteronotus quadridens, P. personatus, P. davyi,* and *P. gymnonotus.* In these forms, the narial pad is flat and unornamented. Another condition is seen in *Pteronotus parnellii* and *P. macleayii,* which have a v-shaped notch in the narial pad between the nostrils. In contrast, both species of *Mormoops* have a narrow, papillated vertical ridge between the nostrils. This structure is quite prominent and has smooth lateral edges, but the anterior face of the ridge gives the impression of being composed of a series of indistinct dermal papillae. Among the outgroups, both species of *Mystacina* have a flat narial pad, while there is a notch in the narial pad between the nostrils in *Saccopteryx bilineata* and both species of *Noctilio. Artibeus jamaicensis* and both species of *Macrotus* and have a ridge between the nostrils, but this ridge is wider and flatter than that seen in *Mormoops* and it lacks a papillated surface, instead having a smooth anterior face. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 86: *Anterodorsal edge of narial pad unadorned, without ridge of skin or noseleaf (0); or with papillated ridge of skin present (1); or with noseleaf present.* Both species of *Mormoops* lack a noseleaf or ridge of skin on the anterodorsal edge of the narial pad. In contrast, all extant species of *Pteronotus* have a ridge of skin on the anterodorsal edge of the narial pad. This ridge has an uneven, papillated dorsal edge that gives the impression of being composed of a series of indistinct dermal papillae. Among the outgroups, the anterodorsal edge of the narial pad is unadorned and lacks a ridge or noseleaf in *Saccopteryx bilineata,* both species of *Mystacina,* and both species of *Noctilio. Artibeus jamaicensis* and both species of *Macrotus* have a well-developed noseleaf that projects from the anterodorsal edge of the narial pad. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect the hypothesis that presence of a ridge of skin on the anterodorsal narial pad represents a necessary intermediate condition between presence of a noseleaf and absence of all structures on the edge of the narial pad. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 87: *No dermal papillae on dorsal surface of nostril (0); or one dermal papillae present on dorsal surface of each nostril (1).* All extant members of the genus *Pteronotus* lack dermal papillae on the dorsal surface of the nostrils. In contrast, both species of *Mormoops* have one dermal papilla on the dorsal surface of each nostril. This papilla is not located on the anterodorsal edge of the narial pad (as are the ridges and noseleaves described in character 86), but the papilla is instead set back approximately midway along the tubelike dorsal aspect of the nostril. All of the outgroups lack dermal papillae on the dorsal surface of the nostrils. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 88: *No dermal projection present lateral to the nostrils (0); or dermal pro-*

jection present, rounded distally, lateral side of projection continuous with the lip (1); or projection triangular and pointed distally, lateral side not continuous with lip (2). Most bats lack dermal projections lateral to the nostrils, but such structures are present in all extant members of *Pteronotus* and *Mormoops.* In these taxa, a single dermal projection of variable form extends anterodorsally from a position lateral to the nostrils. This projection is rounded distally in *Pteronotus parnellii* and *P. personatus,* and its lateral side is continuous with the lip. This arrangement makes the upper lip appear swollen on either side of the narial pad. In contrast, the dermal projection in both species of *Mormoops, P. davyi, P. gymnonotus, P. macleayii,* and *P. quadridens* is triangular in shape and tapers distally to a point. The projections have well-defined lateral sides that are not continuous with the lip. As a result, the lip does not appear swollen in these taxa. Dermal projections lateral to the nostrils are absent in all of the outgroups. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 89: *No dermal tubercle on midline of muzzle posterodorsal to nostrils (0); or prominent dermal tubercle present (1). Pteronotus macleayii, P. quadridens, P. davyi,* and *P. gymnonotus* lack a conspicuous dermal tubercle on the dorsal aspect of the muzzle. In contrast, *Pteronotus parnellii, P. personatus,* and both members of the genus *Mormoops* have a prominent dermal tubercle located on the midline of the muzzle above the nostrils. The dermal tubercle is absent in all of the outgroups. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 90: *Interauricular band absent (0); or prominent interauricular band present (1).* Both species of *Mormoops* have a prominent, v-shaped interauricular band of skin that connects the pinnae across the top of the head. In contrast, all extant species of *Pteronotus* lack an interauricular band. In these taxa, a very low, inconspicuous ridge may be seen to extend medially from the base of each pinna. The degree of prominence of these ridges varies among individuals and perhaps among species (see Smith, 1972), and appears to be significantly affected by preservation in museum specimens (e.g., degree of desiccation in fluid-preserved material). Our investigations led us to conclude that these ridges represent skin-covered auricular muscles. Due to difficulties associated with interpreting the degree of development of these low ridges in preserved specimens (and our inability to clearly identify any taxa that lack them entirely), we chose not to score their presence as a separate character state. Among the outgroups, *Artibeus jamaicensis,* both species of *Noctilio,* both species of *Mystacina,* and *Saccopteryx bilineata* lack an interauricular band, while a prominent interauricular band is present in both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 91: *Pinna not funnel-shaped, base of pinna located well above the level of the mouth (0); or pinna funnel-shaped, base of pinna extends to level or below the level of the mouth (1).* All extant species of *Pteronotus* and *Mormoops* have funnel-shaped pinnae in which the base of the pinnae extends below the level of the mouth. Among the outgroups, both species of *Noctilio* have funnel-shaped pinnae, while the other species do not. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Our scoring of this feature agrees with the descriptions of Smith (1972) and Hall (1981), but differs from some literature accounts which have contrasted the "funnel-shaped" ears in *Mormoops* with "narrow" ears in *Pteronotus* (e.g., Koopman, 1984). The latter distinction refers to the form of the distal pinna, which we treat as a separate character below.

Character 92: *Distal pinna lanceolate, tapers to blunt point (0); or distal pinna squared, pinna height relatively uniform across the entire width of the pinna (1); or distal pinna rounded (2).* All extant species of *Pteronotus* have pinnae that are lanceolate and taper to a blunt point. In contrast, both species of *Mormoops* have pinnae that are squared distally with an edge that is of equal height across most of the breadth of the pinna. Among the outgroups, the distal edge of the pinnae is rounded in both species of *Macrotus* and lancolate in *Artibeus jamaicensis,* both species of *Noctilio,* both species of *Mystacina,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 93: *Lateral edge of distal pinna smooth (0); or serrated (1).* As in most bats, *Pteronotus parnellii, P. davyi, P. gymnonotus,* and both species of *Mormoops* have pinnae with smooth edges. In contrast, *P. macleayii, P. quadridens,* and *P. personatus* have several serrations on the lateral edge of the distal pinna. The outgroups all have pinnae with a smooth lateral edge. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 94: *Distal tip of tragus rounded (0); or tapers to point (1); or bifurcate (2).* The distal tip of the tragus is rounded in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in *Saccopteryx bilineata.* In contrast, the distal tragus tapers to a point in *Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Mystacina.* An alternative state is seen in both species of *Noctilio,* which have a tragus with a bifurcate tip. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 95: *Tragus thin, of uniform thickness throughout (0); or tragus with distinctly thickened area at base (1); or tragus with a thickened central area that extends from midpoint to tip of tragus; lateral and medial edges of tragus thin (2); or tragus uniformly thick (3).* All extant members of the genus *Pteronotus* have a tragus that is relatively thin and of roughly uniform thickness throughout. In contrast, the base of the tragus is thickened in both species of *Mormoops.* Among the outgroups, *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina* have a uniformly thin tragus that resembles that of *Pteronotus.* Both species of *Macrotus* are characterized by a tragus with a vertically oriented, thickened central area that extends up the posterior face of the tragus from its midpoint to its tip. The lateral and medial edges of tragus are thin in this taxon. In contrast, *Artibeus jamaicensis* has a tragus that is uniformly thick. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 96: *Secondary fold on tragus absent (0); or fold present, smaller than body of tragus (1); or fold present, equal to or larger than body of tragus (2).* The secondary fold is a distally rounded fold of skin that extends from the ventromedial aspect of the tragus, lying roughly at a right angle to the main longitudinal axis of that structure (Smith, 1972). The thickness of the fold is related to its size; when the fold is approximately the same size as the body of the tragus, it is approximately the same thickness, while smaller folds are relatively thinner. Most bats lack a secondary fold on the tragus. In contrast, all extant species of the genus *Pteronotus* have a secondary fold that is smaller than the body of the tragus, while both species of *Mormoops* have a secondary fold that is equal to or larger than the body of the tragus. The outgroups all lack a secondary fold. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect the logical sequence of transformation from absence of a secondary fold ("0") to a secondary fold equal to or larger than the body of the tragus ("2"). Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 97: *Two interramal vibrissae present (0); or one interramal vibrissa present (1); or interramal vibrissae absent (2).* Vibrissae ("whiskers") occur in several locations on the face of most mammals including bats. Interramal vibrissae are found under the chin between the rami of the lower jaws, posterior to the mandibular symphysis (Pocock, 1914; Brown, 1971). All extant species of *Pteronotus* are characterized by presence of a single interramal vibrissa. In contrast, both species of *Mormoops* have two interramal vibrissae. Among the outgroups, *Saccopteryx bilineata,* both species of *Noctilio,* and *Artibeus jamaicensis* have two interramal vibrissae. *Mystacina tuberculata* has one interramal vibrissa, and both species of *Macrotus* lack interramal vibrissae entirely. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that the number of vibrissae in the interramal cluster changes by sequential addition (or loss) of individual vibrissae. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 98: *Interramal tubercle well developed (0); or absent (1).* The interramal tubercle (= ventral sinus-hair tubercle of Dalquest and Werner, 1954) is a swelling associated with the interramal vibrissae (see character 97) in some bats. The interramal tubercle is well developed (width greater than one-half the distance between the mandibular rami) in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, this tubercle is similarly well developed in *Saccopteryx bilineata, Mystacina tuberculata,* both species of *Noctilio,* and both species of *Macrotus.* In contrast, the interramal tubercle is absent in *Artibeus.* The interramal vibrissae in this taxon originate from a tiny pitlike perforation in the skin. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 99: *Two genal vibrissae present on each cheek (0); or one genal vibrissa present on each cheek (1); or genal vibrissae absent (2).* Genal vibrissae are located on the cheek ventral to the eye and subocular vibrissae (Pocock, 1914; Brown, 1971). Both species of *Mormoops* lack genal vibrissae entirely. In contrast, all extant species of *Pteronotus* have a single genal vibrissa on each cheek. Among the outgroups, *Saccopteryx bilineata,* both species of *Noctilio,* and *Mystacina tuberculata* have a pair of genal vibrissae on each cheek. Both species of *Macrotus* have a single genal vibrissa on each cheek, and *Artibeus jamaicensis* lacks genal vibrissae entirely. Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that the number of vibrissae in the genal cluster changes by sequential addition (or loss) of individual vibrissae. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 100: *Superciliary vibrissae present (0); or absent (1).* Superciliary (= supraorbital) vibrissae are located dorsal to the eye in many mammals (Pocock, 1914; Brown, 1971). All extant species of *Pteronotus* and *Mormoops* lack superciliary vibrissae. A similar condition is seen among the outgroups in *Mystacina tuberculata* and *Artibeus jamaicensis.* In contrast, a single superciliary vibrissa is present above each eye in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Macrotus.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 101: *Vibrissae on face posterior and lateral to narial pad arranged in a single vertical column (0); or arranged in two roughly parallel vertical columns (1).* Wetterer et al. (2000) noted that there is variation in the arrangement of the vibrissae on the face posterior and lateral to the narial pad. There are two vertical columns of vibrissae in this region in all extant species of *Pteronotus* and *Mormoops*: an anteromedial column located adjacent to the narial pad, and a posterolateral column located posterior to the anteromedial column. These columns are roughly parallel in orientation, and each contains at least two vibrissae. A similar arrangement is seen among the outgroups in both species of *Macrotus* and both species of *Noctilio.* In contrast, the posterolateral column is absent in *Saccopteryx bilineata, Mystacina tuberculata,* and *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 102: *Four vibrissae present in anteromedial column (0); or three vibrissae (1); or two vibrissae (2).* The anteromedial column of vibrissae on the face (which is located adjacent to the narial pad; see character 101) includes only two vibrissae in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition occurs in both species of *Noctilio.* In contrast, this column consists of four vibrissae in *Saccopteryx bilineata,* and three vibrissae in *Mystacina tuberculata,* both species of *Macrotus,* and *Artibeus jamaicensis.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that the number of vibrissae in this column changes by sequential addition (or loss) of individual vibrissae. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Pelage and Patagia

Character 103: *Facial stripes absent (0); or paired stripes present (1).* Facial stripes are absent in all extant species of *Pteronotus* and *Mormoops*. The fur appears to be of uniform color between the narial pad and ears in these taxa. A similar condition is seen among the outgroups in *Saccopteryx bilineata,* both species of *Noctilio,* both species of *Mystacina,* and both species of *Macrotus*. In contrast, *Artibeus* is characterized by a pair of pale facial stripes that run from the anterior rostrum to near the base of the ear. These stripes are roughly parallel, with one dorsal to and one ventral to the eye. Brightness of these stripes may vary among individuals and populations, but facial stripes are present in all adults. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 104: *Dorsal fur unicolored (0); or polymorphic, either unicolored or bicolored (1); or bicolored (2); or polymorphic, either bicolored or tricolored (3); or tricolored (4); or with four bands of color (5).* The fur of adult bats consists of hairs that may have alternating bands of dark and pale colors along the shaft. Hairs may be unicolored (of uniform color along the shaft), bicolored (two bands of color), tricolored (three bands), or have four distinct bands of color. Because the pattern of color banding may vary over the surface of the body (e.g., fur over the rump may have fewer color bands than does fur over the shoulders), in the present analysis we restricted our comparisons to the dorsal fur on the upper back over the scapulae. *Pteronotus davyi* and *P. gymnonotus* have unicolored fur in this region. In contrast, *P. personatus* and *Mormoops blainvillii* have bicolored dorsal fur, and *Pteronotus macleayii* and *P. quadridens* have tricolored fur. *P. parnellii* is polymorphic for this feature, with either bicolored or tricolored fur (see discussion in Smith, 1972). *Mormoops megalophylla* has fur with four color bands. Among the outgroups, *Saccopteryx bilineata* and both species of *Noctilio* have unicolored fur, and bicolored fur occurs in *Mystacina tuberculata* (Dwyer, 1960) and both species of *Macrotus*. *Artibeus jamaicensis* is polymorphic, with either unicolored or bicolored dorsal fur. Transformations in this character were ordered 0 ↔ 1 ↔ 2 ↔ 3 ↔ 4 ↔ 5 to accommodate observed fur-color polymorphisms (which we regard as intermediate conditions between fixed states) and to reflect our hypothesis that changes in fur banding patterns occur in a sequential fashion by adding and subtracting individual color bands. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored "?" for this character.

Character 105: *Ventral fur unicolored (0); or polymorphic, either unicolored or bicolored (1); or bicolored (2); or polymorphic, either bicolored or tricolored (3).* The ventral fur of bats exhibits a range of banding patterns similar to those seen in the dorsal fur. While dorsal and ventral banding patterns in some species are identical, they are often different so we scored these as separate characters. *Pteronotus gymnonotus* has unicolored ventral fur, while *P. parnellii, P. macleayii, P. quadridens, P. personatus, P. davyi,* and *Mormoops blainvillii* have bicolored ventral fur. *Mormoops megalophylla* is polymorphic for this feature, with either bicolored or tricolored ventral fur. Among the outgroups, both species of *Noctilio* have unicolored ventral fur, while bicolored fur occurs in *Saccopteryx bilineata, Mystacina tuberculata* (Dwyer, 1960), and both species of *Macrotus*. *Artibeus jamaicensis* is polymorphic, with either unicolored or bicolored ventral fur. As with character 104, transformations in patterns of ventral fur banding were ordered 0 ↔ 1 ↔ 2 ↔ 3 to accommodate observed fur-color polymorphisms (which we regard as intermediate conditions between fixed states) and to reflect our hypothesis that changes in fur banding patterns occur in a sequential fashion by adding and subtracting individual color bands. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored "?" for this character.

Character 106: *Dorsal fur short, 4–7 mm in length (0); or long, 8–10 mm in length (1).* All extant species of *Pteronotus* have relatively short hair, approximately 4–7 mm in length. In contrast, both species of *Mormoops* have longer hair, approximately 8–10 mm in length. Among the outgroups, both species of *Macrotus, Artibeus jamaicensis,* and *Mystacina tuberculata* and have long hair, while *Saccopteryx bilineata* and both species of *Noctilio* have short hair. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 107: *Dorsal stripes always absent (0); pair of pale dorsal stripes always present (1); or single pale middorsal stripe often present (2).* Contrasting dorsal stripes are present in some species of bats. All extant species of *Pteronotus* and *Mormoops* lack dorsal stripes. A similar condition is seen in both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* A single, dark middorsal stripe is often (but not always) present in both species of *Noctilio. Saccopteryx bilineata* is characterized by a pair of pale dorsal stripes. Data were not available for *Pteronotus pristinus,* which was scored ‘‘?’’ for this character.

Character 108: *Underhair and overhair not differentiated in dorsal pelage (0); or clearly differentiated (1).* Benedict (1957) described hair structure in 165 genera and 243 species representing most families of bats. He found that many bats have clearly differentiated overhair and underhair in the dorsal pelage. In these forms, individual overhairs are straighter (and may thus appear longer) and are coarser than individual underhairs. In contrast, all hairs in the dorsal pelage are of similar waviness and coarseness in species that lack differentiated overhair and underhair (Benedict, 1957). All extant species of *Pteronotus* and *Mormoops* have clearly differentiated underhair and overhair (Benedict, 1957). Among the outgroups, clearly differentiated overhair and underhair is seen only in species of *Noctilio* (Benedict, 1957). The dorsal pelage in *Saccopteryx bilineata, Mystacina tuberculata,* both species of *Macrotus,* and *Artibeus jamaicensis* is not differentiated into overhair and underhair (Benedict, 1957). Due to the variation among outgroups, the primitive condition could not be determined a priori. Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ‘‘?’’ for this character.

Character 109: *Midshaft scales on dorsal hair filaments all entire coronal (0); or scales exhibit a continuous range of variation from entire coronal to repand coronal (1); or alternating entire coronal and hastate coronal scales (2); or all scales dentate coronal (3); or alternating dentate coronal and hastate coronal scales (4); or all scales denticulate coronal (5).* Benedict (1957) described the structure of hair filaments and scales in many bats including all of the taxa in our study. Benedict (1957) recognized two principal types of hair scales: ‘‘imbricate,’’ which overlap laterally, and ‘‘coronal,’’ which encircle the filament like a ring. Seen in lateral view, coronal scales on a hair filament look like cups. ‘‘Entire’’ coronal scales are rings with uniformly level edges, so that each individual scale appears approximately the same height in all views (Benedict, 1957). ‘‘Repand’’ coronal scales are the same shape as entire coronal scales, but have a slightly uneven edge on one side, a feature not seen in entire coronal scales (Benedict, 1957). ‘‘Hastate’’ coronal scales are characterized by having one part of the distal ring edge that is significantly lower than the rest of the edge (Benedict, 1957). The low point on any given scale is not necessarily in the same position as the low points on the surrounding scales. ‘‘Dentate’’ and ‘‘denticulate’’ coronal scales are characterized by presence of serrations along the edges of the scale (Benedict, 1957). These serrations are small and close together in denticulate scales, and are somewhat larger and farther apart in dentate scales (Benedict, 1957). Among mormoopids, *Pteronotus davyi* and *P. gymnonotus* have entire coronal scales (Benedict, 1957). *P. parnellii* has scales that exhibit a continuous range of variation from entire coronal to repand coronal (Benedict, 1957). Denticulate coronal scales are present in *Pteronotus macleayii, P. quadridens,* and *P. personatus* (Benedict, 1957). Dentate coronal scales are present in both species of *Mormoops* (Benedict, 1957). Among the outgroups, *Saccopteryx bilineata* is characterized by denticulate coronal hair scales, and both species of *Noctilio* have scales that range from entire coronal to repand coronal (Benedict, 1957). *Mystacina tuberculata* has only entire coronal scales, and both species of *Macrotus* have alternating entire coronal and hastate coronal scales (Benedict, 1957).

Artibeus jamaicensis has alternating dentate coronal and hastate coronal scales (Benedict, 1957). Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ''?'' for this character.

Character 110: *Midshaft scales on dorsal hair filaments divaricate from hair shaft (0); or scales divergent from hair shaft (1); or appressed to hair shaft (2).* Variation occurs in the degree to which hair scales diverge from the shaft of the filament (Benedict, 1957). Scales that are ''appressed'' lie flat against the filament so that the sides of the scale are parallel with the long axis of the hair shaft, forming a smooth surface with adjacent scales up and down the shaft (Benedict, 1957). In contrast, ''divergent scales'' are flared distally. The proximal portion of each scale has sides that are parallel with each other and the long axis of the hair shaft, much like those of appressed scales, but the distal portion of each scale flares outward away from the axis of the shaft (Benedict, 1957). ''Divaricate'' scales flare even more markedly, with no portion of the side of the scale remaining parallel to the long axis of the hair shaft (Benedict, 1957). Each divaricate scale increases in diameter continuously from its proximal border (where it is narrowest) to its distal edge (where it is widest). All extant species of *Pteronotus* have midshaft hair scales that are appressed to the hair shaft (Benedict, 1957). In contrast, both species of *Mormoops* have divergent hair scales (Benedict, 1957). Among the outgroups, *Mystacina tuberculata* and both species of *Noctilio* have appressed hair scales, *Artibeus jamaicensis* has divergent scales, and *Saccopteryx bilineata* and both species of *Macrotus* have divaricate scales (Benedict, 1957). Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect the seemingly progressive nature of degree of hair scale divergence from the shaft (see discussion in Benedict, 1957). Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* which were scored ''?'' for this character.

Character 111: *Plagiopatagium attaches to the side of the body, dorsal fur exposed on back between right and left wing membranes (0); or plagiopatagium attaches at the mid-dorsal line, right and left membranes meet over spine and cover dorsal fur entirely (1).* The wing membrane of bats are divided into the plagiopatagium (which extends between the body and the fifth digit), dactylopatagium (which extends between the digits), propatagium (which extends between the upper arm and forearm anterior to the elbow), and uropatagium (which extends between the hindlimbs). The medial attachment of the plagiopatagium is on the side of the body in most bats, with dorsal fur exposed between the right and left membranes. This condition is seen in *Pteronotus parnellii, P. macleayii, P. quadridens, P. personatus,* and both species of *Mormoops.* In contrast, the plagiopatagium attaches at the mid-dorsal line in *Pteronotus davyi* and *P. gymnonotus.* The right and left membranes meet over the spine and cover the dorsal fur, which is present but not visible in dorsal view. This arrangement of the patagia gives these bats a ''naked-backed'' appearance. Functional morphology of this trait has not yet been fully investigated, and implications for flight mechanics remain unknown. Bonaccorso et al. (1992) studied thermoregulation in *P. davyi* and concluded that the arrangement of the wing membranes does not appear to strongly increase the rate of heat loss at relatively cool ambient temperatures, but may help facilitate heat dissipation at high ambient temperatures. The plagiopatagium attaches on the side of the body in all of the outgroups. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 112: *Wings folded by flexing proximal phalanx of digits III and IV posteriorly (toward dorsal surface of wing), distal phalanges folded anteriorly (toward underside of wing) (0); or distal phalanges of digits III and IV folded anteriorly, proximal phalanges not folded (1); or all phalanges in digits III, IV, and V folded anteriorly toward the underside of the wing (0).* Bats at rest fold their wings in a variety of different ways that are constrained by anatomy of the joints in the hand and fingers. Every species is characterized by a single folding pattern, and wings cannot be forced into different patterns without damaging the joints, ligaments, and muscles of the limb. All extant species of *Pteronotus* and *Mormoops* fold their wings by flexing all phalanges in digits III, IV, and V anteriorly toward the underside of the wing. A similar pattern is seen among the outgroups in both species of *Macrotus* and *Artibeus jamaicensis.* In contrast, both species of *Noctilio* fold their wings by flexing the distal phalanges of digits III and IV anteriorly without folding the proximal phalanges of those digits. A third pattern is seen in both species of *Mystacina* and *Saccopteryx bilineata,* which flex the proximal phalanx of digits III and IV posteriorly while folding the distal phalanges anteriorly. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 113: *Antebrachial wing sac absent (0); or present (1).* All extant species of *Pteronotus* and *Mormoops* lack an antebrachial wing sac. The same is true of both species of *Noctilio,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus.* In contrast, *Saccopteryx bilineata* is characterized by presence of an antebrachial wing sac. This structure, which is sexually dimorphic (larger in males), is located in the propatagium anterior to the elbow. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 114: *Uropatagium broad (0); or with V-shaped cutout (1); or rudimentary (2).* The extent of the uropatagium varies significantly both among and within families of bats (Schutt and Simmons, 1998). In all extant species of *Pteronotus* and *Mormoops* the uropatagium is broad, completely spanning the area between the hindlegs from the rear end of the body to the calcars. The trailing edge of the membrane extends between the tips of the calcars and is not marked by a notchlike cutout. A similar condition is seen among the outgroups in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Macrotus.* In contrast, the uropatagium in *Artibeus jamaicensis* is less extensive and is characterized by a large, anteriorly directed V-shaped notch in the trailing edge between the calcars. Even more extreme reduction in the uropatagium is seen in both species of *Mystacina,* which have a rudimentary uropatagium that is restricted to narrow strips of membranes along the legs. Transformations in this character were ordered $0 \leftrightarrow 1 \leftrightarrow 2$ to reflect our hypothesis that changes in the extent of the uropatagium occur in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 115: *Uropatagium attaches to calcar, propatagium does not (0); or both plagiopatagium and uropatagium attach to calcar (1).* In most bats, including all of the outgroups in our study, the uropatagium attaches to the calcar while the plagiopatagium attaches directly to the lateral surface of the leg and sometimes the foot. In contrast, both the plagiopatagium and the uropatagium attach to the calcar in all extant species of *Pteronotus* and *Mormoops.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 116: *Calcar not bound to tibia (0); or caudal half of calcar bound to tibia, calcar restricted to position parallel to tibia (1). Pteronotus davyi, P. gymnonotus,* and both species of *Mormoops* have a calcar that is not bound to the tibia. In contrast, the caudal half of the calcar in *P. parnellii, P. macleayii, P. quadridens,* and *P. personatus* is bound to the tibia by connective tissue, thus restricting the possible range of motion of the calcar. All of the outgroups have a calcar that is not bound to the tibia. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

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Character 117: *Ventral processes of sixth cervical vertebra (C6) approximately the same width as those of C2–C5 (0); or C6 ventral processes enlarged to twice the width of C2–C5 ventral processes (1).* The cervical vertebrae of most bats are characterized by a pair of longitudinal, ventrally directed processes located on the centrum. The ventral processes of the sixth cervical vertebra (C6) are twice as wide as those of the other cervical vertebrae in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Mystacina robusta* and both species of *Noctilio.* In contrast, the ventral processes of C6 are similar in width to the ventral processes of C2–C5 in *Saccopteryx bilineata,* both species of *Macrotus,* and *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus* and *Mystacina tuber-*

culata, which were scored ‘‘?’’ for this character.

Character 118: *Seventh cervical vertebra (C7) not fused to first thoracic vertebrae (T1) (0); or C7 fused to T1 (1).* The centrum, zygapophyses, and transverse processes of the seventh cervical vertebra (C7) are partially to fully fused with those first thoracic vertebrae (T1) in members of several bat families (Simmons and Geisler, 1998). C7 and T1 are fused in both species of *Mormoops.* In contrast, there is no evidence of C7/T1 fusion in any extant species of *Pteronotus.* C7 and T1 are not fused in any of the outgroups. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 119: *Thirteen thoracic vertebrae present (0); or 12 present (1); or 11 present (2).* All bats have between 11 and 14 thoracic (rib-bearing) vertebrae (Walton and Walton, 1970). Both species of *Mormoops* have 13 thoracic vertebrae, while all extant species of *Pteronotus* have only 12 thoracic vertebrae. Among the outgroups, both species of *Noctilio* have 11 thoracic vertebrae, *Saccopteryx bilineata* and both species of *Macrotus* have 12, and *Mystacina robusta* and *Artibeus jamaicensis* have 13 thoracic vertebrae. This character was ordered 0 ↔ 1 ↔ 2 to reflect the presumed progressive sequence of changes in vertebral counts. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 120: *Neural spines absent from first four thoracic vertebrae (T1–T4) (0); or spines present on T1–T4 (1).* Neural spines are absent from the first four thoracic vertebrae (T1–T4) in both species of *Mormoops.* In contrast, neural spines are present on T1–T4 in all extant species of *Pteronotus.* Among the outgroups, *Artibeus jamaicensis* has neural spines on T1–T4, while neural spines are absent from these vertebrae in both species of *Macrotus, Saccopteryx bilineata,* both species of *Noctilio,* and *Mystacina robusta.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 121: *Height of neural spines decreases from T1–T4 (0); or neural spines on T1–T4 of equal height (1).* The relative height of the neural spines on T1–T4 varies among bats that have neural spines on these vertebrae. The height of the neural spines progressively decreases from T1 through T4 in *Pteronotus macleayii, P. quadridens, P. davyi, P. gymnonotus,* and *P. personatus.* In contrast, the neural spines on T1–T4 are of equal height in *P. parnellii.* Among the outgroups, the height of the neural spines decreases from T1 through T4 in *Artibeus jamaicensis.* The remaining outgroups, which lack neural spines on T1–T4 (see character 120), and were scored ‘‘–’’ for this character. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 122: *Ridges on ventral surface of T4 absent (0); or two parallel ridges present on ventral surface of T4 (1).* A pair of parallel ridges are present on the ventral surface of T4 in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Macrotus californicus* and *Mystacina robusta.* In contrast, these ridges are absent in *Macrotus waterhousii, Artibeus jamaicensis,* both species of *Noctilio,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 123: *Neural spines absent from posterior thoracic vertebrae (T8 and above) (0); or spines present on posterior thoracic vertebrae (1).* Neural spines are absent from the posterior thoracic vertebrae (T8 and above) in *Pteronotus personatus, P. quadridens,* and both species of *Mormoops.* In contrast, neural spines are present on the posterior thoracic vertebrae in *Pteronotus parnellii, P. macleayii, P. gymnonotus,* and *P. davyi.* Among the outgroups, *Artibeus jamaicensis* and *Mystacina robusta* each have neural spines on the posterior thoracic vertebrae. Neural spines are absent from the posterior thoracic vertebrae in both species of *Macrotus, Saccopteryx bilineata,* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ‘‘?’’ for this character.

Character 124: *No fusion between posterior thoracic and anterior lumbar vertebrae (0); or two posteriormost thoracic ver-*

tebrae, L1, and L2 fused (1). Vertebral fusion is absent in the lower back of most bats. However, the last two thoracic and first two lumbar vertebrae fused together in all extant species of *Pteronotus* and both species of *Mormoops.* These vertebrae are not fused in any of the outgroups. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 125: *Ridges on ventral surface of third lumbar vertebra (L3) absent (0); or two parallel ridges present on ventral surface of L3 (1).* The third lumbar vertebra (L3) lacks ridges on its ventral surface in *Mormoops megalophylla.* In contrast, *M. blainvillii* and all extant species of *Pteronotus* have two parallel ridges present in this location. Among the outgroups, *Saccopteryx bilineata, Mystacina robusta,* and *Artibeus jamaicensis* exhibit similar ventral ridges on L3, but both species of *Macrotus* and both species of *Noctilio* lack these ridges. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 126: *Ridges on ventral surface of fourth and fifth lumbar vertebra (L4 and L5) absent (0); or two parallel ridges present on ventral surface of both L4 and L5 (1).* The fourth and fifth lumbar vertebrae (L4 and L5) lack ridges on the ventral surface in both species of *Mormoops.* In contrast, all extant species of *Pteronotus* have two parallel ventral ridges on the ventral surface of both L4 and L5. Among the outgroups, paired ventral ridges are present on L4 and L5 in *Artibeus jamaicensis,* both species of *Macrotus,* and *Mystacina robusta,* but are absent in *Saccopteryx bilineata* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 127: *Anterior face of manubrium small (0); or broad, defined by elevated ridges (1).* The anterior face of the manubrium of the sternum is the site of origin for the anterior division of m. pectoralis (Vaughan, 1959, 1970b; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The anterior face of the manubrium is relatively small and poorly defined in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in both species of *Macrotus,* both species of *Noctilio,* and *Saccopteryx bilineata.* In contrast, the anterior face of the manubrium is a broad, triangular surface that extends onto the lateral processes and is defined by three elevated ridges in *Artibeus jamaicensis* and *Mystacina robusta.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 128: *Angle between axis of ventral process of manubrium and body of manubrium approximately 90° (0); or greater than 90° (1).* The ventral process of the manubrium is a bony projection that provides the anterior attachment point for a series of ligamentous sheets that run down the midline of the sternum. Together with these ligamentous sheets, the ventral process of the manubrium forms the origin for the m. pectoralis complex, which provides most of the power for the downstroke during flight (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The angle between the axis of the ventral process (defined as the long axis of the thickened base and central body of the process) and the body of the manubrium varies among bats (Simmons and Geisler, 1998). All extant species of *Pteronotus* have an angle of more than 90° between the axis of ventral process and the body of the manubrium. As a result, the ventral process appears to project anteroventrally in these species. In contrast, the angle between the axis of the ventral process and the body of the manubrium is approximately 90° and the ventral process projects ventrally in both species of *Mormoops.* Among the outgroups, the angle between the axis of the ventral process and the body of the manubrium is approximately 90° in *Saccopteryx bilineata,* both species of *Macrotus,* and *Artibeus jamaicensis,* but this angle is greater than 90° in both species of *Noctilio* and *Mystacina robusta.* The primitive condition could not be determined a priori due to variation among the outgroups. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 129: *Distal tip of ventral process of manubrium laterally compressed, keel-like (0); or blunt and rounded (1).* The distal tip of the ventral process of the manubrium is laterally compressed and keel-like in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, a laterally compressed, keel-like ventral process is also seen in *Artibeus jamaicensis,* both species of *Macrotus,* both species of *Noctilio,* and *Saccopteryx bilineata.* In contrast, the distal tip of the ventral process is blunt and rounded in *Mystacina robusta.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 130: *Length of manubrium approximately equal to maximum width (0); or less than maximum width (1).* The length of the manubrium posterior to the lateral processes is less than the transverse width of this portion of the manubrium in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Mystacina robusta,* both species of *Noctilio, Artibeus jamaicensis,* and both species of *Macrotus.* In contrast, the length of the manubrium posterior to the lateral processes is approximately equal to its width in *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 131: *Mesosternum with medial keel low or absent (0); or with high keel (1).* The mesosternum has a low median keel, or lacks the keel altogether, in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in *Artibeus jamaicensis, Mystacina robusta,* both species of *Noctilio,* and *Saccopteryx bilineata.* In contrast, a high keel (maximum keel height > width of mesosternum) is present in both species of *Macrotus.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 132: *Xiphisternum with prominent median keel (0); or without keel (1).* The xiphisternum has a prominent median keel in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, this condition is a also seen in *Mystacina robusta* and *Saccopteryx bilineata.* In contrast, the xiphisternum lacks a keel in both species of *Noctilio,* both species of *Macrotus,* and *Artibeus* jamaicensis. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 133: *Second costal cartilage articulates with sternum at manubrium-mesosternum joint (0); or second rib articulates with manubrium only (1).* The second costal cartilage articulates with the sternum at the manubrium-mesosternum joint in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in *Saccopteryx bilineata* and *Mystacina robusta.* In contrast, the second rib articulates with the manubrium and there is no contact between the rib (or costal cartilage) and the mesosternum in *Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 134: *Mesosternum articulates with five costal cartilages posterior to second rib (0); or with six costal cartilages (1).* Variable numbers of costal cartilages connect the mesosternum with the bony ribs in bats (Simmons and Geisler, 1998). On each side of the body, the mesosternum articulates with six costal cartilages posterior to the second rib in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen in both species of *Macrotus.* In contrast, the mesosternum articulates with only five costal cartilages posterior to the second rib in *Artibeus jamaicensis,* both species of *Noctilio, Mystacina robusta,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 135: *Ribs with no anterior laminae (0); or narrow anterior laminae present (1); or wide anterior laminae present (2).* Anterior laminae are thin plates of bone that run along the leading edges of ribs anterior to the main body of the rib (Simmons and Geisler, 1998). These structures, which are often nearly transparent, appear to provide an increased area for muscle attachment (Simmons and Geisler, 1998). The anterior laminae are relatively narrow (lamina width less than that of the main body of the rib) in *Pteronotus macleayii, P. quadridens, P. personatus, P. davyi, P. gymnonotus,* and *Mormoops blainvillii.* In contrast, the anterior laminae are relatively wide (lamina width equal to or greater than that of the main body of the rib) in *Pteronotus parnellii* and *Mormoops megalophylla.* Among the outgroups, wide anterior laminae are seen in both species of *Noctilio,* narrow laminae occur in *Saccopteryx bilineata,* and anterior laminae are entirely absent in *Mystacina robusta,* both species of *Macrotus,* and *Artibeus jamaicensis.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in size of the laminae occur in a progressive fashion. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 136: *Ribs with no posterior laminae (0); or narrow posterior laminae present (1); or wide posterior laminae present (2).* Posterior laminae are thin plates of bone that run along the leading edges of ribs posterior to the main body of the rib (Simmons and Geisler, 1998). Wide posterior laminae (lamina width equal to or greater than that of the main body of the rib) are seen in all extant species of *Pteronotus* and *Mormoops megalophylla.* In contrast, the posterior laminae are relatively narrow (lamina width less than that of the main body of the rib) in *Mormoops blainvillii.* Narrow posterior laminae are present among the outgroups in *Saccopteryx bilineata,* both species of *Noctilio, Artibeus jamaicensis,* and both species of *Macrotus.* The posterior laminae are entirely absent in *Mystacina robusta.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in size of the laminae occur in a progressive fashion. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 137: *Distal clavicle articulates with or lies in contact with coracoid process (0); or clavicle suspended by ligaments between acromion and coracoid processes of scapula (1).* The distal (dorsolateral) clavicle articulates with the scapula in the region between the tip of the acromion process and the base of the coracoid process. The articulation can be accomplished in several different ways, depending on whether the clavicle is associated principally with the acromion, principally with the coracoid, or is suspended between these two processes by a series of ligaments (Strickler, 1978; Simmons and Geisler, 1998). The clavicle articulates with or lies in contact with the coracoid process in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in *Saccopteryx bilineata,* both species of *Macrotus,* and *Artibeus jamaicensis.* In contrast, the clavicle is suspended by ligaments between the acromion and coracoid processes in both species of *Noctilio* and *Mystacina robusta.* The primitive condition could not be determined a priori due to variation among the outgroups. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 138: *Pit for attachment of clavicular ligament absent from scapula (0); or present anterior and medial to glenoid fossa (1).* The clavicular ligament extends between the base of the coracoid process and the clavicle (Strickler, 1978). A distinct pit for the attachment of the clavicular ligament is present anterior and medial to the glenoid fossa in all extant species of *Pteronotus* and *Mormoops.* In contrast, there is no evidence of a pit for attachment of the clavicular ligament in any of the outgroups. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 139: *Coracoid process elongate, tip approximately the same width as the shaft (0); or coracoid process elongate, tip distinctly flared (1); or coracoid process reduced to a small triangular process (2).* The coracoid process in most bats is an elongate bar of bone with a distinct shaft and tip (Simmons and Geisler, 1998). The tip of the coracoid process is blunt and is approximately the same width as the shaft of the coracoid in both species of *Mormoops.* In contrast, the tip of the coracoid process is distinctly flared (wider than the shaft) in all extant species of *Pteronotus.* Among the outgroups, *Artibeus jamaicensis* and both species of *Macrotus* have a coracoid process with a flared tip, while the tip of the coracoid in *Saccopteryx bilineata* and both species of *Noctilio* is not flared. In contrast to these conditions (all of which involve a relatively elongate coracoid), the coracoid process of both species of *Mystacina* is reduced to a small triangular process that lacks a definable shaft. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 140: *Distal acromion process without anteromedial projection (0); or with triangular anteromedial projection that does not contact rim of scapula (1); with elongate projection that extends anteriorly and medially to fuse with anteromedial rim of scapula (2).* A triangular anteromedial projection is present just ventral and medial to the tip of the acromion process in all extant species of *Pteronotus* and *Mormoops.* This projection is directed toward (but does not contact) the anteromedial rim of the scapula. Among the outgroups, a similar process is present in both species of *Noctilio.* A different condition is seen in both species of *Mystacina,* which have a very long anterior projection that extends anteriorly and medially to contact and fuse with the anteromedial rim of the scapula medial to the suprascapular notch. The resulting bar of bone forms a complete bridge over the supraspinous fossa. A secondary sutural contact is also present between the lateral surface of the bony bridge and the tip of the suprascapular process (see character 142), enclosing the suprascapular notch to form a small canal. In contrast, the distal acromion process lacks an anterior projection entirely in *Saccopteryx bilineata, Artibeus jamaicensis,* and both species of *Macrotus.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in extent of the anterior projection of the acromion process occur in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 141: *Distal acromion process without posterolateral projection (0); or with triangular posterolateral projection (1).* A triangular projection from the distal acromion process is present in *Pteronotus davyi* and *P. gymnonotus.* In contrast, this process is absent in *Pteronotus personatus, P. quadridens, P. macleayii, P. parnellii,* and both species of *Mormoops.* Among the outgroups, a posterolateral projection is present in both species of *Noctilio,* but this projection is absent in *Saccopteryx bilineata,* both species of *Mystacina,* both species of *Macrotus,* and *Artibeus* jamaicensis. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 142: *Suprascapular process absent (0); or present (1).* The suprascapular process is a projection that extends medially and somewhat anteriorly from the anterolateral border of the suprascapular notch at the base of the coracoid process, just medial to the anterior edge of the glenoid fossa and just anterior to the pit for the clavicular ligament (in those forms that have this pit; Simmons and Geisler, 1998). A suprascapular process is present in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, this process is similarly present in both species of *Mystacina* and both species of *Noctilio.* In contrast, the suprascapular process is absent in *Saccopteryx bilineata, Artibeus jamaicensis,* and both species of *Macrotus.* The primitive condition could not be determined a priori due to variation among the outgroups. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 143: *Dorsal articular facet on scapula absent (0); or dorsal articular facet faces dorsolaterally, consists of a small groove on the anteromedial rim of the glenoid fossa (1); or faces dorsolaterally, consists of oval facet on anteromedial rim of glenoid fossa (2); or faces dorsally, consists of a large, flat facet clearly separated from the glenoid fossa (3).* A secondary articulation between the humerus and scapula occurs in many bats when the humerus is abducted and the trochiter (= greater tuberosity) contacts a dorsal articular facet on the scapula (Vaughan, 1959, 1970b; Hill, 1974; Strickler, 1978; Altenbach and Hermanson, 1987; Schlosser-Strum and Schleimann, 1995; Simmons and Geisler, 1998). The dorsal articular facet faces dorsolaterally and consists of an oval facet on the anteromedial rim of the glenoid fossa in all extant species of *Pteronotus* and *Mormoops.* The same condition is seen in *Artibeus jamaicensis* and both species of *Macrotus.* Dorsal articular facet in *Saccopteryx bilineata* also faces dorsolaterally, but consists of a small groove on the anteromedial rim of the glenoid fossa. In contrast, the dorsal articular facet faces dorsally and consists of a large, flat facet clearly separated from the glenoid fossa in both species of *Mystacina.* Both species of *Noctilio* lack a dorsal articular facet. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 144: *Infraspinous fossa of scapula wide, maximum width greater than 50% of maximum length (0); or infraspinous fossa narrow, maximum width less than or equal to 50% of maximum length (1).* The infraspinous fossa, located on the dorsal aspect of the scapula posterolateral to the scapular spine, is the site of origin for m. infraspinatus and m. teres major, muscles that act to flex, rotate, and (in the case of m. infraspinatus) abduct the humerus (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The infraspinous fossa is relatively wide in *Mormoops blainvillii* and all extant species of *Pteronotus.* In these taxa, the maximum width of the fossa is greater than 50% of its maximum length. In contrast, *M. megalophylla* has an infraspinous fossa that is relatively narrow, with maximum width less than 50% of length. Among the outgroups, a wide infraspinous fossa is seen in *Saccopteryx bilineata, Mystacina robusta,* both species of *Noctilio,* and *Artibeus jamaicensis.* Both species of *Macrotus* have a narrow infraspinous fossa. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 145: *Intermediate infraspinous facet narrower than posterolateral facet (0); or facets subequal (1).* The infraspinous fossa of the scapula has three facets in all of the taxa in our study[2]: an anteromedial facet (located adjacent to the spine of the scapula), an intermediate facet, and a posterolateral facet (adjacent to the axillary border of the scapula). The intermediate infraspinous facet is narrower than the posterolateral facet in *Pteronotus personatus* and *Mormoops megalophylla.* In contrast, these facets are subequal in *Pteronotus parnellii, P. macleayi, P. quadridens, P. davyi, P. gymnonotus,* and *Mormoops blainvillii.* A similar condition is seen in *Saccopteryx bilineata.* The intermediate facet is narrower than the posterolateral facet in both species of *Noctilio,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 146: *Axillary border of scapula flat, level within dorsoventral plane (0); or axillary border curved in dorsoventral plane, concave ventrally (1).* The axillary border of the scapula is that edge which faces the axilla or armpit. The axillary border of the scapula is flat and lies level within the dorsoventral plane in all extant species of *Pteronotus.* In contrast, both species of *Mormoops* have a scapula with a curved axillary border that is concave ventrally. All of the outgroups have a scapula with a flat axillary border that is level within the dorsoventral plane. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 147: *Anterior portion of axillary border of scapula rounded (0); or flattened (1).* The anterior portion of the axillary border of the scapula is flattened to form a sharp edge in both species of *Mormoops* and all extant species of *Pteronotus.* The anterior portion is similarly flattened in both species of *Macrotus.* In contrast, the anterior portion is rounded with no definitive sharp edge in *Artibeus jamaicensis,* both species of *Noctilio, Mystacina robusta,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 148: *Head of humerus round in outline in medial view (0); or oval or elliptical (1).* The head of the humerus, which articulates with the glenoid fossa on the scapula, is oval or elliptical in outline when seen in medial view[3] in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in both species *Noctilio.* In contrast, *Saccopteryx bilineata,* both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis* have a humeral head that is round in outline in when seen in medial view. Data were not available

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[2] Our observations differ from those of Simmons and Geisler (1998), who erroneously reported that *Mystacina* has only two facets in the infraspinous fossa.

[3] Determination of anatomical directions for bat limb elements is complicated by the unusual orientation of the limbs during flight. In specifying "medial view" in this character, we have followed Smith (1972) and assumed that the wing is folded and the humerus adducted.

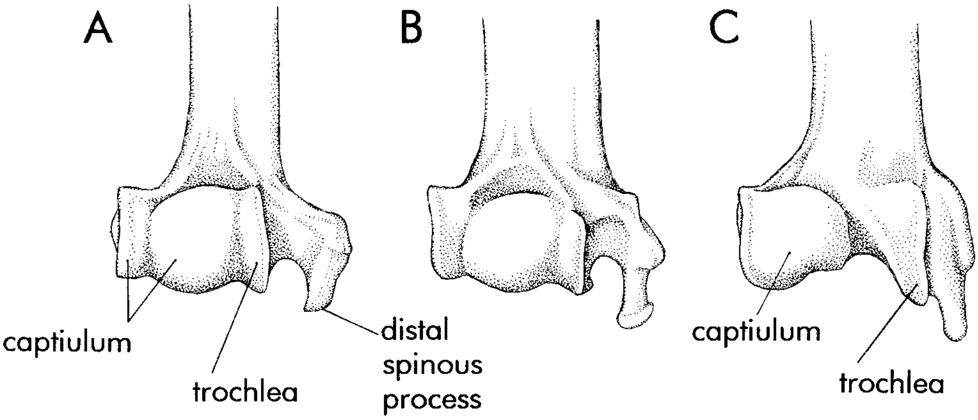

Fig. 8. Anterior views of the distal end of the humerus of (**A**) *Pteronotus parnellii,* (**B**) *Pteronotus personatus,* and (**C**) *Mormoops megalophylla* (redrawn from Vaughan and Bateman, 1970: fig. 5). Note the differences between *Pteronotus* and *Mormoops* in degree of development of the capitulum, location of the trochlea relative the shaft, and presence/absence of a deep groove between the trochlea and distal spinous process.

for *Pteronotus pristinus,* which was scored "?" for this character.

Character 149: *Trochiter extends proximally just to the level of the proximal edge of the humeral head (0); or extends proximally well beyond the level of the head (1).* The trochiter (= greater tuberosity) of the humerus in bats extends varying distances proximally relative to the head of the humerus (Simmons and Geisler, 1998). The trochiter extends proximally just to the level of the proximal edge of the head in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in *Saccopteryx bilineata* and both species of *Noctilio.* In contrast, the trochiter extends proximally well beyond the level of the humeral head in both species of *Mystacina,* both species of *Macrotus,* and *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 150: *Humerus with distal articular facets in line with shaft, not displaced laterally (0); or articular facets displaced laterally from line of shaft (1).* The articular facets of the distal humerus include the trochlea, capitulum, and lateral surface of the capitulum (fig. 8; Vaughan and Bateman, 1970; Smith, 1972). The articular surfaces lie adjacent to one another and are distinguished on the basis of a series of ridges and grooves. The combined articular surface typically forms a spool-shaped structure, although the form of this structure varies considerably among and within families of bats (Smith, 1972; Simmons and Geisler, 1998). The structural unit formed by the three distal articular surfaces lies in line with the shaft of the humerus in both species of *Mormoops.* The medial edge of the trochlea minimally lies in line with the medial surface of the humeral shaft (e.g., fig. 8C) and may extend medially beyond this level. In contrast, the distal articular facet complex is laterally displaced from the line of the humeral shaft in all extant species of *Pteronotus.* In these forms, the edge of the trochlea does not extend medially as far as the medial surface of the humeral shaft (fig. 8A, B). Among the outgroups, the distal articular facets are in line with the shaft in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina.* These facets are displaced laterally in *Artibeus jamaicensis* and both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 151: *Central surface of capitulum of humerus not reduced, height equal to that of trochlea (0); or central surface of the capitulum reduced, height less than that of trochlea (1).* The capitulum on the distal end of the humerus is an articular surface comprised of two ridges with a groove between them (fig. 8). The central surface of the capitulum is more medial of these ridges, lying adjacent to a third ridge, the trochlea (Vaughan, 1959; Vaughan and Bateman, 1970; Smith, 1972). The central capitulum surface is the same height as the trochlea in all extant species of *Pteronotus* (fig. 8). In contrast, both species of *Mormoops* have a reduced central capitulum whose height is less than that of the trochlea (fig. 8). All of the outgroups all have an unreduced central capitulum surface that is equal in height to the trochlea. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 152: *Distal spinous process of humerus separated from trochlea by deep notch (0); or process located directly adjacent to trochlea, notch absent (1).* The distal spinous process of the humerus is a bony projection that extends distally from the medial epicondyle of the humerus in bats (fig. 8; Vaughan and Bateman, 1970; Smith, 1972). This process is the site of origin for m. flexor carpi ulnaris, which is a flexor of the fifth metacarpal (Vaughan, 1959; Vaughan and Bateman, 1970; Smith, 1972). The distal spinous process is separated from the trochlea by a deep notch in all extant species of *Pteronotus* (fig. 8). In contrast, this process lies directly adjacent to the trochlea (and the notch is absent) in both species of *Mormoops* (fig. 8). Among the outgroups, the distal spinous process is separated from the trochlea by a deep notch in *Saccopteryx bilineata,* both species of *Noctilio, Artibeus jamaicensis,* and both species of *Macrotus.* Both species of *Mystacina* have the distal spinous process located adjacent to the trochlea and lack the notch. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 153: *Height of distal spinous process of humerus less than or equal to height of trochlea (0); or greater than height of trochlea (1).* The height of the distal spinous process of the humerus (measured along the long axis of the spinous process, which runs roughly parallel to the long axis of the humeral shaft) is greater than the height of the trochlea in all extant species of *Pteronotus* and *Mormoops* (fig. 8). A similar condition is seen in *Mystacina tuberculata.* In contrast, the height of the distal spinous process is less than or equal to the height of the trochlea in *Mystacina robusta, Artibeus jamaicensis,* both species of *Macrotus,* both species of *Noctilio,* and *Saccopteryx bilineata.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 154: *Distal spinous process of humerus with no ventral projection (0); or with ventral projection (1).* The distal spinous process of the humerus lacks a ventral projection in *Mormoops megalophylla* and all extant species of *Pteronotus* (fig. 8). In contrast, the distal spinous process of *Mormoops blainvillii* is characterized by a ventral projection that extends perpendicular to the shaft of the humerus. A similar ventral projection is seen in both species of *Macrotus. Artibeus jamaicensis,* both species of *Mystacina,* both species of *Noctilio,* and *Saccopteryx bilineata* lack a ventral projection from the distal spinous process. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 155: *Olecranon process of ulna well developed, extends proximally beyond end of radius (0); or reduced, does not extend beyond end of the radius (1).* Both species of *Mormoops* have a well-developed olecranon process that extends proximally beyond the end of the radius. In contrast, all extant species of *Pteronotus* have a reduced olecranon process that does not extend beyond the end of the radius. The olecranon process is well -developed in all of the outgroup species. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 156: *Pisiform bone rodlike, of uniform width throughout (0); or dumbbell-shaped, enlarged at both ends (1).* The pisiform bone in bats lies on the ventral surface of the carpus where it is attached by fascia to the trapezium and the metacarpal of the fifth digit (Vaughan, 1959). All extant species of *Pteronotus* have a pisiform bone that is rodlike in form, roughly uniform in width throughout its length. In contrast, both species of *Mormoops* have a pisiform that is enlarged at both ends, giving it a dumbbell shape. A similar condition is seen among the outgroups in *Saccopteryx* bilineata and both species of *Macrotus. Mystacina robusta,* both species of *Noctilio,* and *Artibeus* jamaicensis have rodlike pisiform bone. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 157: *Metacarpal formula 5<4<3 (0); or 5<4=3 (1); or 3=4=5 (2); or 3=5<4 (3); or 3<4<5 (4).* Metacarpal formulae in bats describe the relative length of the third, fourth and fifth digits. For example, the formula 5<4<3 describes the condition in which the third metacarpal is longest and the fifth is shortest. All extant species of *Pteronotus* have a metacarpal formula of 5<4<3, where metacarpals 4 and 3 are only slightly longer than 5. In contrast, both species of *Mormoops* have a metacarpal formula of 5<4=3, where metacarpals 4 and 3 are much longer than 5. Among the outgroups, both species of *Noctilio* have a metacarpal formula of 3=5<4, where metacarpal 4 is only slightly longer than 3 and 5. Both species of *Macrotus* have a metacarpal formula of 3<4<5, where each is only slightly longer than the preceding, and both species of *Mystacina* have a formula of 5<4=3, with the relative lengths similar to *Mormoops. Saccopteryx bilineata* has a metacarpal formula of 5<4<3, similar to *Pteronotus.* All three metacarpals are subequal in length (3=4=5) in *Artibeus jamaicensis.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 158: *Wing digit I with first phalanx longer than metacarpal (0); or first phalanx and metacarpal subequal in length (1).* Phalanges in both the manus and pes are numbered from proximal to distal. The first phalanx of each wing digit is identified by its articulation with the distal end of the corresponding metacarpal. The first phalanx in wing digit I is longer than the metacarpal of that digit in both species of *Mormoops.* In contrast, all extant species of *Pteronotus* are characterized by a wing digit I in which the first phalanx and metacarpal are subequal in length. These elements are similarly subequal in length in both species of *Noctilio* and *Artibeus jamaicensis,* but the first phalanx is markedly longer than the metacarpal in *Saccopteryx bilineata,* both species of *Mystacina,* and both species of *Macrotus.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 159: *Wing digit II with long, ossified first phalanx (0); or first phalanx absent or tiny and unossified (1).* The first phalanx in wing digit II is relatively long (length more than four times the diameter of the shaft) and ossified in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in both species of *Noctilio, Artibeus jamaicensis,* and both species of *Macrotus.* In contrast, the first phalanx is apparently absent in both species of *Mystacina* and *Saccopteryx bilineata.* It is possible that a minute, unossified remnant of the first phalanx remains in these forms, but we were unable to detect it in standard museum preparations. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 160: *Wing digit III with long, completely ossified third phalanx (0); or with long third phalanx that is ossified at the base and unossified at the tip (1); or with long but completely unossified third phalanx (2); or with minute, unossified third phalanx (3).* The third phalanx of wing digit III is long (length more than four times the diameter of the shaft) and fully ossified in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in *Artibeus jamaicensis* and both species of *Macrotus.* In contrast, the third phalanx is long but is ossified only at its base in both species of *Mystacina,* and is completely unossified in both species of *Noctilio.* The third phalanx of wing digit III is a very tiny, unossified element in *Saccopteryx bilineata.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 ↔ 3 to reflect our hypothesis that changes in phalangeal proportions and degree of ossification occur in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 161: *Second phalanx of wing digit IV longer than first phalanx (0); or phalanges subequal in length (1); or second phalanx shorter than first phalanx (2).* The second phalanx of wing digit IV is longer than the first phalanx of that digit in all extant species of *Pteronotus.* In contrast, the first and second phalanges of digit IV are subequal in both species of *Mormoops*. Among the outgroups, the second phalanx is longer than the first phalanx in *Artibeus jamaicensis,* both species of *Noctilio,* and *Saccopteryx bilineata.* These phalanges are subequal in both species of *Mystacina* and the second phalanx is shorter than the first phalanx in *Macrotus.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that changes in phalangeal proportions occur in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 162: *Sacral vertebrae do not contact ischium (0); or posterior sacral vertebrae fused with posterior ischium (1).* The principal articulation between the pelvis and the vertebral column in bats occurs between the sacral vertebrae and the ilium. In some species, a secondary articulation occurs between the posterior sacral vertebrae and the posterior portion of the ischium. This secondary articulation is separated from the main iliosacral articulation by a gap across which there is no contact between the pelvis and vertebral column. A secondary articulation in which the posterior sacral vertebrae are fused with the ischium occurs in all extant species of *Pteronotus.* In contrast, the ischium does not contact the vertebral column in either species of *Mormoops.* A similar condition is seen among the outgroups in *Saccopteryx bilineata, Mystacina robusta, Artibeus jamaicensis,* and both species of *Macrotus.* Both species of *Noctilio* are characterized by presence of contact and fusion between the ischium and posterior sacral vertebrae. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored "?" for this character.

Character 163: *Dorsomedial edge of ascending process of ilium not upturned, does not extend dorsally beyond the level of the iliosacral articulation, iliac fossa not large or well defined (0); or dorsomedial edge upturned, flares dorsally above the level of the iliosacral articulation, iliac fossa large and well defined (1).* The dorsomedial edge of the ascending process of the ilium in bats forms the origin for m. tensor fascia latae and m. gluteus medius (Vaughan, 1959, 1970b). The dorsomedial edge of the ascending process of ilium is strongly upturned and flares dorsally above the level of the iliosacral articulation in *Mormoops megalophylla, Pteronotus parnellii,* and *P. personatus.* In these forms, the iliac fossa is large and well defined. In contrast, the dorsomedial edge of the ascending process of ilium is not upturned, does not extend dorsally beyond the level of the iliosacral articulation, and the iliac fossa is not large or well defined in *Mormoops blainvillii, Pteronotus macleayii, P. quadridens, P. davyi,* and *P. gymnonotus.* This condition (low ascending process and small, poorly defined iliac fossa) is also seen in *Saccopteryx bilineata,* both species of *Mystacina, Artibeus jamaicensis,* and both species of *Macrotus.* An upturned, flared ascending process with a large, well-defined iliac fossa occurs in both species of *Noctilio.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 164: *Ischium with ischial tuberosity small or absent, does not project dorsally beyond level of ramus (0); or with large ischial tuberosity that projects dorsally from posterior horizontal ramus (1).* The dorsal ischial tuberosity is a projection that extends dorsally and/or posteromedially from the posterior end of the ischium, originating from the "corner" of the pelvis at the junction between the horizontal and vertical rami of the ischium (Vaughan, 1959, 1970a; Simmons and Geisler, 1998). Two muscles may originate from the ischial tuberosity: m. semitendinosus and m. semimembranosus, both of which act to extend the femur and flex the lower leg (Vaughan, 1959, 1970b). A large, dorsally projecting ischial tuberosity is absent in all extant species of *Pteronotus* and *Mormoops.* A similar condition is seen among the outgroups in *Artibeus jamaicensis,* both species of *Macrotus,* and *Saccopteryx bilineata.* In contrast, a large, dorsally projecting ischial tuberosity is present in both species of *Mystacina* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 165: *Length of pubic spine less than or equal to one-third the length of the ilium (0); or equal to or greater than one-half the length of the ilium (1).* The pubic spine is an elongate projection from the anteroventral corner of the pubis (Vaughan, 1959; Walton and Walton, 1970). Presence of a pubic spine is a synapomorphy of bats (Simmons, 1994; Simmons and Geisler, 1998). All extant species of *Pteronotus* and *Mormoops* have a pubic spine whose length is equal to or greater than one-half the length of the ilium. A similar condition is seen among the outgroups in *Artibeus jamaicensis* and both species of *Macrotus.* In contrast, the length of the pubic spine in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina* is less than or equal to one-third the length of the ilium. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 166: *Articulation between right and left pubes in male restricted to a small area, consists of an ossified interpubic ligament (0); or articulation between pubes broad, consists of a symphysis that is long in an anteroposterior dimension (1).* The contact between the right and left pubes in male bats varies considerably. *Pteronotus parnellii, P. personatus, P. davyi, P. gymnonotus,* and both species of *Mormoops* are characterized by a broad symphysis that is long in an anteroposterior dimension. A similar condition is seen in *Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Noctilio.* In contrast, the articulation between the pubes in male *Saccopteryx bilineata* is restricted to a small area. The right and left pubes are not in direct contact, but are joined by a short, ossified interpubic ligament. Data were not available for *Pteronotus pristinus, P. macleayii, P. quadridens,* and both species of *Mystacina,* which were scored "?" for this character.

Character 167: *Greater and lesser trochanters of femur well developed, flanges extend well beyond sides of femoral head (0); or both trochanters reduced, flanges do not extend beyond sides of femoral head (1).* Most bats have well-developed greater and lesser trochanters on the femur. In these forms, the flanges that comprise the trochanters extend well beyond the sides of the head of the femur. In contrast, all extant species of *Pteronotus* and *Mormoops* have reduced trochanters that are more closely appressed to the shaft and do not extend much beyond the sides of the femoral head. All of the outgroups have well-developed trochanters that extend far beyond the femoral head. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 168: *Femur with well-developed ridge present distal to lesser trochanter (0); or with well-developed ridge present dorsal to lesser trochanter (1); or ridge absent from femoral shaft (1).* A high, longitudinally oriented ridge is present on the shaft of the femur distal to the lesser trochanter in all extant species of *Mormoops* and *Pteronotus.* Among the outgroups, a similar ridge is present in *Artibeus jamaicensis* and *Saccopteryx bilineata.* In contrast, both species of *Macrotus* have a ridge present dorsal to the lesser trochanter. The femoral shaft lacks any such ridges in both species of *Noctilio* and both species of *Mystacina.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 169: *Shaft of femur straight (0); or with bend that directs the distal shaft dorsally (1).* The shaft of the femur is straight in all extant species of *Pteronotus* and *Mormoops.* A similar state is seen in *Artibeus jamaicensis,* both species of *Mystacina,* both species of *Noctilio,* and *Saccopteryx bilineata.* In contrast, in both species of *Macrotus* the shaft of the femur is bent somewhat so that the distal end is directed more dorsally (the equivalent of a lateral bend if the femur were in the position typical of nonvolant mammals). Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 170: *Fibula well developed and fully ossified (0); or thin and threadlike, often only partly ossified (1); or absent or entirely unossified (2).* The fibula in most mammals is well developed (relatively robust) and complete (ossified from knee to ankle). In contrast, the fibula in all extant species of *Pteronotus* and *Mormoops* is relatively much thinner, almost threadlike. This element is often only partially ossified, which makes it appear incomplete in dried skeleton preparations. A similar condition is seen in *Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Noctilio.* The fibula is either absent or entirely unossified (no remnant present in dried skeletons) in *Saccopteryx bilineata.* In contrast, the fibula is well developed and fully ossified in both species of *Mystacina.* The primitive condition could not be determined a priori due to variation among outgroups. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 171: *Tail absent (0); or tail length approximately one-half the length of the tibia (1); or approximately three-fourths the length of the tibia (2); or approximately the same length as the tibia (3); or one and one-half times the length of the tibia (4).* Tail length in bats can vary enormously among species. The tail of all extant species of *Pteronotus* and *Mormoops* is approximately the same length as the tibia. Among the outgroups, a similar condition is seen in *Mystacina tuberculata.* In contrast, the tail is one and one-half times the length of the tibia in both species of *Macrotus,* three-fourths the length of the tibia in *Mystacina robusta* and *Saccopteryx bilineata,* one-half the length of the tibia in both species of *Noctilio,* and the tail is absent in *Artibeus jamaicensis.* Transformations in this character were ordered 0 ↔ 1 ↔ 2 ↔ 3 ↔ 4 to reflect our hypothesis that reduction or increase in length of the tail occurs in a progressive fashion. Data were not available for *Pteronotus pristinus,* which was scored ''?'' for this character.

Character 172: *Calcaneum not expanded or flattened (0); or expanded and flattened (1).* The calcaneum of all extant species of *Pteronotus* and *Mormoops* is a rectangular bone that is not noticeably flattened or expanded. A similar condition is seen among the outgroups in *Artibeus jamaicensis,* both species of *Macrotus,* both species of *Mystacina,* and *Saccopteryx bilineata.* In contrast, the calcaneum in both species of *Noctilio* is flattened and expanded into a nearly triangular bone when seen in anterior view. Data were not available for *P.pristinus,* which was scored ''?'' for this character.

Character 173: *Calcar entirely cartilaginous (0); or cartilaginous distally, with clearly demarcated calcified base (1); or calcar entirely calcified (2).* The degree of calcification of the calcar varies among and within families of microchiropteran bats (Schutt and Simmons, 1998). Although thin and distally flexible, the calcar is apparently entirely calcified in all extant species of *Pteronotus* (Schutt and Simmons, 1998; Schutt, personal commun.). In contrast, the base of the calcar is calcified but the distal portion of this element is cartilaginous in both species of *Mormoops* (Schutt and Simmons, 1998; Schutt, personal commun.). A transitional zone is clearly visible between the calcified and cartilaginous portions of the calcar in these species. Among the outgroups, both species of *Macrotus* and both species of *Noctilio* also have a calcar that is cartilaginous distally with a clearly demarcated calcified base (Schutt and Simmons, 1998). The calcar in *Saccopteryx bilineata* is entirely calcified (Schutt and Simmons, 1998). *Mystacina robusta* and *Artibeus jamaicensis* exhibit a third condition in which the calcar is entirely cartilaginous (Schutt and Simmons, 1998). Transitions in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that increased or decreased calcification of the calcar occurs in a progressive fashion. Data were not available for *Pteronotus pristinus* and *Mystacina tuberculata,* which were scored ''?'' for this character.

Character 174: *Calcar length less than or approximately equal to one-half the length of the hind foot (0); or approximately the same length as hind foot (1); or one and one-half times the length of the hind foot (2); or twice the length of the hind foot (3).* The relatively length of the calcar can be assessed by comparing its length (from base to tip) with the length of the hind foot (including claws). The calcar is approximately the same length as the hind foot in *Pteronotus parnellii, P. quadridens,* and *P. personatus.* In contrast, the calcar is approximately one and one-half times the length of the hind foot in *P. macleayii, P. gymnonotus,* and *P. davyi.* The calcar is even longer—approximately twice the length of the hind foot—in both species of *Mormoops.* Among the outgroups, the calcar is less than or equal to one-half the length of the hind foot in both species of *Mystacina* and *Artibeus jamaicensis,* approximately one and one-half times the length of the hind foot in *Saccopteryx bilineata* and both species of *Macrotus,* and is twice the length of the hind foot in both species of *Noctilio.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 175: *Length of foot less than or equal to one-half the length of the tibia (0); or greater than three-fourths the length of the tibia (1).* The relative length of the hind foot varies among bats. The length of the foot (including claws) is less than or equal to one-half the length of the tibia in all extant species of *Pteronotus* and *Mormoops.* Among the outgroups, a similar condition is seen in *Saccopteryx bilineata* and both species of *Macrotus.* In contrast, the hind foot is at least three-fourths the length of the tibia in *Artibeus jamaicensis,* both species of *Noctilio,* and both species of *Mystacina.* Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Character 176: *Claws without basal talons (0); or with basal talons (1).* The claws on the thumb and hind feet of most bats, including extant species of *Pteronotus* and *Mormoops,* lack basal talons or spurs. A similar condition is seen among the outgroups in both species of *Macrotus, Artibeus jamaicensis,* both species of *Noctilio,* and *Saccopteryx bilineata.* In contrast, the claws of both species of *Mystacina* are characterized by well-developed basal talons. Data were not available for *Pteronotus pristinus,* which was scored "?" for this character.

Postcranial Myology

Character 177: *M. humeropatagialis present (0); or absent (1).* Humeropatagialis is a muscle unique to bats that originates from the humerus (and sometimes the ulna) and inserts into the plagiopatagium. It apparently functions to tense the plagiopatagium posterior and lateral to the elbow (Strickler, 1978). M. humeropatagialis is present in extant species of *Pteronotus* and *Mormoops.* This muscle is present among the outgroups in *Saccopteryx bilineata* and both species of *Noctilio* (Strickler, 1978). In contrast, this muscle is absent in both species of *Macrotus* (Vaughan, 1959). The primitive condition could not be determined a priori due to variation among the outgroups. Data were not available for *Pteronotus pristinus,* both species of *Mystacina,* and *Artibeus jamaicensis,* so these taxa were scored "?" in our analysis.

Character 178: *M. occipitopollicalis with tendinous attachments to the anterior division of m. pectoralis profundus (0); or with no tendinous attachment to the anterior division of m. pectoralis profundus (1).* M. occipitopollicalis originates from the posterior surface of the skull, runs along the leading edge of the wing membrane, and inserts into structures in the region of the wrist (Strickler, 1978). This muscle is variable in structure, including different combinations of segments of muscle, tendon, and elastic tissue, having variable insertion points, and exhibiting different tendinous connections to other muscles in different taxa (Strickler, 1978). M. occipitopollicalis has a tendinous attachment to the anterior division of m. pectoralis profundus in *Pteronotus parnellii, Pteronotus davyi,* and *Mormoops megalophylla* (Strickler, 1978). Among the outgroups, a similar tendinous attachment is seen in *Saccopteryx bilineata* and both species of *Macrotus,* but no such attachment is present in either species of *Noctilio* (Vaughan, 1959; Strickler, 1978). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii, Artibeus jamaicensis,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 179: *M. occipitopollicalis insertional complex includes muscle fibers distal to band of elastic tissue (0); or entirely tendinous distal to band of elastic tissue (1).* The insertional complex of m. occipitopollicalis is entirely tendinous distal to band of elastic tissue in *Pteronotus parnellii, Pteronotus davyi,* and *Mormoops megalophylla* (Strickler, 1978). Among the outgroups, a similar arrangement is seen in both species of *Macrotus,* but the insertional complex includes muscle fibers distal to the band of elastic tissue in *Saccopteryx bilineata* and both species of *Noctilio* (Vaughan, 1959; Strickler, 1978). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii, Artibeus jamaicensis,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 180: *M. spinodeltoideus orig-*

inates from vertebral border of scapula only (0); or from vertebral border of scapula plus one-half to two-thirds of the transverse scapular ligament (1); or from vertebral border of scapula plus more than three-fourths of the transverse scapular ligament (1). M. spinodeltoideus in bats originates from the scapula and associated ligaments, and inserts on the dorsal ridge of the humerus (Strickler, 1978). Contraction of this muscle acts to flex, abduct, and supinate the humerus (Strickler, 1978). M. spinodeltoideus originates from the vertebral border of scapula plus one-half to two-thirds of the transverse scapular ligament in *Pteronotus parnellii* and *P. davyi* (Strickler, 1978). The origin of this muscle is even more extensive in *M. megalophylla,* where m. spinodeltoideus originates from the vertebral border of scapula plus more than three-fourths of the transverse scapular ligament (Strickler, 1978). Among the outgroups, m. spinodeltoideus originates from the vertebral border of scapula plus one-half to two-thirds of the transverse scapular ligament in *Artibeus jamaicensis* and both species of *Macrotus,* but the origin is restricted to the vertebral border of the scapula in *Saccopteryx bilineata* and both species of *Noctilio* (Vaughan, 1959; Strickler, 1978; Hermanson and Altenbach, 1985). Transformations in this character were ordered 0 ↔ 1 ↔ 2 based on our assumption that changes resulting in increased or decreased extent of origin from the transverse scapular ligament occur in a progressive fashion. Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 181: *M. teres major originates from one-half to three-fourths of the axillary border of the scapula (0); or originates from one-fourth to two-fifths of the axillary border (1); or origin restricted to the ventral tip of the axillary border (2).* M. teres major in bats originates from the scapula and associated fascia, and inserts onto the humerus (Vaughan, 1959; Strickler, 1978). Contraction of this muscle acts to flex and rotate the humerus (Vaughan, 1959; Strickler, 1978). The origin of m. teres major includes approximately one-fourth to two-fifths of the total axillary border of the scapula in *Pteronotus parnellii* and *P. davyi* (Strickler, 1978). In contrast, the origin of this muscle is restricted to just the tip of the axillary border in *M. megalophylla* (Strickler, 1978). Among the outgroups, the origin of m. teres major includes approximately one-fourth to two-fifths of the axillary border in *Artibeus jamaicensis,* both species of *Macrotus,* and *Saccopteryx bilineata,* and it is even more extensive—extending from one-half to three-fourths of the axillary border—in both species of *Noctilio* (Vaughan, 1959; Strickler, 1978; Hermanson and Altenbach, 1985). Transformations in this character were ordered 0 ↔ 1 ↔ 2 based on our assumption that changes resulting in increased or decreased extent of origin occur in a progressive fashion. Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 182: *M. teres major inserts into ventral ridge of humerus (0); or into ventral base of pectoral crest (1).* The insertion point of m. teres major onto the humerus varies among bats (Strickler, 1978). This muscle inserts into the ventral base of the pectoral crest of the humerus in *Pteronotus parnellii, P. davyi,* and *Mormoops megalophylla* (Strickler, 1978). A similar condition is seen among the outgroups in *Artibeus jamaicensis* and both species of *Macrotus* (Vaughan, 1959; Hermanson and Altenbach, 1985). In contrast, m. teres major inserts into the ventral ridge of the humerus in *Saccopteryx bilineata* and both species of *Noctilio* (Strickler, 1978). Data were not available for *Pteronotus macleayii, P. quadridens, P. personatus, P. gymnonotus, P. pristinus, Mormoops blainvillii,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 183: *M. triceps brachii caput medialis present (0); or absent (1).* Vaughan and Bateman (1970) described the myology of the forelimb of all species of *Pteronotus* and *Mormoops.* M. triceps brachii is a tripartite muscle with three heads: caput lateralis, caput medialis, and caput longus. The caput medialis originates from the posterior surface of the distal humerus and inserts into the common tendon of the triceps; it may also be attached by connective tissue to the olecranon process of the ulna (Vaughan, 1959). M. triceps caput medialis is present in *Pteronotus,* but is absent in both species of *Mormoops* (Vaughan and Bateman, 1970). This muscle is present in *Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Macrotus* (Vaughan, 1959; Strickler, 1978). Data were not available for *P. pristinus,* both species of *Mystacina,* and *Artibeus jamaicensis,* so these taxa were scored "?" in our analysis.

Character 184: *M. coracobrachialis the same size or smaller than coracoid head of m. biceps brachii, originates from tip of coracoid process (0); or approximately twice the size of coracoid head of biceps, originates proximal to tip of coracoid process (1).* M. coracobrachialis and m. biceps brachii are muscles that originate from the coracoid process and insert on the humerus and radius, respectively (Vaughan, 1959). M. coracobrachialis acts to adduct and extend the humerus, while m. biceps brachii flexes and rotates the forearm and adducts the wing (Vaughan, 1959). M. coracobrachialis originates from the tip of the coracoid process and is roughly the same size or smaller than the coracoid head of the biceps in *Pteronotus parnellii* and both species of *Mormoops* (Vaughan and Bateman, 1970). In contrast, m. coracobrachialis is twice the size of the coracoid head of the biceps in *P. macleayii, P. quadridens, P. personatus, P. davyi,* and *P. gymnonotus,* and its origin is proximal to the tip of the coracoid process (Vaughan and Bateman, 1970). M. coracobrachialis originates at the tip of the coracoid process and is the same size or smaller than the coracoid head of the biceps in *Saccopteryx bilineata,* both species of *Macrotus,* and both species of *Noctilio* (Vaughan, 1959; Strickler, 1978). Data were not available for *P. pristinus,* both species of *Mystacina,* and *Artibeus jamaicensis,* so these taxa were scored "?" in our analysis.

Character 185: *M. biceps brachii insertional tendons not encased in sling (0); or encased in sling (1).* The insertional tendons of m. biceps brachii are encased in a sling of connective tissue that is attached to the dorsal surface of the humerus in both species of *Mormoops* (fig. 9; Vaughan and Bateman, 1970). In contrast, these tendons are not encased in a sling in any extant species of *Pteronotus* (Vaughan and Bateman, 1970). The sling is similarly lacking in *Artibeus jamaicensis,* both species of *Macrotus,* and both species of *Noctilio* (Vaughan, 1959; Strickler, 1978; Hermanson and Altenbach, 1985). Data were not available for *P. pristinus, Saccopteryx bilineata,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 186: *M. brachialis present (0); or absent (1).* M. brachialis in bats originates on the medial portion of the anterior surface of the humerus and inserts on the radius (Vaughan, 1959). It acts to flex and rotate the radius, and may help to stabilize the wing during flight (Vaughan, 1959). M. brachialis is absent in both species of *Mormoops,* but this muscle is present in all species of *Pteronotus* (fig. 9; Vaughan and Bateman, 1970). M. brachialis is present in *Saccopteryx bilineata,* both species of *Macrotus,* and both species of *Noctilio* (Vaughan, 1959; Strickler, 1978), suggesting that presence of m. brachialis may be the primitive condition. Data were not available for *P. pristinus,* both species of *Mystacina,* and *Artibeus jamaicensis,* so these taxa were scored "?" in our analysis.

Character 187: *No sesamoid in tendon of m. extensor carpi radialis longus (0); or sesamoid present (1).* M. extensor carpi radialis originates from the lateral epicondyle and

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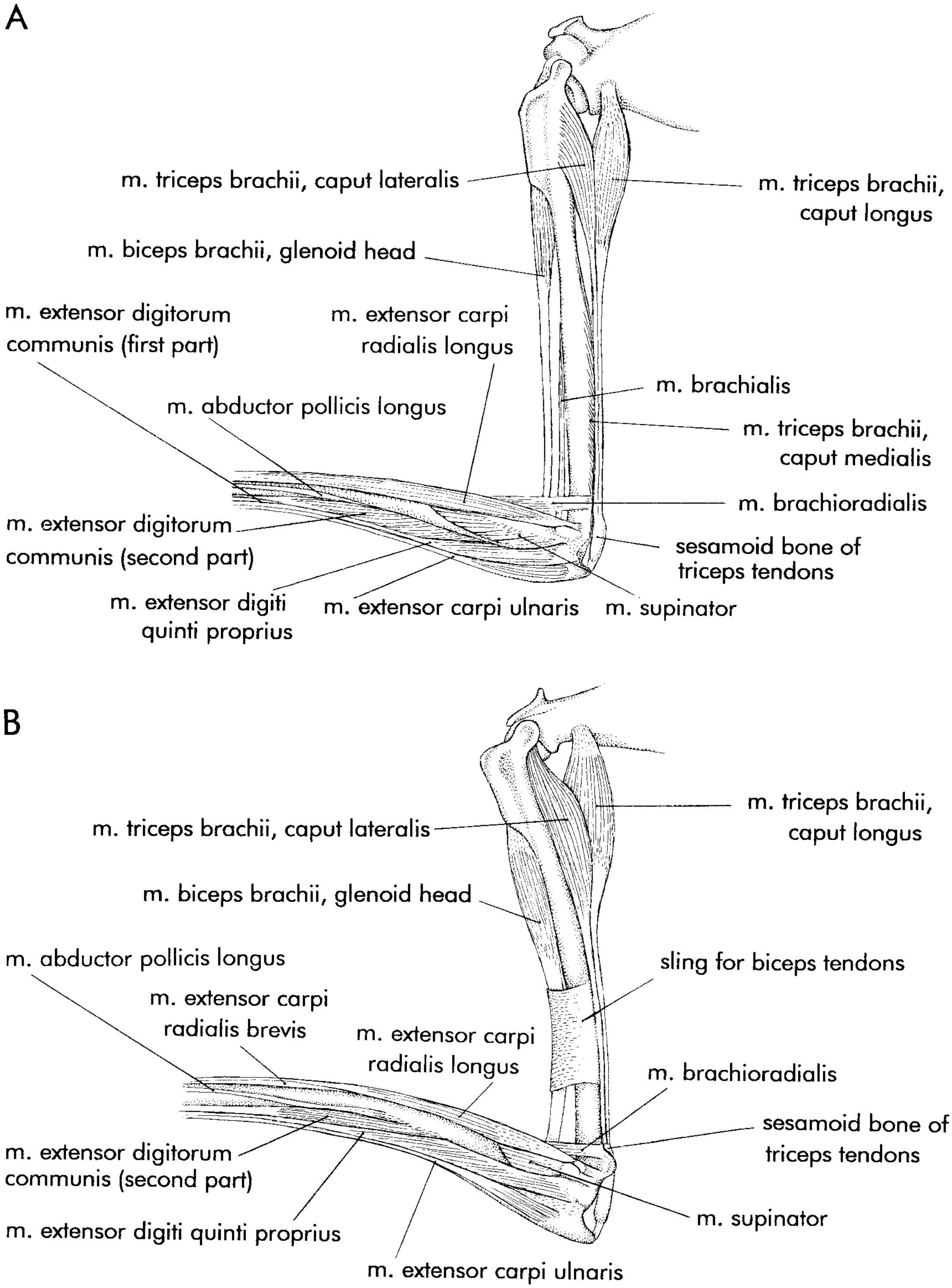
Fig. 9. Dorsal views of the arm of (**A**) *Pteronotus personatus* and (**B**) *Mormoops megalophylla* (redrawn from Vaughan and Bateman, 1970: figs. 1, 2). In each figure, the shoulder is shown at the top and the wrist (not included in this view) is to the left. Note the sling for the biceps tendons in *Mormoops* (a structure absent in *Pteronotus*) and presence of m. brachialis in *Pteronotus* (absent in *Mormoops*). M. triceps caput medialis, which is absent in *Mormoops* but present in *Pteronotus,* cannot be seen in this dorsal view.


A
m. triceps brachii, caput lateralis
m. triceps brachii, caput longus
m. biceps brachii, glenoid head
m. extensor digitorum communis (first part)
m. extensor carpi radialis longus
m. brachialis
m. abductor pollicis longus
m. triceps brachii, caput medialis
m. brachioradialis
m. extensor digitorum communis (second part)
sesamoid bone of triceps tendons
m. extensor digiti quinti proprius
m. extensor carpi ulnaris
m. supinator
B
m. triceps brachii, caput longus
m. triceps brachii, caput lateralis
m. biceps brachii, glenoid head
sling for biceps tendons
m. abductor pollicis longus
m. extensor carpi radialis brevis
m. extensor carpi radialis longus
m. brachioradialis
sesamoid bone of triceps tendons
m. extensor digitorum communis (second part)
m. supinator
m. extensor digiti quinti proprius
m. extensor carpi ulnaris

distal shaft of the humerus, and inserts on the dorsal bases of the metacarpals of the first and second digits (Vaughan, 1959; Vaughan and Bateman, 1970). This muscle acts to extend the metacarpals and may serve to spread the distal part of the wing (Vaughan, 1959; Vaughan and Bateman, 1970). No sesamoid is present in the tendon of m. extensor carpi radialis longus in any extant species of *Pteronotus* (Vaughan and Bateman, 1970). In contrast, a sesamoid is associated with the tendon of this muscle in both species of *Mormoops* (Vaughan and Bateman, 1970). Among the outgroups, a sesamoid in this location is absent in both species of *Macrotus* (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 188: *M. extensor policis brevis originates from ulna (0); or from both ulna and radius (1).* M. extensor policis brevis is an extensor of the thumb that inserts on the metacarpophalangeal joint and second phalanx of the first digit (Vaughan, 1959; Vaughan and Bateman, 1970). M. extensor policis brevis originates from the dorsal surface of the ulna in both species of *Mormoops* (Vaughan and Bateman, 1970). In contrast, this muscle originates from the dorsal surface of the ulna and the adjacent surface of the radius in all extant species of *Pteronotus* (Vaughan and Bateman, 1970). In both species of *Macrotus* the origin of this muscle is restricted to the dorsal surface of the ulna (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 189: *M. extensor digitorum communis originates from radius, ulna, and humerus (0); or from radius and ulna only (1).* M. extensor digitorum communis is a digital extensor that inserts onto the third, fourth, and fifth digits of the wing. This muscle originates from the proximal half of the radius and ulna in all extant species of *Pteronotus* and *Mormoops* (Vaughan and Bateman, 1970). In contrast, in both species of *Macrotus,* m. extensor digitorum communis has a more extensive origin that includes the proximal radius, proximal ulna, and the lateral epicondyle of the humerus (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 190: *Tendon from m. extensor digitorum communis inserts on second phalanx of fifth digit (0); or on shaft of metacarpal of fifth digit (1).* The tendon of m. extensor digitorum communis inserts on the second phalanx of the fifth digit in *Pteronotus parnellii, P. davyi, P. gymnonotus, Mormoops megalophylla,* and *M. blainvillii.* In contrast, the tendon of m. extensor digitorum communis inserts on the shaft of the metacarpal of the fifth digit in *P. macleayii, P. quadridens,* and *P. personatus* (Vaughan and Bateman, 1970). In both species of *Macrotus* the tendon inserts on the second phalanx of the fifth digit (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 191: *M. extensor digiti quinti proprius originates from lateral epicondyle of humerus and dorsal base of ulna (0); or from lateral epicondyle only (1); or from second division of m. extensor digitorum communis and posterodorsal base of radius (2).* M. extensor digiti quinti proprius is a digital extensor that inserts on the second phalanx of the fifth digit of the wing. M. extensor digiti quinti proprius originates from the lateral epicondyle of humerus and the dorsal base of the ulna in *Pteronotus macleayii, P. quadridens, P. davyi,* and *P. gymnonotus.* In contrast, this muscle originates from the lateral epicondyle of the humerus only in *P. personatus* and both species of *Mormoops*; an ulnar origin is lacking in these taxa. A third condition is seen in *P. parnellii,* in which m. extensor digiti quinti proprius originates from the second division of m. extensor digitorum communis and the posterodorsal base of the radius (Vaughan and Bateman, 1970). In both species of *Macrotus* the muscle originates from the lateral epicondyle and the dorsal base of the ulna (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 192: *M. flexor digitorum profundus inserts via tendon onto second pha-*

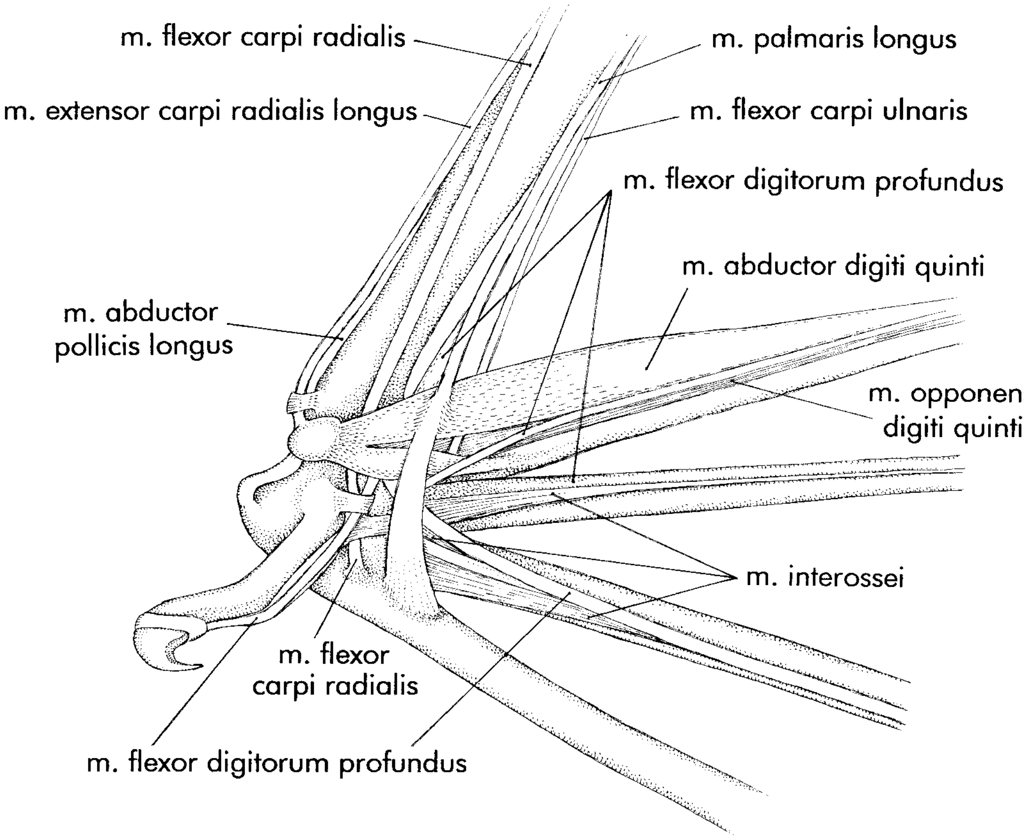


Fig. 10. Ventral view of the hand of *Mormoops megalophylla* (redrawn from Vaughan and Bateman, 1970: fig. 6).

lanx of digit IV of wing (0); or does not insert onto digit IV (1). M. flexor digitorum profundus is a digital flexor that originates from the distal humerus and inserts via tendons onto a variable number of wing digits (fig. 10; Vaughan, 1959; Vaughan and Bateman, 1970). This muscle inserts onto the second phalanx of digit IV of the wing in all extant species of *Pteronotus* and *Mormoops* (fig. 10; Vaughan and Bateman, 1970). In contrast, m. flexor digitorum profundus does not insert on digit IV in either species of *Macrotus* (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

Character 193: *M. flexor digitorum profundus inserts via tendon onto second phalanx of digit V of wing (0); or does not insert onto digit V (1).* M. flexor digitorum profundus inserts onto the second phalanx of digit V of the wing in all extant species of *Pteronotus* and *Mormoops* (fig. 10; Vaughan and Bateman, 1970). In contrast, m. flexor digitorum profundus does not insert on digit V in either species of *Macrotus* (Vaughan, 1959). Data were not available for the other outgroups in our study, which were scored "?" for this character, as was *Pteronotus pristinus.*

It may be noted that the taxonomic distribution of states of this character is identical to that of character 192, which also describes the insertion of m. flexor digitorum profundus. We opted to score these as separate characters because the taxonomic distribution of these two features is not identical when additional taxa are considered. For example, m. flexor digitorum profundus inserts on digit IV, but not on digit V, in *Phyllostomus has-*

tatus (Vaughan and Bateman, 1970). These observations indicate that insertion on digit IV and digit V may vary independently.

Character 194: *M. palmaris longus robust (0); or vestigial (1).* M. palmaris longus originates on the spinous process of the medial epicondyle of the humerus and inserts on the metacarpals of the second and/or third digits of the wing (see characters 195 and 196; Vaughan, 1959; Vaughan and Bateman, 1970). M. palmaris longus is a vestigial muscle that is much narrower than m. flexor digitorum profundus in all extant species of *Pteronotus* (Vaughan and Bateman, 1970). In contrast, this muscle is relatively robust (approximately the same size as m. flexor digitorum profundus) in both species of *Mormoops* (fig. 10). A similar condition is seen among the outgroups in both species of *Macrotus, Artibeus jamaicensis,* and both species of *Noctilio* (Vaughan, 1959; Vaughan and Bateman, 1970). Data were not available for *Pteronotus pristinus, Saccopteryx bilineata,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis.

Character 195: *M. palmaris longus inserts onto metacarpal of digit II (0); or does not insert onto metacarpal of digit II (1).* M. palmaris longus inserts onto the metacarpal of digit II of the wing in *Pteronotus parnellii, P. macleayi, P. gymnonotus, Mormoops megalophylla,* and *M. blainvillii* (fig. 10; Vaughan and Bateman, 1970). A similar insertion is seen among the outgroups in *Artibeus jamaicensis* (Vaughan and Bateman, 1970). In contrast, m. palmaris longus lacks an insertion onto the metacarpal of digit II in both species of *Macrotus* (Vaughan, 1959). Data were not available for *Pteronotus pristinus, Saccopteryx bilineata,* both species of *Noctilio,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis. Vaughan and Bateman (1970) attempted to trace the insertion of m. palmaris longus in *Pteronotus personatus, P. quadridens,* and *P. davyi,* but found that the tendons were too small to follow. We accordingly scored these taxa "–" for this character.

Character 196: *M. palmaris longus inserts onto metacarpal of digit III (0); or does not insert onto metacarpal of digit III (1).* M. palmaris longus inserts onto the metacarpal of digit III of the wing in *Pteronotus parnellii, P. macleayi, P. gymnonotus, Mormoops megalophylla,* and *M. blainvillii* (Vaughan and Bateman, 1970). A similar insertion is seen among the outgroups in *Macrotus* (Vaughan, 1959). In contrast, m. palmaris longus lacks an insertion onto the metacarpal of digit III in *Artibeus jamaicensis* and both species of *Noctilio* (Vaughan and Bateman, 1970; Straney, 1980). Data were not available for *Pteronotus pristinus, Saccopteryx bilineata,* and both species of *Mystacina,* so these taxa were scored "?" in our analysis. As noted above, Vaughan and Bateman (1970) attempted to trace the insertion of m. palmaris longus in *Pteronotus personatus, P. quadridens,* and *P. davyi,* but found that the tendons were too small to follow. We accordingly scored these taxa "–" for this character.

Character 197: *Digital tendon locking mechanism absent from digits of hind feet (0); or ratchetlike lock present, consists of tubercles on the proximal flexor tendon and plicae on the adjacent tendon sheath (1); or friction lock present, consists of retinaculum on flexor tendon sheath (2).* The hind feet of many bats are equipped with a digital tendon locking mechanism (TLM) that apparently facilitates hindlimb hanging with minimal muscular effort (Schaffer, 1905; Schutt, 1993; Bennett, 1993; Quinn and Baumel, 1993; Simmons and Quinn, 1994). All extant species of *Pteronotus* and *Mormoops* lack a TLM (Simmons and Quinn, 1994; Schutt, personal commun.). Among the outgroups, *Mystacina tuberculata* also lacks a TLM (Simmons and Quinn, 1994). In contrast, a ratchetlike TLM, consisting of tubercles on the proximal flexor tendon and plicae on the adjacent tendon sheath, is present in *Saccopteryx bilineata* and both species of *Noctilio* (Simmons and Quinn, 1994; Schutt, personal commun.). Both species of *Macrotus* and *Artibeus jamaicensis* lack a ratchetlike TLM, instead having a friction-lock on the digital tendons that consists of a bandlike retinaculum in the tendon sheath (Schutt, 1993; Simmons and Quinn, 1994). Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" for this character.

Reproductive Tract

Character 198: *Female external genitalia with transverse vulval opening (0); or vulval opening oriented anteroposteriorly (1).* The female external genitalia in bats consists of a clitoris and vulval opening. The vulval opening is oriented anteroposteriorly in all extant species of *Pteronotus* and *Mormoops.* A similar arrangement is seen among the outgroups in *Artibeus jamaicensis,* both species of *Macrotus,* and *Mystacina tuberculata.* In contrast, the vulval opening is oriented transversely in *Saccopteryx bilineata* and both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and *Mystacina robusta,* so these taxa were scored "?" for this character.

Character 199: *Clitoris of moderate size, length approximately equal to width at base (0); or clitoris elongated, length approximately twice width at base (1).* The clitoris of mormoopid bats varies in relative length. The clitoris is of moderate size (clitoris length approximately equal to width at base) in *Pteronotus parnellii, P. personatus, P. quadridens, P. davyi, P. gymnonotus,* and both species of *Mormoops.* In contrast, the clitoris is elongated (clitoris length approximately twice width at base) in *Pteronotus macleayii.* Among the outgroups, the clitoris is of moderate size in *Saccopteryx bilineata,* both species of *Macrotus,* and *Artibeus jamaicensis,* but it is elongated in both species of *Noctilio.* Data were not available for *Pteronotus pristinus* and both species of *Mystacina,* so these taxa were scored "?" for this character.

Character 200: *External uterine horns more than three-fourths the length of the external common uterine body (0); or one-half the length of the common uterine body (1); or one-fourth the length of the common uterine body (2); or uterus fully simplex, uterine horns not distinct from common uterine body (3).* Hood and Smith (1982, 1983) examined morphology of the female reproductive tract in representatives of most bat families and found considerable variation in the extent of external fusion of the uterine horns. Four mormoopids were included in their study: *Mormoops blainvillii, Pteronotus parnellii, P. macleayi,* and *P. quadridens.* All were found to be characterized by a similar uterine morphology in which the uterine horns are approximately one-half the length of the common uterine body (Hood and Smith, 1982, 1983). Among the outgroups, *Saccopteryx bilineata* and *Mystacina robusta* have uterine horns that are more than three-fourths the length of the common uterine body, both species of *Noctilio* have uterine horns that are one-half the length of the common uterine body, *Macrotus californicus* has uterine horns that are one-fourth the length of the common uterine body, and *Artibeus jamaicensis* has a fully simplex uterus that lacks free uterine horns (Hood and Smith, 1982, 1983). No data were available for *Pteronotus personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops megalophylla, Mystacina tuberculata,* and *Macrotus waterhousii,* so these taxa were scored "?" for this character.

Following Hood and Smith (1982, 1983), we ordered this character 0 ↔ 1 ↔ 2 ↔ 3 to reflect the presumed process by which a duplex uterus (such as that seen in pteropodids and some emballonurids) may be transformed into a simplex uterus by progressive fusion of the uterine horns beginning at the cervical end of the uterus. As fusion progresses, the common uterine body is thought to increase in length at the expense of decreased length of the free uterine horns. This process seems confirmed (at least in bats) by observations of an inverse relationship between length of the common uterine body and length of the free uterine horns (Hood and Smith, 1982). Transformations in this series may have worked both ways in at least some groups (e.g., within Phyllostomidae), with reversals accomplished by progressive splitting of the uterine horns and reduction in relative size of the common uterine body (see discussion in Wetterer et al., 2000).

Character 201: *Common uterine lumen relatively short, coronal lumina join well within common uterine body (0); or common uterine lumen large, coronal lumina join immediately within the common uterine body (1); or common uterine lumen very large, coronal lumina either reduced to a tubular intramural uterine cornua or entirely absent (2).* Internal uterine fusion in bats is broadly correlated with external uterine fusion, but these two features are decoupled to some extent because the degree of external fusion is not always indicative of a similar degree of fusion of the internal spaces (coronal lumina) within the common uterine body (Hood and Smith, 1982, 1983). In *Mormoops blainvillii, Pteronotus parnellii, P. macleayi,* and *P. quadridens,* the common uterine lumen is relatively large and the coronal lumina join immediately upon their entry into the common uterine body (Hood and Smith, 1982, 1983). Among the outgroups, a similar condition is seen in *Macrotus californicus.* In contrast, the common uterine lumen is relatively short and the coronal lumina join well within common uterine body in *Saccopteryx bilineata, Mystacina robusta,* and both species of *Noctilio* (Hood and Smith, 1982, 1983). Another distinct condition is seen in *Artibeus jamaicensis,* which has a very large common uterine lumen and lacks any remnants of coronal lumina (Hood and Smith, 1982, 1983). As with the preceding character, we followed Hood and Smith (1982, 1983) in ordering this character 0 ↔ 1 ↔ 2 to reflect the presumed process by which a duplex uterus may be transformed into a simplex uterus (or vice versa) by progressive fusion uterine horns and lumina. No data were available for *Pteronotus personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops megalophylla, Mystacina tuberculata,* and *Macrotus waterhousii,* so these taxa were scored ‘‘?’’ for this character.

Character 202: *Uterotubal junction with oviductal papilla (0); or oviductal papilla absent (1).* Bats of many families have a uterotubal junction characterized by an oviductal papilla that projects into the lumen of the uterine horn (Hood and Smith, 1982, 1983). In contrast, *Mormoops blainvillii, Pteronotus parnellii, P. macleayi,* and *P. quadridens* have a simple uterotubal junction and lack oviductal papilla (Hood and Smith, 1982, 1983). Among the outgroups, *Saccopteryx bilineata,* both species of *Noctilio, Macrotus californicus,* and *Artibeus jamaicensis* similarly have a simple uterotubal junction lacking an oviductal papilla, but an oviductal papilla is present in *Mystacina robusta* (Hood and Smith, 1982, 1983). No data were available for *Pteronotus personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops megalophylla, Mystacina tuberculata,* and *Macrotus waterhousii,* so these taxa were scored ‘‘?’’ for this character.

Character 203: *Oviductal mucosal folds occur throughout the oviduct (0); or folds restricted to extramural oviduct (1). Mormoops blainvillii, Pteronotus parnellii, P. macleayi,* and *P. quadridens* have oviductal mucosal folds that occur throughout the oviduct, including the intramural portion that is enclosed within the wall of the uterus (Hood and Smith, 1982, 1983). This condition also occurs among the outgroups in *Saccopteryx bilineata,* both species of *Noctilio,* and *Mystacina robusta* (Hood and Smith, 1982, 1983). In contrast, *Macrotus californicus* and *Artibeus jamaicensis* are characterized by restriction of oviductal mucosal folds to the extramural oviduct; the intramural portion of the oviduct is smooth and lacks any such folds (Hood and Smith, 1982, 1983). No data were available for *Pteronotus personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops megalophylla, Mystacina tuberculata,* and *Macrotus waterhousii,* so these taxa were scored ‘‘?’’ for this character.

Character 204: *Ovarian ligament extends from ovary to external entry of oviduct (0); or to lateral border of common uterine body (1).* The ovarian ligament extends from the ovary to the external entry of the oviduct into the uterus in *Mormoops blainvillii, Pteronotus parnellii, P. macleayi,* and *P. quadridens*(Hood and Smith, 1982, 1983). This condition also occurs among the outgroups in *Saccopteryx bilineata, Mystacina robusta,* both species of *Noctilio,* and *Macrotus californicus* (Hood and Smith, 1982, 1983). In contrast, the ovarian ligament extends from the ovary to the lateral border of the common uterine body in *Artibeus jamaicensis* (Hood and Smith, 1982, 1983). No data were available for *Pteronotus personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops megalophylla, Mystacina tuberculata,* and *Macrotus waterhousii,* so these taxa were scored ‘‘?’’ for this character.

DIGESTIVE TRACT

Character 205: *Submaxillary glands of mucous type (0); or of serous type (1); or absent (2).* Submaxillary glands are salivary glands located adjacent to the upper jaw of bats (Dalquest and Warner, 1954). Two types of submaxillary glands are found in bats: (1) mucous glands, which are nongranular, have an epithelial membrane, and secrete mucous, and (2) serous glands (= albuminous glands), which are granular, have a layer of mesothelium, and secrete a watery fluid. Mucous-type submaxillary glands are found in *Pteronotus parnellii* and *P. davyi* (Dalquest and Warner, 1954). In contrast, *Mormoops megalophylla* is characterized by serous-type submaxillary glands (Dalquest and Warner, 1954). Among the outgroups, mucous-type submaxillary glands are present in *Saccopteryx bilineata,* and submaxillary glands are absent in *Artibeus jamaicensis* (Dalquest and Warner, 1954). No data were available for *Pteronotus personatus, P. quadridens, P. macleayi, P. gymnonotus, P. pristinus, Mormoops blainvillii,* both species of *Noctilio,* both species of *Mystacina,* and both species of *Macrotus,* so these taxa were scored "?" for this character.

Character 206: *Cardiac vestibule of stomach very small or absent (0); or large (1).* Foreman (1971, 1972, 1973, 1979) described the structure and histology of the stomach and duodenum of a wide variety of bats, and our observations of character variation in these structures are based entirely on his work. Foreman (1971, 1972, 1973, 1979) defined the cardiac vestibule as that part of the stomach which is immediately adjacent to the esophageal opening. The cardiac vestibule is very small or absent in *Pteronotus parnellii* and *Mormoops megalophylla* (Foreman, 1971, 1972, 1973). A similar condition is seen among the outgroups in *Saccopteryx bilineata,* both species of *Noctilio,* and *Macrotus waterhousii* (Foreman, 1971, 1972, 1973, 1979). In contrast, the cardiac vestibule is large in *Artibeus jamaicensis* (Foreman, 1979). Data were not available for *Pteronotus quadridens, P. macleayii, P. personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii,* both species of *Mystacina,* and *Macrotus californicus,* so these taxa were scored "?" in our study.

Character 207: *Mucous-producing pyloric glands distributed in extremely narrow zone immediately adjacent to pyloric sphincter (0); or distributed in broad zone (1).* Mucous-producing pyloric glands are distributed in an extremely narrow zone immediately adjacent to pyloric sphincter in *Pteronotus parnellii* and *Mormoops megalophylla* (Foreman, 1971, 1972, 1973). Among the outgroups, a similar condition is seen in *Saccopteryx bilineata* and both species of *Noctilio* (Foreman, 1971, 1972, 1973). In contrast, mucous-producing pyloric glands are distributed in a much broader zone of the stomach in *Macrotus waterhousii* and *Artibeus jamaicensis* (Foreman, 1979). Data were not available for *Pteronotus quadridens, P. macleayii, P. personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii,* both species of *Mystacina,* and *Macrotus californicus,* so these taxa were scored "?" in our study.

Character 208: *Pyloric sphincter asymmetrical, valve in lesser curvature smaller than valve in greater curvature (0); or sphincter symmetrical, valves of similar size (1).* The pyloric sphincter separates the stomach from the duodenum (Foreman, 1971, 1972, 1973, 1979). The pyloric sphincter is asymmetrical, with the valve in the lesser curvature of the stomach smaller than the valve in the greater curvature, in *Pteronotus parnellii* and *Mormoops megalophylla* (Foreman, 1971, 1972, 1973). A similar condition is seen among the outgroups in both species of *Noctilio* and *Macrotus waterhousii* (Foreman, 1971, 1972, 1973, 1979). In contrast, the pyloric sphincter is symmetrical, with the valves of similar size, in *Saccopteryx bilineata* and *Artibeus jamaicensis* (Foreman, 1973, 1979). Data were not available for *Pteronotus quadridens, P. macleayii, P. personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii,* both species of *Mystacina,* and *Macrotus californicus,* so these taxa were scored "?" in our study.

Character 209: *Brunner's glands at gastroduodenal junction present in small to moderate numbers, with broad tubules and moderate to large cells with large, spherical nuclei that are juxtaposed to the basement membrane (0); or glands abundant, with tubules of moderate breadth and small cells with extremely small, spherical nuclei that are juxtaposed to the basement membrane (0); or glands unusually abundant, with narrow tubules and small cells with extremely* *small, flattened nuclei that are not juxtaposed to the basement membrane (1).* Brunner's glands occur in most bats in the gastroduodenal junction just distal to the pyloric sphincter (Foreman, 1971, 1972, 1973, 1979). These glands are unusually abundant in *Pteronotus parnellii* and *Mormoops megalophylla* (Foreman, 1971, 1972, 1973). Brunner's glands in these taxa are characterized by narrow tubules and small cells with extremely small, flattened nuclei that are not juxtaposed to the basement membrane (Foreman, 1971, 1972, 1973). Among the outgroups, a similar condition is seen in both species of *Noctilio* (Foreman, 1971, 1972, 1973). In contrast, in *Macrotus waterhousii* and *Artibeus jamaicensis* have Brunner's glands present in small to moderate numbers, with broad tubules and moderate to large cells with large circular nuclei that are juxtaposed to the basement membrane (Foreman, 1979). *Saccopteryx bilineata* is characterized by an intermediate condition in which the Brunner's glands are abundant, with tubules of moderate breadth and small cells with extremely small, spherical nuclei that are juxtaposed to the basement membrane (Foreman, 1972, 1973). Transformations in this character were ordered 0 ↔ 1 ↔ 2 to reflect our hypothesis that transformations in structure and abundance of Brunner's glands occurred in a progressive fashion. Data were not available for *Pteronotus quadridens, P. macleayii, P. personatus, P. davyi, P. gymnonotus, P. pristinus, Mormoops blainvillii,* both species of *Mystacina,* and *Macrotus californicus,* so these taxa were scored "?" in our study.

RESULTS

As noted under "Materials and Methods," we conducted several separate phylogenetic analyses of our data to investigate the effects of different assumptions and the inclusion of the fossil species *Pteronotus pristinus.* Results of each of these analyses are described individually below. Decay values, branch lengths, bootstrap values, and jackkinfe values for clades recovered in these analyses are summarized in tables 2 and 3.

ANALYSIS 1: EXTANT TAXA ONLY, ORDERED CHARACTERS

Our first analysis included all of the extant taxa in our study (*Pteronotus pristinus* was excluded) and used the ordered character transformations described above under individual character descriptions. Parsimony analysis of these data resulted in a single most-parsimonious tree (fig. 11) of 438 steps (CI = 0.653; CI excluding uninformative characters = 0.619; RI = 0.750). Monophyly of Mormoopidae was very well supported (fig. 11; tables 2, 3). Within the family, very strong support was also found for monophyly of *Pteronotus* and *Mormoops.* Within *Pteronotus,* monophyly of a clade consisting of *P. davyi* + *P. gymnonotus* was similarly well supported. The sister group of this lineage was a larger clade consisting of *P. parnellii, P. personatus, P. quadridens,* and *P. macleayi,* but monophyly of this group was only weakly supported. Within this group, *P. parnellii* occupied the basal branch, with the remaining species forming a poorly supported clade. Within the latter group, weak support was found for a clade consisting of *P. quadridens* + *P. macleayi* (fig. 11; tables 2, 3).

With the exception of the *P. davyi* + *P. gymnonotus* clade, support values for most groupings within *Pteronotus* were disappointingly low (e.g., bootstrap and jackknife values = 58–66%, decay values = 1; tables 2, 3). However, support values for alternative arrangements of *Pteronotus* species were considerably worse in the bootstrap and jackknife analyses. Other than those clades that appeared in the most-parsimonious tree (fig. 11), only six clades received support in more than 5% of the bootstrap and jackknife iterations: *P. parnellii* + *P. personatus* (bootstrap and jackknife support values = 25–26%), *P. davyi* + *P. gymnonotus* + *P. personatus* + *P. macleayii* + *P. quadridens* (support values = 23%), *P. personatus* + *P. quadridens* (support values = 20%), *P. parnellii* + *P. davyi* + *P. gymnonotus* (support values = 11%), *P. parnellii* + *P. personatus* + *P. quadridens* (support values = 9–10%), and *P. parnellii* + P. *macleayii* + *P. quadridens* (support values = 5–6%). These results indicate that while the hypothesis of *Pteronotus* relationships shown in figure 11

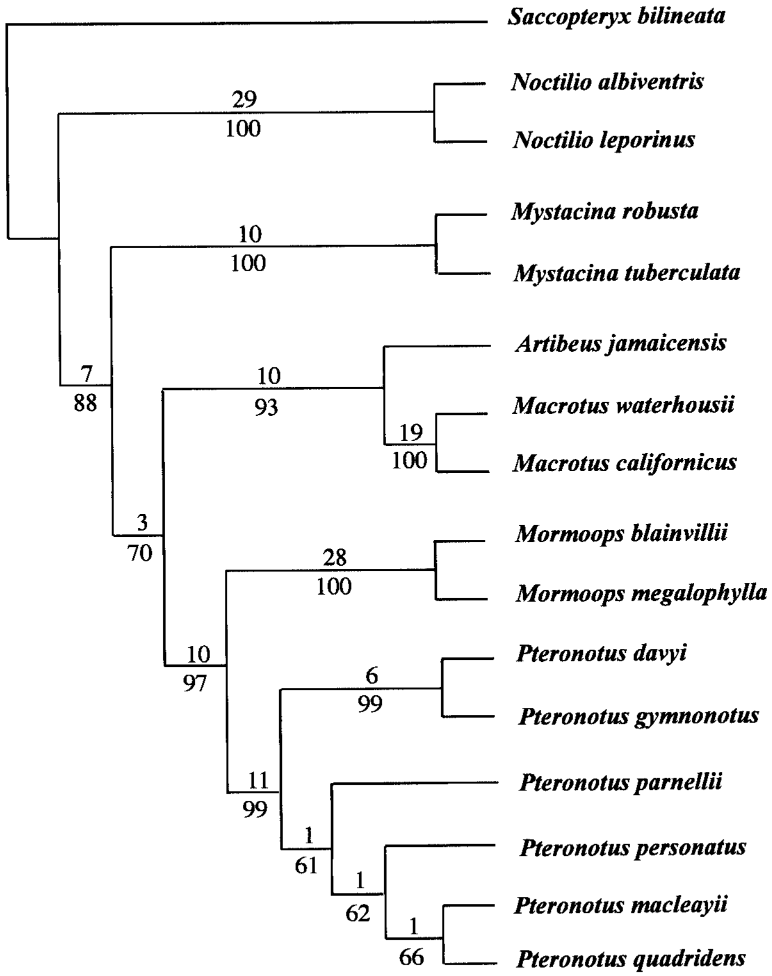


Fig. 11. Tree showing the results of our Analysis 1, which used ordered characters and did not include the fossil *Pteronotus pristinus*. This tree shows the topology of the single most-parsimonious tree recovered (438 steps; CI = 0.653; CI excluding uninformative characters = 0.619; RI = .750). Decay values are given above each branch; bootstrap values are below (see tables 2 and 3 for associated branch length values and results of jackknife analysis).

is not strongly supported, it nevertheless appears much more likely than any of the alternatives.

Among the outgroups, very strong support was found for monophyly of Noctilionidae and Mystacinidae. Although our taxonomic sampling within Phyllostomidae was admittedly very poor, monophyly of this family (represented by *Artibeus jamaicensis* and two species of *Macrotus*) was also well supported in our analysis. Moderate support was found for a sister-group relationship between Mormoopidae and Phyllostomidae, with Noctilionidae and Mystacinidae falling outside this clade. Virtually no support was found for alternative arrangements grouping Mormoopidae and Noctilionidae as sister taxa (bootstrap and jackknife support values = 3%) or Noctilionidae and Phyllostomidae as sister taxa (support values <1%). Similarly, there was no support for monophyly of Noctilionoidea as traditionally recognized (e.g., excluding Mystacinidae; support values ≤1%). Indeed, such relationships were contraindi-

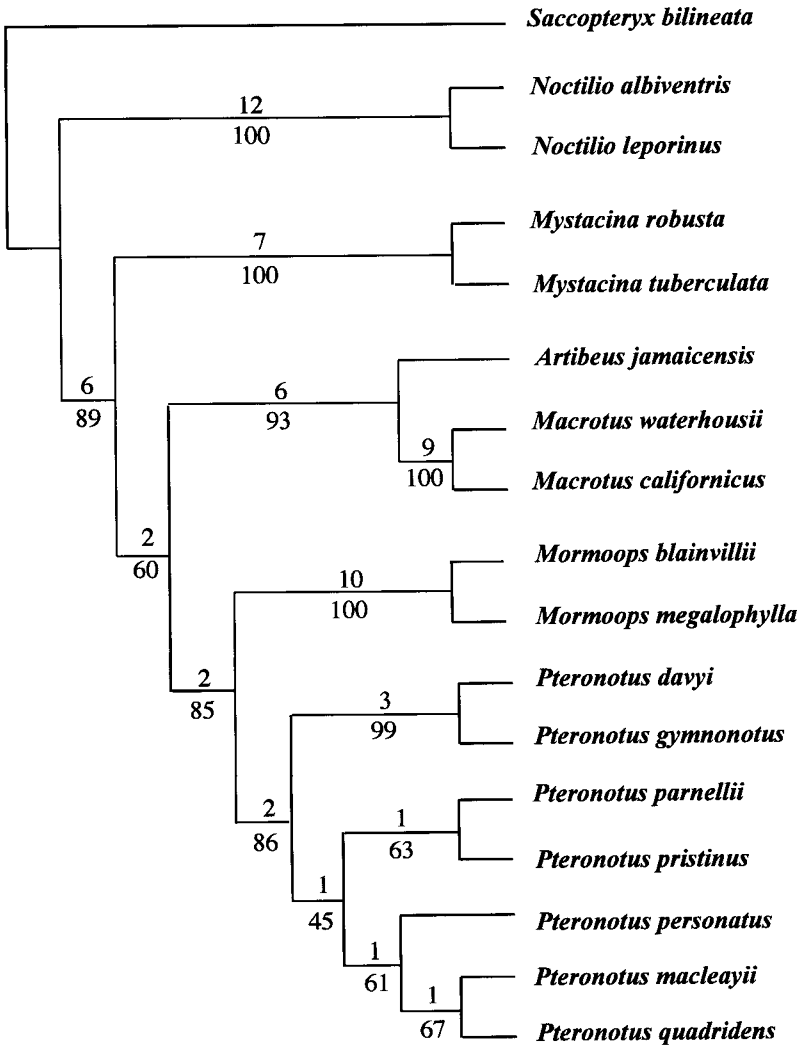


Fig. 12. Tree showing the results of our Analysis 2, which used ordered characters and included the fossil *Pteronotus pristinus.* This tree shows the topology of the single most-parimonious tree recovered (439 steps; CI = 0.652; CI excluding uninformative characters = 0.618; RI = .749). Decay values are given above each branch; bootstrap values are below (see tables 2 and 3 for associated branch length values and results of jackknife analysis). Results of our Analysis 3, which included the same taxa but treated all characters as unordered, produced an identical tree topology; see text for discussion.

cated by the strong support found for a Mormoopidae + Phyllostomidae + Mystacinidae clade that excludes Noctilionidae.

ANALYSIS 2: ALL TAXA, ORDERED CHARACTERS

Our second analysis included all of the taxa in our study (including the fossil species *Pteronotus pristinus*) and used the ordered character transformations described above under individual character descriptions. Parsimony analysis of these data resulted in a single most-parsimonious tree of 439 steps (fig. 12; CI = 0.652; CI excluding uninformative characters = 0.618; RI = 0.749). The topology of the branching pattern among the extant taxa was identical to that found in our Analysis 1. *Pteronotus pristinus* was unambiguously placed as the sister group of *P.*

TABLE 2
Bootstrap and Jacknife Support[a] for Identified Clades

Clade	Analysis 1 (fossil excluded)	Analysis 2 (all taxa)	Analysis 3 (characters unordered)
Noctilionidae	100/100[b]	100/100	100/100
Mystacinidae + Phyllostomidae + Mormoopidae	88/88	89/88	79/79
Mystacinidae	100/100	100/99	100/99
Phyllostomidae + Mormoopidae	70/69	60/61	46/46
Phyllostomidae	93/93	93/92	92/91
Macrotus	100/100	100/100	100/100
Mormoopidae	97/96	85/84	87/85
Mormoops	100/100	100/100	100/100
Pteronotus	99/99	86/84	86/82
Pteronotus davyi + P. gymnonotus	99/98	99/96	98/94
Pteronotus parnellii + P. pristinus + P. personatus + P. macleayii + P. quadridens	NA	45/41	39/35
Pteronotus parnellii + P. personatus + P. macleayii + P. quadridens	59/58	NA	NA
Pteronotus parnellii + P. pristinus	NA	63/54	65/53
Pteronotus personatus + P. macleayii + P. quadridens	62/63	61/61	62/63
Pteronotus macleayii + P. quadridens	66/64	67/64	60/57

[a] Results represent percentages of 10,000 replicate branch-and-bound searches.
[b] Bootstrap value/jackknife value.

parnellii. As in Analysis 1, no support was found for alternative arrangements placing Mormoopidae as the sister group of families other than Phyllostomidae (bootstrap and jackkinfe values ≤3% for all such arrangements), and little support was found for other arrangements of taxa within *Pteronotus* (bootstrap and jackknife values ≤22% for all alternative clades)

The only substantive differences between the results of Analysis 1 and Analysis 2 were in perceived support for several groupings, mostly along the backbone of the tree (tables 2, 3). Bootstrap and jackknife support for monophyly of Mormoopidae and a Mormoopidae + Phyllostomidae clade decreased approximately 10% when the incomplete fossil *P. pristinus* was included, and support for monophyly of *Pteronotus* was reduced by 15% (table 2). Support for these clades in decay analyses was even more strongly affected (table 3), with Analysis 2 decay values reduced by 65–85% in comparison to Analysis 1. Within *Pteronotus,* decay values for the *P. davyi + P. gymnonotus* clade (which was very strongly supported by bootstrap and jackknife results) were reduced 50% with the inclusion of *P. pristinus.* Although no decrease in support for monophyly of Noctilionidae, Mystacinidae, Phyllostomidae, *Macrotus,* and *Mormoops* was detected in the bootstrap and jackknife analyses, the decay values for each of these clades were reduced by 25–65% when *Pteronotus pristinus* was included in the analysis (tables 2, 3).

ANALYSIS 3: ALL TAXA, UNORDERED CHARACTERS

Our third analysis included all of the taxa in our study, but differed from the previous analyses in treating all character transformations as unordered. Parsimony analysis of this data set resulted in a single most-parsimonious tree of 416 steps (CI = 0.688; CI excluding uninformative characters = 0.655; RI = 0.767). To-

TABLE 3
Decay Values and Branch Lengths for Identified Clades

Clade	Analysis 1 (fossil excluded)	Analysis 2 (all data)	Analysis 3 (characters unordered)
Noctilionidae	29/29–54[a]	12/29–54	11/24–54
Mystacinidae + Phyllostomidae + Mormoopidae	7/15–42	6/15–42	5/12–40
Mystacinidae	10/11–52	7/11–52	7/9–49
Phyllostomidae + Mormoopidae	3/8–39	2/8–39	1/7–39
Phyllostomidae	10/18–45	6/18–45	6/16–46
Macrotus	19/20–44	9/20–44	9/17–44
Mormoopidae	10/16–46	2/16–46	3/14–47
Mormoops	28/29–48	10/29–48	9/26–47
Pteronotus	11/13–33	2/13–33	2/14–35
Pteronotus davyi + *P. gymnonotus*	6/6–11	3/6–11	3/4–10
Pteronotus parnellii + *P. pristinus* + *P. personatus* + *P. macleayii*+ *P. quadridens*	NA	1/2–13	1/2–13
Pteronotus parnellii + *P. personatus* + *P. macleayii* + *P. quadridens*	1/2–13	NA	NA
Pteronotus parnellii + *P. pristinus*	NA	1/1–25	1/1–24
Pteronotus personatus + *P. macleayii* + *P. quadridens*	1/4–10	1/4–10	1/4–10
Pteronotus macleayii + *P. quadridens*	1/2–6	1/2–6	1/2–5

[a] Decay value/miminum branch length–maximum branch length.

pology of this tree (not figured) was identical to that found in Analysis 2. Results of Analysis 3 differed from those of Analysis 2 only in the degree of perceived support for various clades (see tables 2 and 3). Decay values for most clades were not significantly changed when the characters were treated as unordered (table 3); however, bootstrap and jackknife support for some groupings were somewhat reduced. Bootstrap and jackknife support for the Mystacinidae + Mormoopidae + Phyllostomidae clade decreased approximately 10%, and support for Mormoopidae + Phyllostomidae decreased 15% (table 2). Values for many clades within *Pteronotus* remained relatively constant, although support for the *P. parnellii* + *P. pristinus* + *P. personatus* + *P. macleayii* + *P. quadridens* clade, as well as the *P. macleayii* + *P. quadridens* clade, was reduced by 6–7% (table 2).

Alternative Hypotheses

In addition to the analyses described above, we also attempted to evaluate previous phylogenetic arrangements by searching for the shortest trees compatible with those hypotheses. The shortest tree compatible with Smith's (1972) phylogeny (fig. 1) was found to be 443 steps long, 4 steps longer than the most-parsimonious tree (see results of Analysis 2 above). The shortest fully resolved tree compatible with the phylogeny of Arnold et al. (1982; fig. 2) was 449 steps long, 10 steps longer than the most-parsimonious tree. Finally, the shortest tree compatible with the trees published by Kennedy et al. (1999) was 468 steps long, 29 steps longer than the most-parsimonious tree. Topology of our most-parsimonious tree is entirely congruent with Van Den Bussche and Hoofer's (2000) phylogeny of noctilionoid relationships.

DISCUSSION AND CONCLUSIONS

Intrafamilial Relationships of Mormoopids

The results of our phylogenetic analyses were remarkably congruent with one another.

Monophyly of Mormoopidae, *Mormoops,* and *Pteronotus* was confirmed in all analyses regardless of taxonomic sampling or character ordering. Within *Pteronotus,* several clades were recovered: (1) *P. davyi* + *P. gymnonotus*; (2) *P. macleayi* + *P. quadridens*; (3) *P. personatus* + *P. macleayi* + *P. quadridens*; (4) *P. parnellii* + *P. pristinus* + *P. personatus* + *P. macleayi* + *P. quadridens*; and (5) *P. parnellii* + *P. pristinus.* These results support monophyly of all of the subgenera recognized by Smith (1972), and additionally indicate that the subgenera *Pteronotus* and *Chilonycteris* are sister taxa.

Our experiments with including and excluding the fossil taxon *Pteronotus pristinus* from otherwise identical analyses (Analyses 1 and 2) indicated that this species, known only from cranial material, can be placed unambiguously relative to extant species of mormoopids. The levels of support for its placement as the sister group of *P. parnellii* equalled values associated with several clades of extant taxa (tables 2, 3). It is clear from these results that the information preserved in fossils of *P. pristinus* was phylogenetically informative despite the fact that we could score this species for less than 16% of the characters in our study (table 1). However, there is a downside to including incompletely known taxa in a phylogenetic study. Inclusion of *P. pristinus* in the analysis did not affect tree topology, but it did negatively influence the decay, bootstrap, and jackknife values at many nodes, particularly those defining the family Mormoopidae and the genus *Pteronotus.* Decay values were most strongly influenced. These effects are likely due to the large amounts of missing data and correspondingly small numbers of informative characters associated with *P. pristinus.* Placement of *P. pristinus* in many alternative positions in the tree (e.g., as the sister group to all extant species of *Pteronotus,* to all extant mormoopids, or to Mystacinidae or Noctilionidae) requires only a few additional steps. As a result, inclusion of this taxon in our analyses had the effect of reducing decay values at many nodes in these regions of the tree. Bootstrap and jackknife analyses were also affected by the relatively small numbers of informative characters, some of which were undoubtedly excluded during the resampling process in many replicates.

Comparison of the results of Analyses 2 and 3 indicates that ordering character transformations did not bias tree topology in our study, as identical trees were recovered in both analyses. The only effect of ordering transformations in this study was to slightly increase perceived levels of support at most nodes, an expected outcome given the extra steps required by ordered characters under some circumstances. Overall length of the shortest tree was increased by 23 steps (5%) when we included ordered characters. Because the transformations implied by our ordering of character states are logical from an evolutionary and constructional standpoint (see justifications under individual character descriptions above), it is our view that these data are phylogenetically informative. We therefore regard the results (including the support values) from Analyses 1 and 2 as best representing the outcome of our study.

Comparisons of our tree with the shortest trees compatible with phylogenies of other authors indicated that our hypothesis is only slightly better supported by morphological data than that of Smith (1972). This is not surprising, given the general congruence of these hypotheses (figs. 1, 11, 12). Smith's (1972) hypothesis was based on morphology (indeed, we considered many of the same characters), and our tree differs from his only in placement of two taxa, *Pteronotus parnellii* and *P. personatus.* Greater incongruence exists between our tree and that of Arnold et al. (1982). Arnold et al.'s (1982) phylogeny, which was based on morphology, allozymes, immunology, and chromosome data, differs in the position of *P. parnellii* within *Pteronotus* and, more significantly, placement of Noctilionidae as the sister group of Mormoopidae (figs. 2, 11, 12). As noted above under ''Results'', we found no support for the latter hypothesis in our data set.

The greatest incongruence between our results and those of other authors involves trees based on cytochrome-*b* sequence data recently published by Kennedy et al. (1999). As noted in the ''Introduction'', those authors found that Mormoopidae was paraphyletic, with *Noctilio* placed as the sister group of *Pteronotus* (i.e., Noctilionidae nesting *within* Mormoopidae). This novel hypothesis was refuted in our analyses, which found strong support for monophyly of Mormoopidae under all analysis parameters. Given the sparse sampling of Mormoopidae in the Kennedy et al. (1999) study (which included only one species of *Mormoops* and two species of *Pteronotus*) and the heavy character weighting employed by those authors (see ''Introduction''), we believe that it is too early to assess the real level of incongruence between the phylogenetic signal preserved in cytochrome-b and morphological data.

Interestingly, there does not appear to be any significant incongruence between our morphological data and the 12S rRNA—tRNA^{Val}– 16S rRNA data of Van Den Bussche and Hoofer (2000). Eight species from their study were included in our analyses (*Saccopteryx bilineata, Noctilio albiventris, Noctilio leporinus, Mystacina tuberculata, Artibeus jamaicensis, Macrotus waterhousii, Mormoops megalophylla,* and *Pteronotus parnellii*), and the recovered phylogenetic relationships among these taxa were identical in our trees and theirs. This degree of congruence between morphological and molecular data is remarkable, and suggests that future combined-data analyses will be very profitable. In our opinion, Kennedy et al.'s (1999) finding of mormoopid paraphyly is unlikely to be substantiated in future analyses. At least three separate data sets support monophyly of Mormoopidae: morphology (Arnold et al., 1982; this study), karyotype data (Arnold et al., 1982), and 12S rRNA—tRNA^{Val}– 16S rRNA gene sequences (Van Den Bussche and Hoofer, 2000). In this context, mormoopid monophyly clearly represents the best-supported working hypothesis.

CLASSIFICATION AND TAXONOMIC DIAGNOSES OF MORMOOPID CLADES

Results of our study indicate that the classification of Mormoopidae developed by Smith (1972) is entirely appropriate from a phylogenetic standpoint. All of the higher-level taxa recognized in Smith's classification (i.e., families, genera, subgenera) are apparently monophyletic. The only alteration that we suggest is placement of the extinct species *Pteronotus pristinus* (which was described after Smith's revision) in the subgenus *Phyllodia* to reflect its close relationships to *Pteronotus parnellii.* The classification we propose is given in table 4.

TABLE 4

Proposed Classification of Mormoopid Bats

- Superfamily Noctilionoidea
  - Family Mormoopidae
    - Genus *Mormoops*
      - *Mormoops blainvillii*
      - *Mormoops megalophylla*
    - Genus *Pteronotus*
      - Subgenus *Pteronotus*
        - *Pteronotus davyi*
        - *Pteronotus gymnonotus*
      - Subgenus *Phyllodia*
        - *Pteronotus parnellii*
        - *Pteronotus pristinus* (extinct)
      - Subgenus *Chilonycteris*
        - *Pteronotus personatus*
        - *Pteronotus macleayii*
        - *Pteronotus quadridens*

Below we provide taxonomic diagnoses of all mormoopid clades based on DELTRAN and ACTRAN optimizations of our data (with characters ordered) on our shortest tree (including *Pteronotus pristinus*; fig. 12). Unambiguously derived conditions that represent synapomorphies are shown in italic type. Synapomorphies that are unique and unreversed in the context of our data set are additionally highlighted in boldface type. Plesiomorphic states, derived conditions that apply at higher taxonomic levels (e.g., derived features shared between mormoopids and phyllostomids), and states whose optimizations are ambiguous are listed in standard (Roman) type. Many of the latter features may represent synapomorphies of the taxa under which they are listed, but their status remains unclear in the absence of additional polarity information. In cases where missing data make the level of transformation of a character uncertain, we list each derived state (putative synapomorphy) under the smallest group in which it can be demonstrated to occur and note the other levels at which the transformation might apply.

The taxonomic diagnoses presented here should be interpreted as hypotheses subject to further testing. These hypotheses are obviously directly dependent on tree topology and taxonomic sampling. If future studies indicate phylogenetic relationships incongruent with topology of our shortest tree, then these diagnoses will require modification. Even if the topology remains stable, it is possible some features interpreted as unique synapomorphies in the context of the present analysis may have evolved convergently in groups not sampled in this study (e.g., in other phyllostomid genera). Conversely, additional polarity information may in the future make it possible to identify other unique, unreversed synapomorphies from among those characters whose polarity is unclear at present. In the mean time, the diagnoses presented below offer working hypotheses that may be used for identification and other purposes.

FAMILY MORMOOPIDAE

EMENDED DIAGNOSIS: Size small to medium (forearm length = 35–66 mm, condylobasal length = 12–22 mm; 3–28 g); premaxilla fused to maxilla ; palatal branch of premaxilla well developed, right and left premaxillae fused across midline of palate; pair of incisive foramina present; hard palate extends posteriorly into interorbital region; ***nasals concave upward in lateral view***; nasal foramina small or absent; postorbital process absent; epitympanic recess deep and constricted in area; fossa for m. stapedius indistinct; fenestra cochleae (= fenestra rotundum) enlarged, maximum diameter >25% of the external width of the first half-turn of the cochlea; pars cochlearis of petrosal loosely attached to basisphenoid via ligaments and/or thin splints of bone; cochlea greatly enlarged; tympanic annulus semivertical, lies at angle of 75–90° relative to basicranial plane; angular process of lower jaw projects above the level of the occlusal plane of cheekteeth; coronoid process of lower jaw does not extend dorsally above level of condyloid process; two pairs of upper incisors (I1 and I2) present; inner upper incisors (I1) bilobed; height of outer upper incisors (I2) less than one-half that of inner incisors (I1); two pairs of lower incisors (i1 and i2) present; inner lower incisors (i1) trilobed; two upper premolars (P3 and P4) present, (P1) absent; ***crown height of P3 subequal to that of P4***; three lower premolars (p1, p3, and p4) present; three upper molars (M1, M2, M3) present; three lower molars (m1, m2, m3) present; cristid obliqua on m1 and m2 extends from hypoconid to middle of posterior wall of protocristid; inferior colliculi partially exposed on dorsal surface of brain; ***first 5–8 tracheal rings enlarged to form tracheal expansion posterior to larynx***; basihyal with entoglossal process present; ceratohyal reduced to half the length of epihyal; m. mylohyoideus inserts on basihyal and basihyal raphe only; m. mandibulo-hyoideus absent; m. stylohyoideus absent or reduced to a few fibers fused with m. stylopharyngeus, deep to the digastric muscles; *m. geniohyoideus originates by long tendon from the mandible*; paired m. geniohyoideus muscles partially or completely fused across midline; midline hyoid strap muscles with m. genioglossus and m. hyoglossus attached directly to basihyal via fleshy fibers; m. styloglossus with one belly; m. ceratohyoideus insertion included ceratohyal but does not include stylohyal; m. sternothyroideus originates from clavicle; m. omohyoideus originates from scapula; m. cricopharyngeus consists of a single large slip of muscle; ***m. cricothyroideus complex consists of two separate muscles, m. cricothyroideus anterior and m. cricothyroideus posterior***; lateral circumvallate papillae present; basketlike medial-posterior mechanical papillae present; *pharyngeal region of tongue totally bare of papillae*; internal labial papillae absent; cheek pouches absent; lower lip with multiple dermal papillae; *one or more transverse flaps present below lower lip*; anterior edge of labio-nasal region does not protrude anteriorly beyond edge of lower lip; *one dermal projection present lateral to each nostril*; *pinnae funnel-shaped*; *distal tip of tragus rounded*; ***secondary fold present on tragus***; interramal vibrissae present; interramal tubercle well developed; superciliary vibrissae absent; vibrissae on face posterior and lateral to narial pad arranged in two roughly parallel vertical columns; two vibrissae present in anteromedial column; facial stripes absent; dorsal stripes absent; *underhair and overhair clearly differentiated*; scales on dorsal hairs divergent or appressed, not divaricate; wings folded by flexing all phalanges in digits III, IV, and V anteriorly toward the underside of the wing; antebrachial wing sac absent; uropatagium broad; ***both uropatagium and plagiopatagium attach to calcar***; C6 with enlarged ventral processes; 12 or more thoracic vertebrae present; pair of parallel ridges present on ventral surface of T4; ***last two thoracic and first two lumbar vertebrae fused***; L3 with pair of parallel ridges on ventral surface; anterior face of manubrium of sternum small, not defined by elevated ridges; distal tip of ventral process of manubrium laterally compressed and keel-like; length of manubrium less than width; mesosternum without large keel; second rib contacts sternum at manubrium–mesosternum joint; mesosternum articulates with six costal cartilages posterior to second rib; xiphisternum with prominent median keel; clavicle articulates with or lies in contact with coracoid process of scapula; ***pit for attachment of clavicular ligament present on scapula***; tip of acromion process with triangular anterior projection; suprascapular process present; dorsal articular facet consists of an oval facet on the anteromedial rim of the glenoid fossa, faces dorsolaterally; anterior portion of axillary border of scapula flattened; *head of humerus oval or elliptical in medial view (not round)*; trochiter extends proximally just to the level of the proximal edge of the humeral head; *height of distal spinous process of humerus greater than height of trochlea*; metacarpal of digit V of wing shorter than metacarpals of digits III and IV; first phalanx in wing digit II long, length more than four times shaft diameter; third phalanx of wing digit III long and completely ossified; ischial tuberosity small or absent; length of public spine equal to or greater than one-half length of ilium; pubic symphysis in male relatively long; ***greater and lesser trochanters of femur reduced, flanges do not extend beyond sides of femoral head***; well-developed ridge present on femoral shaft distal to lesser trochanter; distal femur straight; fibula thin and threadlike, often only partly ossified; tail length approximately the same as length of tibia; calcaneum not expanded or flattened; calcar at least partly ossified; length of hind foot less than or equal to one-half tibia length; claws without basal talons; m. humeropatagialis present; m. occipitopollicalis with a tendinous attachment to the anterior division of m. pectoralis profundus; m. occipitopollicalis insertional complex entirely tendinous distal to band of elastic tissue; m. teres major inserts into ventral ridge of humerus; m. extensor digitorum communis originates from radius and ulna only, no humeral origin; m. flexor digitorum profundus inserts onto second phalanges of digits I, III, IV, and V; m. palmaris longus inserts onto metacarpal of digits II and III; digital tendon locking mechanism absent from digits of hind feet; female external genitalia with vulval opening oriented anteroposteriorly; external uterine horns one-half length of common uterine body; common uterine body large, coronal lumina join immediately within the common uterine body; oviductal papilla absent; oviductal mucosal folds occur throughout oviduct; ovarian ligament extends from ovary to external entry of oviduct; cardiac vestibule of stomach very small or absent; mucous-producing pyloric glands distributed in an extremely narrow zone immediately adjacent to pyloric sphincter; pyloric sphincter asymmetrical, valve in lesser curvature smaller than valve in greater curvature; Brunner's glands at gastroduodenal junction unusually abundant, with narrow tubules and small cells with extremely small, flattened nuclei that are not juxtaposed to the basement membrane.

Genus *Mormoops*

EMENDED DIAGNOSIS: Size small to medium (forearm length = 43–61 mm; condylobasal length = 12–14 mm; 6–20 g); ***rostrum strongly upturned, angle between long axis of anterior half of zygomatic arch and occlusal surface of molar toothrow 28–34°***; maximum rostral breadth less than or equal to length of maxillary toothrow; rostral length less than one-half of total length of skull; infraorbital foramen not enlarged, diameter less than one-eighth the height of rostrum; *infraorbital foramen located above posterior half of P4; anterior rim of orbit terminates above M1*; zygomatic breadth greater than mastoid breadth; ***parietals inflated***; cochlea phanerocochlear; ectotympanic bulla extends medially across two-thirds or more of cochlea; longitudinal furrows in basisphenoid wide and shallow; basioccipital not constricted between cochlea; *lingual cingulae absent on upper incisors (I1 and I2)*; diastema present between outer upper incisor (I2) and canine; outer lower incisors (i2) trilobed; *diastema present between upper P3 and P4*; *lower p3 double-rooted*; crown length of lower p3 and p4 subequal; no cuspule present on premetacrista on M1 and M2; *lower first and second molars (m1 and m2) nyctalodont*; horny papillae on tongue of different sizes, largest near midline; distal tips of medial-posterior mechanical papillae directed toward pharyngeal region; lower lip of moderate size, dorsoventral height less than height of nostrils; ***lower lip with horseshoe-shaped dermal pad***; two transverse flaps present below lower lip; nostrils tubelike, openings face slightly laterally and are not adjacent; ***narial pad with narrow, papillated vertical ridge between nostrils***; anterodorsal edge of narial pad unadorned, without ridge of skin or noseleaf; ***one dermal papilla present on dorsal surface of each nostril***; dermal projection lateral to nostril triangular and pointed distally, lateral side not continuous with lip; prominent dermal tubercle present on midline of muzzle posterodorsal to nostrils; *prominent interauricular band present*; ***distal pinna squared, pinna height relatively uniform across the entire width of the pinna***; lateral edge of distal pinna smooth; ***tragus with distinctly thickened area at base***; ***secondary fold equal to or larger than body of tragus***; two interramal vibrissae present; ***genal vibrissae absent***; dorsal and ventral fur with two or more bands of color; dorsal fur long, 8–10 mm; ***dorsal hairs with dentate coronal scales***; dorsal hair scales divergent; plagiopatagium attaches to the side of the body, dorsal fur exposed on back between right and left membranes; calcar not bound to tibia; ***seventh cervical vertebra fused to first thoracic vertebra***; 13 thoracic vertebrae present; neural spines absent from all thoracic vertebrae; *pair of parallel ridges absent from ventral surface of fourth and fifth lumbar vertebra*; angle between axis of ventral process of manubrium and body of manubrium approximately 90°; anterior and posterior laminae present on ribs; tip of coracoid process not flared, approximately the same width as coracoid shaft; tip of acromion process without a posterolateral projection; ***axillary border of scapula curved in dorsoventral plane, concave ventrally***; humerus with distal articular facets in line with shaft, not displaced laterally; ***central surface of capitulum of humerus reduced, height less than that of trochlea***; *distal spinous process of humerus located directly adjacent to trochlea, no notch present between process and trochlea*; olecranon process of ulna well developed, extends beyond proximal end of radius; *pisiform dumbbell-shaped, enlarged at both ends*; metacarpal formula $5 < 4 = 3$; wing digit I with first phalanx longer than metacarpal; first and second phalanges of wing digit IV subequal in length; sacral vertebrae not fused to ischium posteriorly; calcar cartilaginous distally, with clearly demarcated calcified base; *calcar length approximately twice length of hind foot*; ***m. triceps caput medialis absent***; m. coracobrachialis smaller than coracoid head of m. biceps brachii, originates from tip of coracoid process of scapula; ***m. biceps brachii insertional tendons encased in sling of connective tissue***; ***m. brachialis absent***; ***sesamoid present in tendon of m. extensor carpi radialis longus***; m. extensor policis brevis originates from ulna; tendon from m. extensor digitorum communis inserts on second phalanx of digit V; ***m. extensor digiti quinti proprius originates from lateral epicondyle of humerus only***; m. palmaris longus robust; clitoris of moderate size.

Mormoops blainvillii

EMENDED DIAGNOSIS: Size medium-small (forearm length = 43–50 mm; condylobasal length = 12–14 mm; 6–11 g); dorsal fur bicolored; ventral fur bicolored; pair of parallel ridges present on ventral surface of third lumbar vertebra; ribs with narrow anterior laminae; ribs with narrow posterior laminae; infraspinous fossa of scapula wide, maximum width greater than 50% of maximum length; intermediate infraspinous facet and posterolateral facet subequal in width; *distal spinous process of humerus with ventral projection that extends perpendicular to shaft;* ascending process of ilium without flared or upturned dorsomedial edge upturned, iliac fossa small and poorly defined.

No information on structure of the vomeronasal complex, hyoid apparatus, shoulder myology, or submaxillary glands is available for this species.

Mormoops megalophylla

EMENDED DIAGNOSIS: Size medium-large (forearm length = 49–61 mm; condylobasal length = 12–22 mm; 12–20 g); vomeronasal epithelial tube rudimentary, lacking a neuroepithelial medial lining (may apply at level of *Mormoops*); vomeronasal cartilage curved in cross section, "J", "C", "U", or "O" shaped (may apply at level of *Mormoops*); nasopalatine duct present (may apply at level of *Mormoops*); accessory olfactory bulb absent (may apply at level of *Mormoops*); m. sternohyoideus originates from entire surface of manubrium, no clavicular origin (may apply at level of *Mormoops* or *Mormoopidae*); ***dorsal fur with four bands of color***; ***ventral fur polymorphic, either bicolored or tricolored***; *pair of parallel ridges absent from ventral surface of third lumbar vertebra; ribs with wide anterior laminae*; ribs with wide posterior laminae; *infraspinous fossa of scapular narrow, maximum width less than or equal to 50% of maximum length*; intermediate infraspinous facet narrower than posterolateral facet; distal spinous process of humerus without ventral projection; *ascending process of ilium with dorsomedial edge upturned, flares dorsally above the level of the iliosacral articulation, iliac fossa large and well defined*; *m. spinodeltoideus originates from vertebral border of scapula plus more than three-fourths of the transverse scapular ligament* (may apply at level of *Mormoops*); *m. teres major origin restricted to tip of axillary border of scapula* (may apply at level of *Mormoops*); *submaxillary glands of serous type* (may apply at level of *Mormoops*).

Genus *Pteronotus*

EMENDED DIAGNOSIS: Size small to medium (forearm length = 35–66 mm; condylobasal length = 12–22 mm; 3–28 g); rostrum slightly upturned, angle between long axis of anterior half of zygomatic arch and occlusal surface of molar toothrow 13–26°; *anterior rim of orbit terminates above posterior half of M2*; parietals not inflated; lingual cingulae present on upper incisors (I1 and I2); diastema absent between upper P3 and P4; lower p3 single-rooted; *crown length of lower p3 less than or equal to one-half crown length of p4*; *horny papillae on tongue of uniform size*; ***medial-posterior mechanical papillae basin-shaped with no clear inclination***; ***lower lip large and platelike, dorsoventral height equal to or greater than height of nostrils***; lower lip without horseshoe-shaped dermal pad; ***one transverse flap present below lower lip***; nostrils open directly adjacent to each other and face anteriorly; anterodorsal edge of narial pad with papillated ridge of skin present; no dermal papillae on dorsal surface of nostril; interauricular band absent; distal pinna lancolate, tapers to blunt point; tragus thin, of uniform thickness throughout; secondary fold smaller than body of tragus; one interramal vibrissa present; one genal vibrissa present on each cheek; *dorsal fur short, 4–7 mm*; dorsal hairs with appressed scales; seventh cervical vertebra not fused to first thoracic vertebra; 12 thoracic vertebrae present; *neural spines present on first four thoracic vertebrae*; pair of parallel ridges present on ventral surface of third, fourth, and fifth lumbar vertebrae; angle between axis of ventral process of manubrium and body of manubrium greater than 90°; ribs with wide posterior laminae; tip or coracoid process distinctly flared; infraspinous fossa of scapula wide, maximum width greater than 50% of maximum length; *intermediate and posterolateral infraspinous facets subequal* (reversed in *P. personatus*); axillary border of scapula flat, level within dorsoventral plane; humerus with distal articular facets displaced laterally from line of shaft; central surface of capitulum of humerus not reduced, height equal to that of trochlea; distal spinous process of humerus separated from trochlea by a deep notch; distal spinous process of humerus without ventral projection; ***olecranon process of ulna reduced, does not extend beyond the proximal end of radius***; pisiform rodlike, of uniform width throughout; metacarpal formula 5 < 4 < 3; *first phalanx of wing digit I longer than metacarpal*; second phalanx of wing digit IV longer than first phalanx; *posterior sacral vertebrae fused to posterior ischium*; *calcar entirely calcified*; m. spinodeltoideus originates from vertebral border of scapula and one-half to two-thirds of transverse scapular ligament; m. teres major originates from one-fourth to two-fifths of axillary border of scapula; m. triceps caput medialis present; m. biceps brachii insertional tendons not encased in sling; m. brachialis present; no sesamoid present in tendon of m. extensor carpi radialis longus; ***m. extensor policis brevis originates from both ulna and radius***; ***m. palmaris longus vestigial***; submaxillary glands of mucous type.

Subgenus *Pteronotus*

Emended Diagnosis: Size small to medium (forearm length = 40–56 mm; condylobasal length = 13–17 mm; 5–18 g); *maximum rostral breadth greater than length of maxillary toothrow*; rostral length less than one-half of total length of skull; infraorbital foramen not enlarged, diameter less than one-eighth height of rostrum; *infraorbital foramen located above posterior half of M1*; zygomatic breadth greater than mastoid breadth; cochlea phanerocochlear; ectotympanic bulla extends medially across two-thirds or more of cochlea; longitudinal furrows in basisphenoid wide and shallow; basioccipital not constricted between cochlea; diastema present between outer upper incisor (I2) and canine; outer lower incisors (i2) trilobed; no cuspule present on premetacrista on M1 and M2; lower first and second molars (m1 and m2) myotodont; narial pad flat, with no notch or ridge between nostrils; dermal projection lateral to nostril triangular and pointed distally, lateral side not continuous with lip; no dermal tubercle on midline of muzzle posterodorsal to nostrils; lateral edge of distal pinna smooth; *dorsal fur unicolored*; midshaft scales on dorsal hair filaments all entire coronal; ***plagiopatagium attaches at mid-dorsal line, right and left membranes meet over spine and cover dorsal fur***; calcar not bound to tibia; neural spines decrease in height from first thoracic through fourth thoracic vertebra; neural spines present on T8–T12; ribs with narrow anterior laminae; *distal acromion process with triangular posterolateral projection*; ascending process of ilium without flared or upturned dorsomedial edge upturned, iliac fossa small and poorly defined; calcar length approximately one and one-half times length of hind foot; m. coracobrachialis approximately twice the size of coracoid head of m. biceps brachii, originates proximal to tip of coracoid process of scapula; tendon from m. extensor digitorum communis inserts on second phalanx of digit V; m. extensor digiti quinti proprius originates from lateral epicondyle of humerus and dorsal base of ulna; clitoris of moderate size.

Pteronotus davyi

Emended Diagnosis: Size medium-small (forearm length = 40–50 mm; condylobasal length = 13–16 mm; 5–11 g); m. sternohyoideus originates from entire surface of manubrium, no clavicular origin (may apply at level of subgenus *Pteronotus* or Mormoopidae); ventral fur bicolored.

Pteronotus gymnonotus

Emended Diagnosis: Size medium-large (forearm length = 49–56 mm; condylobasal length = 15–17 mm; 11–18 g); ***ventral fur unicolored.***

Unnamed Clade 1 (*Phyllodia* + *Chilonycteris*)

Diagnosis: Size small to medium (forearm length = 35–66 mm; condylobasal length = 12–22 mm; 3–28 g); maximum rostral breadth less than or equal to length of maxillary toothrow; vomeronasal cartilage bar-shaped in cross section; dorsal fur bicolored or tricolored; ventral fur bicolored; plagiopatagium attaches to the side of the body, dorsal fur exposed on back between right and left membranes; ***caudal half of calcar bound to tibia, calcar restricted to position parallel to tibia***; tip of acromion process without a posterolateral projection; *length of calcar and hindfoot subequal* (reversed in *P. macleayi*).

Subgenus *Phyllodia*

Emended Diagnosis: Size medium (forearm length = 48–66 mm; condylobasal length = 16–22 mm; 10–28 g); rostral length less than one-half of total length of skull; infraorbital foramen located above anterior half of M1; zygomatic breadth greater than mastoid breadth; *longitudinal furrows in basisphenoid narrow and deep*; no cuspule present on premetacrista on M1 and M2; lower first and second molars (m1 and m2) myotodont.

Because one member of this clade (*Pteronotus pristinus*) is a fossil species known only from cranial material, we have chosen not to include postcranial and soft-tissue characters in the diagnosis of *Phyllodia*. However, numerous derived states in these character systems are found in *Pteronotus parnellii* (see below), and many of these may actually apply at the level of *Phyllodia*.

Pteronotus parnellii

EMENDED DIAGNOSIS: Size medium (forearm length = 35–66 mm; condylobasal length = 16–22 mm; 10–28 g); infraorbital foramen not enlarged, diameter less than one-eighth height of rostrum; *cochlea cryptocochlear* (may apply to all *Phyllodia*); ***ectotympanic bulla extends medially across no more than one-third of cochlea*** (may apply at level of *Phyllodia*); *basioccipital markedly constricted between cochlea* (may apply at level of *Phyllodia*); *diastema present between outer upper incisor (I2) and canine (C); outer lower incisors (i2) bilobed*; *vomeronasal epithelial well developed, neuroepithelium medial lining present* (may apply at level of *Phyllodia*); nasopalatine duct absent; *accessory olfactory bulb present* (may apply at level of *Phyllodia*); ceratohyal reduced to approximately one-half length of epihyal; *m. mylohyoideus occurs as an undivided sheet of muscle with an anterior aponeurosis* (may apply at level of *Phyllodia, Phyllodia* + *Chilonycteris,* genus *Pteronotus,* or Mormoopidae); m. sternohyoideus origin includes clavicle; m. styloglossus with two bellies; ***m. sphincter coli profundus absent*** (may apply at level of *Phyllodia, Phyllodia* + *Chilonycteris,* genus *Pteronotus,* or Mormoopidae); *narial pad with V-shaped notch present between nostrils* (may apply at level of *Phyllodia*); dermal projection lateral to nostrils rounded distally, lateral side of projection continuous with lip (may apply at level of *Phyllodia* or *Phyllodia* + *Chilonycteris*); prominent dermal tubercle present on midline of muzzle posterodorsal to nostrils; lateral edge of distal pinna smooth; ***dorsal fur polymorphic, either bicolored or tricolored*** (may apply at level of *Phyllodia*); dorsal hairs with alternating entire coronal and hastate coronal scales; ***height of neural spines subequal on first four thoracic vertebrae*** (may apply at level of *Phyllodia*); neural spines present on T8–T12; *ribs with wide anterior laminae* (may apply at level of *Phyllodia*); ascending process of ilium with dorsomedial edge upturned, flares dorsally above the level of the iliosacral articulation, iliac fossa large and well defined; m. coracobrachialis smaller than coracoid head of m. biceps brachii, originates from tip of coracoid process of scapula; tendon from m. extensor digitorum communis inserts on second phalanx of digit V; ***m. extensor digiti quinti proprius originates from second division of m. extensor digitorum communis and posterodorsal base of radius*** (may apply at level of *Phyllodia*); clitoris of moderate size

Pteronotus pristinus (extinct)

EMENDED DIAGNOSIS: Size medium (greatest length of skull 17–18 mm [condylobasal length not available]); *infraorbital foramen enlarged, diameter one-quarter to one-third height of rostrum*; diastema absent between outer upper incisor (I2) and canine (C); outer lower incisors (i2) trilobed.

No information on postcranial skeletal morphology or soft-tissue characters is available for this species.

Subgenus *Chilonycteris*

EMENDED DIAGNOSIS: Size small to medium (forearm length = 35–49 mm; condylobasal length = 13–16 mm; 3–11 g); infraorbital foramen not enlarged, diameter less than one-eighth the height of rostrum; ***zygomatic breadth less than mastoid breadth***; cochlea phanerocochlear; ectotympanic bulla extends medially across two-thirds or more of cochlea; longitudinal furrows in basisphenoid wide and shallow; basioccipital not constricted between cochlea; diastema present between outer upper incisor (I2) and canine; outer lower incisors (i2) trilobed; *lower first and second molars (m1 and m2) nyctalodont*; ***lateral edge of distal pinna serrated***; dorsal fur either bicolored or tricolored; ***dorsal hairs with denticulate coronal scales***; neural spines decrease in height from first thoracic through fourth thoracic vertebra; ribs with narrow anterior laminae; m. coracobrachialis approximately twice the size of coracoid head of m. biceps brachii, originates proximal to tip of coracoid process of scapula; ***tendon from m. extensor digitorum communis inserts on shaft of metacarpal of digit V.***

Pteronotus personatus

EMENDED DIAGNOSIS: Size medium-small (forearm length = 40–49 mm; condylobasal length = 13–16 mm; 5–11 g); rostral length less than one-half of total length of skull; ***infraorbital foramen located above anterior half of M2***; ***cuspule present on premetacrista on M1 and M2***; *vomeronasal epithelial tube absent* (may apply at level of *Chilonycteris*); nasopalatine duct present; accessory olfactory bulb absent; *ceratohyal unreduced, approximately equal in length to epihyal* (may apply at level of *Chilonycteris*); narial pad flat, with no notch or ridge between nostrils; dermal projection lateral to nostrils rounded distally, lateral side of projection continuous with lip; prominent dermal tubercle present on midline of muzzle posterodorsal to nostrils; dorsal fur bicolored; neural spines absent on T8–T12; *intermediate infraspinous facet narrower than posterolateral facet*; ascending process of ilium with dorsomedial edge upturned, flares dorsally above level of iliosacral articulation, iliac fossa large and well defined; *m. extensor digiti quinti proprius originates from lateral epicondyle of humerus only.*

Unnamed Clade 2 (*P. macleayi* + *P. quadridens*)

EMENDED DIAGNOSIS: Size small (forearm length = 35–46 mm; condylobasal length = 13–16 mm; 3–8 g); ***rostral length equal to or greater than one-half of total length of skull***; infraorbital foramen located above anterior half of M1; no cuspule present on premetacrista on M1 and M2; dermal projection lateral to nostril triangular and pointed distally, lateral side not continuous with lip; no dermal tubercle on midline of muzzle posterodorsal to nostrils; ***dorsal fur tricolored***; ascending process of ilium without flared or upturned dorsomedial edge, iliac fossa small and poorly defined; m. extensor digiti quinti proprius originates from lateral epicondyle of humerus and dorsal base of ulna.

Pteronotus macleayii

EMENDED DIAGNOSIS: Size small (forearm length = 41–46 mm; condylobasal length = 14–16 mm; 4–8 g); *narial pad with V-shaped notch present between nostrils*; neural spines present on T8–T12; *calcar length approximately one and one-half times length of hind foot*; *clitoris elongated.*

Pteronotus quadridens

EMENDED DIAGNOSIS: Size small (forearm length = 35–40 mm; condylobasal length = 12–14 mm; 3–6 g); narial pad flat, with no notch or ridge between nostrils; neural spines absent on T8–T12; length of calcar and hind foot subequal; clitoris of moderate size.

MONOPHYLY AND DIAGNOSES OF NOCTILIONOID FAMILIES

In addition to the diagnoses of mormoopid taxa presented above, our study also has implications for the diagnoses of Phyllostomidae, Noctilionidae, and Mystacinidae, all of which appear monophyletic in our study. As noted previously, our sampling within Phyllostomidae was poor given the diversity of that family (3 species sampled out of more than 140), but our sample of Noctilionidae and Mystacinidae was complete (2 out of 2 species in each family). Lack of data for many characters in *Mystacina robusta* and *M. tuberculata* (73% and 62% complete in the context of our character set; see table 1) and absence of additional outgroups to Noctilionoidea (e.g., vespertilionids, nataloids, molossoids) rendered polarity of many characters uncertain at the base of our tree. In recognition of these multiple sources of uncertainty, we have not attempted to produce complete diagnoses of Phyllostomidae, Mystacinidae, and Noctilionidae. Instead, we provide here lists of synapomorphies of these families identified in our study. Features that are unique and unreversed in the context of our data set and tree are shown in bold.

Unambiguous synapomorphies supporting monophyly of Phyllostomidae include: (1) **epitympanic recess shallow and broad**; (2) diastema absent between outer upper incisor (I2) and canine; (3) inner lower incisor (i1) bilobed; (4) outer lower incisor (i2) bilobed; (5) vomeronasal epithelial tube well developed, neuroepithelium medial lining present; (6) **m. cricopharyngeus consists of 3 or more slips;** (7) **narial pad with wide, smooth-sided vertical ridge between nostrils**; (8) **noseleaf present**; (9) ventral processes of C6 not enlarged, similar in width to those of C2–C5; (10) xiphisternum without median keel; (11) second costal cartilage articulates with manubrium only (no contact with mesosternum); (12) tip of acromion process without triangular anterior projection; (13) suprascapular process absent; (14) **friction tendon locking mechanism present on digits of hind feet**; (15) **length of external uterine horns less than or equal to one-fourth length of common uterine body**; (16) **oviductal mucosal folds restricted to extramural oviduct**; (17) **mucous-producing pyloric glands distributed in a broad zone in stomach**; and (18) **Brunner's glands at gastroduodenal junction present in small to moderate numbers, with broad tubules and moderate to large cells with large spherical nuclei that are juxtaposed to the basement membrane.** Other derived conditions that were incompletely sampled in our study might represent additional synapomorphies of Phyllostomidae if future studies demonstrate that they apply at the base of the phyllostomid tree. These include: (19) accessory olfactory bulb present; (20) **m. humeropatagialis absent**; and (21) **submaxillary glands absent.**

Unambiguous synapomorphies supporting monophyly of Mystacinidae include: (1) infraorbital foramen enlarged, diameter one-quarter to one-half height of rostrum; (2) infraorbital foramen located above posterior half of M1; (3); anterior rim of orbit terminates above posterior half of M2; (4) **uropatagium rudimentary**; (5) **coracoid process reduced to a small triangular process**; (6) **distal acromion process with elongate projection that extends anteriorly and medially to fuse with anteromedial rim of scapula**; (7) **dorsal articular facet on scapula faces dorsally, consists of a large, flat facet clearly separated from the glenoid fossa**; (8) distal spinous fossa of humerus located directly adjacent to trochlea, no notch present between these structures; (9) calcar length equal to approximately one-half hind foot length; and (10) **claws of thumb and hindfoot with basal talons.** Several other derived conditions that we could score in only one species of *Mystacina* (but which may occur in both taxa) would represent additional synapomorphies of Mystacinidae if they can be shown to occur in both species: (11) **vomeronasal cartilage absent**; (12) **m. mandibulo-hyoideus present;** (13) **origin of m. sternohyoideus restricted to medial manubrium**; (14) insertion of m. ceratohyoideus does not include ceratohyal; (15) **m. sternothyroideus originates from lateral manubrium (no clavicular origin)**; (16) **m. omohyoideus absent**; (17) anterior face of manubrium broad, defined by elevated ridges; (18) **distal tip of ventral process of manubrium blunt and rounded (not keel-like)**; (19) **ribs with no posterior laminae**; (20) calcar entirely cartilaginous; and (21) uterotubal junction with oviductal papilla present.

Unambiguous synapomorphies supporting monophyly of Noctilionidae include: (1) **incisive foramina absent**; (2) **pair of large nasal foramina present in posterior nasal region below forehead**; (3) maximum rostral breadth greater than length of maxillary toothrow; (4) cochlea cryptocochlear; (5) **cristid obliqua on lower first and second molars (m1 and m2) extends from hypoconid to metaconid**; (6) basketlike medial-posterior mechanical papillae absent; (7) **cheek pouches present;** (8) two rows of transverse flaps present below lower lip; (9) pinna funnel-shaped; (10) **distal tip of tragus bifurcate**; (11) two vibrissae present in anteromedial column (adjacent to narial pad); (12) ventral fur unicolored; (13) **single pale middorsal stripe often present**; (14) overhair and underhair clearly differentiated in dorsal pelage; (15) **scales on dorsal hairs exhibit continuous range of variation from entire coronal to repand coronal**; (16) **wings folded by flexing the distal phalanges of digits III and IV anteriorly, proximal phalanges not folded**; (17) **11 thoracic**

vertebrae present; (18) third lumbar vertebra without pair of ridges on ventral surface; (19) xiphisternum without prominent median keel; (20) second costal cartilage articulates with manubrium only (no contact with mesosternum); (21) ribs with wide anterior laminae; (22) distal acromion process with triangular posterolateral projection; (23) **dorsal articular facet on scapula absent**; (24) head of humerus oval or elliptical, not round; (25) **metacarpal formula 3 = 5 < 4**; (26) first phalanx and metacarpal of wing digit I subequal in length; (27) posterior sacral vertebrae fused with posterior ischium; (28) ascending process of ilium with dorsomedial edge upturned, flares dorsally above the level of the iliosacral articulation, iliac fossa large and well defined; (29) tail length approximately equal to one-half of tibia length; (30) **calcaneum expanded and flattened**; (31) calcar length approximately twice length of hind foot; (32) **m. occipitopollicalis with no tendinous attachment to anterior division of m. pectoralis profundus**; (33) **m. teres major originates from one-half to three-fourths of axillary border of scapula**; and (34) clitoris elongated, length approximately twice width at base. Two derived conditions that we could score in only one species of *Noctilio* would represent additional synapomorphies of Noctilionidae if they can be shown to occur in both species: (35) **ceratohyal reduced to a tiny cartilaginous element**; and (36) **right and left m. geniohyoideus not fused across midline.**

INTERFAMILIAL RELATIONSHIPS

Phylogenetic relationships among noctilionoid families have been the source of considerable debate in recent years. As noted in the ‘‘Introduction,’’ previous phylogenetic analyses have placed Mormoopidae either with Noctilionidae (e.g., Patton and Baker, 1978; Arnold et al., 1982; Simmons, 1998; Simmons and Geisler, 1998; Kennedy et al., 1999) or as the sister group of Phyllostomidae (Van Valen, 1979; Novacek, 1991; Kirsch et al., 1998; Van Den Bussche and Hoofer, 2000). Results of our study support the latter hypothesis. The phyllostomid and mormoopid taxa in our study together formed a clade (excluding both Mystacinidae and Noctilionidae) in our shortest trees (figs. 11, 12), and support was found for this grouping in all analyses (tables 2, 3). Bootstrap and jackknife support for the alternative grouping (Mormoopidae + Noctilionidae) was much lower in all analyses (bootstrap and decay values ≤3). No support was found for a Phyllostomidae + Noctilionidae clade in any analysis (bootstrap and decay values ≤1).

Echoing the results of Van Den Bussche and Hoofer’s (2000) study of mitochondrial gene sequences, results of our analyses indicated that Mystacinidae is the sister group of the Mormoopidae + Phyllostomidae clade. These three families formed a clade (excluding Noctilionidae) in our shortest trees (figs. 11, 12), and strong support for was found for this grouping in all analyses (tables 2, 3).

As with the family diagnoses presented above, we provide lists below of unambiguous synapomorphies of the larger noctilionoid clades identified in our study. Features that are unique and unreversed in the context of our data set and tree are shown in bold. Our data cannot provide a diagnosis for Noctilionoidea because our study did not include enough outgroups (e.g., nataloids, molossoids, or vespertilionoids).

Unambiguous synapomorphies supporting monophyly of a Phyllostomidae + Mormoopidae clade include: (1) **tympanic annulus semivertical, lies at angle of 75–90° to basicranial plane**; (2) vomeronasal epithelial tube present; (3) **anterior edge of labio-nasal region does not protrude anteriorly beyond edge of lower lip, muzzle appears blunt**; (4) narial pad flat, with no notch or ridge between nostrils; (5) **genial vibrissae reduced to one on each cheek or absent entirely**; (6) **wings folded by flexing all phalanges in digits III, IV, and V anteriorly toward the underside of the wing**; (7) **third phalanx of wing digit III long and fully ossified**; (8) **pubic spine length equal to or greater than one-half length of ilium**; (9) **m. occipitopollicalis insertional complex entirely tendinous distal to band of elastic tissue** (this feature could not be scored in either species of *Mystacina*, so it may apply at the next higher level); (10) m. spinodeltoideus originates from vertebral border of scapula plus one-half to two-thirds of the transverse scapular ligament (this feature could not be scored in either species of *Mystacina,* so it may apply at the next higher level); (11) **m. teres major inserts into ventral base of pectoral crest** (this feature could not be scored in either species of *Mystacina,* so it may apply at the next higher level); and (12) **common uterine lumen large or very large, coronal lumina either join immediately within the common uterine body, are reduced to tubular intramural cornua, or are absent entirely.**

Unambiguous synapomorphies of a Mystacinidae + Mormoopidae + Phyllostomidae clade include: (1) anterior rim of orbit terminates at or posterior to the anterior half of M2; (2) ectotympanic bulla extends medially across two-thirds or more of the cochlea; (3) **upper P3 present**; (4) horny papillae on tongue of different sizes, largest near midline; (5) **lateral vallate papillae present**; (6) distal tips of medial-posterior mechanical papillae directed toward pharyngeal region; (7) superciliary vibrissae absent; (8) dorsal fur bicolored; (9) dorsal fur 8–10 mm in length; (10) pair of ridges present on ventral surface of L4 and L5; (11) third phalanx of wing digit III long and at least partially ossified; (12) **ratchet-like digital tendon locking mechanism absent for digits of foot**; and (13) **female external genitalia with vulval opening oriented anteroposteriorly.**

Directions for Future Research

The results of our phylogenetic analyses allowed us to test monophyly of the family Mormoopidae, to test previous hypotheses of interrelationships among mormoopid species, and to evaluate the affinities of the fossil *Pteronotus pristinus* to extant species. Based on character optimizations, we were also able to provide revised diagnoses for Mormoopidae and all superspecific clades (e.g., genera and subgenera) within the family. However, our results were not entirely satisfactory. Levels of support for several clades within *Pteronotus* were relatively weak, and problems with polarizing many characters made their interpretation difficult. Addressing these issues will require further analyses including additional morphological data (e.g., more complete sampling of many soft-tissue character systems), as well as data analysis in the context of more outgroups. New data sets should also be explored, particularly DNA sequence data. Some of this work is now under way (Van Den Bussche, personal commun.), and such studies should provide additional tests of our phylogeny in the future.

With a relatively well-resolved phylogeny of Mormoopidae, it will be possible to address a number of questions concerning the evolutionary and ecological history of this group. Detailed analyses of morphological evolution, historical biogeography, and the evolution of echolocation call structure and foraging strategies—topics beyond the scope of the present study—can in the future be conducted in a phylogenetic context. Intriguing areas for future research include the evolution of mormoopid wing morphology, which is characterized by phylogenetically structured variation in membrane attachment sites, osteology, and myology, evolution of mormoopid craniodental morphology and diet, patterns of change in brain structure, evolution of high-duty-cycle CF echolocation, and biogeographic history of mormoopids in the Caribbean. It is our hope that the present study will facilitate studies such as these and thereby contribute to a better understanding of the biology and evolution of mormoopid bats.

Our phylogeny may also have interesting implications for understanding the biogeographic history of the major noctilionoid clades. Noctilionidae, Phyllostomidae, and Mormoopidae are all entirely Neotropical in distribution. In contrast, Mystacinidae is an Old World family with Recent species restricted to New Zealand, and Miocene fossil representatives in Australia (Hand et al., 1998; Kirsch et al., 1998). Kirsch et al. (1998) proposed a complex historical biogeographic hypothesis to explain the geographic and temporal distribution of noctilionoid taxa, but this hypothesis was developed under the assumption that Mystacinidae was the sister group to a Noctilionidae + Mormoopidae + Phyllostomidae clade. Our results, which agree with those of Van Den Bussche and Hoofer (2000) in placing Mystacinidae *within* the Neotropical radiation, suggest that Kirsch et al.'s (1998) biogeographic hypothesis should be reevaluated.

Recognizing that all phylogenies are themselves hypotheses that require continued testing, the present study provides an important starting point for more comprehensive phylogenetic analyses of bats using a dense-sampling approach. Future work on noctilionoid relationships will require more comprehensive sampling within Phyllostomidae as well as inclusion of additional putative outgroups. Further testing of monophyly of Noctilionoidea as defined here (i.e., including Mystacinidae) will minimally require addition of representatives of other yangochiropteran families to the data set (e.g., Myzopodidae, Thyropteridae, Furipteridae, Natalidae, Molossidae, Vespertilionidae). Expansion of taxonomic sampling will necessitate integration of many new morphological characters relevant to relationships among these taxa. Some such characters have been described previously (e.g., in Simmons and Geisler [1998] and Wetterer et al. [2000]), but many new characters will doubtless prove to be relevant in the context of improved species-level sampling. Finally, we believe that combined-data analyses including morphological and molecular data will ultimately provide the most robust tests of current hypotheses of bat relationships, including those presented in this contribution.

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APPENDIX 1: SPECIMENS EXAMINED

Pteronotus parnelli parnelli: **Cuba:** Oriente; Siboney, Cueva de Los Majaes (AMNH 176182); Pinar del Rio, La Mulata, Pan de Guajaibon (AMNH 176181); **Jamaica:** St. Catherine; St. Clair (AMNH 247594); St. Elizabeth; Balaclava, Oxford Cave (AMNH 45206–17); Hanover; Lusea (AMNH 12382–83, 12385); Trelawny; 5 mi N and 2.5 mi WNW Quick Step (USNM 545139–40).

Pteronotus parnelli pusillus: **Dominican Republic:** Santiago, 4 km SW Monción, Cueva Durán (AMNH 212996); San Rafael; Rancho La Guardia (AMNH 213893); **Haiti:** Sud; Sapoti (19 km SW Beaumont) (AMNH 236655).

Pteronotus parnelli portoricensis: **United States:** Puerto Rico; Trujillo Alto, Cueva de Trujillo Alto (AMNH 39369–70).

Pteronotus parnelli mexicanus: **Mexico:** Colima; Pueblo Juarez (AMNH 188747–48); Jalisco; 2.3 mi SW La Cuesta (AMNH 254606); Jalisco; 7.5 km W Jama, Cueva D.C.V. (AMNH 204958); Jalisco; Los Masos (AMNH 27293); Mexico; 6 km SEE Tunatico; Cueva del Coyote (188311–12, 188314–19, 188321–24); Oaxaca; Juchitan, 3 mi N El Jicaro (AMNH 185771); Oaxaca; Juchitan, Tapanatepec (AMNH 177738); Tamaulipas; Acuña, Sierra de Tamaulipas (AMNH 249063–64).

Pteronotus parnelli mesoamericanus: **Mexico:** Chiapas; 1.3 mi SE Zapaluta (AMNH 252516); **Honduras:** Lempira; Las Flores (AMNH 129009–34, 129741, 129743–50); **Guatemala:** Sta. Rosa; 2 km NE Chiquimilla (AMNH 243727); Sta. Rosa; 13 km N Avellana (AMNH 243728); **Nicaragua:** León; 50 mi N Sébaco (AMNH 177740); **Costa Rico:** San José; Las Pavas (AMNH 135243, 135245, 135249).

Pteronotus parnelli rubiginosus: **Panama:** Canal Zone; Chilobrillo (AMNH 143797); **Venezuela:** Araqua; Rancho Grande (AMNH 144389–90); **Trinidad and Tobago:** St. Andrew; Tamaná, Mt. Tamaná (AMNH 175540, 246152–53, 246155); St. George; Blanchisseuse, Las Cueves (AMNH 182693); **Brazil:** Amazonas; Rio Bronco, Serra de Cuchy (AMNH 78121–25, 78127–31, 78133–34, 78173).

Pteronotus parnelli fuscus: **Colombia:** Magdalena; Cacagualito (AMNH 23656); **Venezuela:** Aragua; Rancho Grande (AMNH 144842, 144845); Carabobo; Las Quiguas (AMNH 31563, 31578–79); Carabobo; San Esteban (AMNH 31564–31570, 31574–31576); Yaracui; Aroa, Boliviar R.R. (AMNH 32099–103, 32126).

Pteronotus macleayii macleayii: **Cuba:** Habana; Bucaranao (AMNH 174250); Oriente; Baracoa, Cueva de Mojana (AMNH 61151–53); Pinar del Rio; San Vicente (AMNH 17618–88).

Pteronotus macleayii grisea: **Jamaica:** Hanover; Lucea (AMNH 12359); St. Elizabeth; Balaclava, Oxford Cave (AMNH 45256, 45268–75); St. James; Montego Bay (AMNH 12390, 60917, 60896, 60899, 60902, USNH 260730); St. James, Monetgo Bay, Providence Cave (34884–86, 45257–67); Trelawny, Windsor (ANMH 61022).

Pteronotus quadridens fuliginosus: **United States:** Puerto Rico; San Juan, Pueblo Viejo, Cueva de Fari (AMNH 39353–59, 39363–67); Trujillo Alto (39396–03); **Dominican Republic:** between Cabra and Nagua, Cueva de Muricelagos (AMNH 238138); La Altagracia; Boca de Yuma (AMNH 238139); Santo Domingo; Cana Honda (AMNH 25760); **Haiti:** Cerca La Source (USNH 253631–32); Sud; Sapoti (19 km SW Beaumont) (AMNH 236654); **Jamiaca:** St. Elizabeth; Balaclava, Oxford Cave (AMNH 45248–55).

Pteronotus quadridens torrei: **Cuba:** [No additional information] (AMNH 60637–38); 8 mi E Baracoa (USNH 121061); La Habana; Bararanao, Cueva de El Fantasma (AMNH 176061); Las Villo; Punta Caquanes, Yaguajay ‘‘Cueva de Colon’’ (AMNH 186970–71).

Pteronotus personatus psilotis: **Mexico:** Morelos; Tequesquitengo (AMNH 180443–44, 180446); Nayarit; Nayarit–-Sinaloa state line, Rio Canas, near la Concha (USNH 508415); Oaxaca; Juchitan, Tapanatpec (175018–19, 177672–93, 177695–96, 178468).

Pteronotus personatus personatus: **Colombia:** Bolivar; Cartagena (USNH 433517, 433531); **Panama:** San Blas; Armila (Quebrada Venado) (USNH 335085–86); **Venezuela:** Sucre; la Brea (AMNH 33300); Yaracui; Aroa, Bolivar R.R. (33112, 32123–24, 32127–32133, 32136–37); **Trinidad and Tobago:** St. George; Tacariquas; St. Augustine (AMNH 175560).

Pteronotus davyi davyi: **Dominica:** Roseau (AMNH 35923); **Trinidad and Tobago:** St. George**:** Arima Heights of Aripo (AMNH 29694); St. George; Diego Martin, Carenage (AMNH 29703–04); St. George; Port of Spain (AMNH 7445, 19122); Nariva (AMNH 207060); St. Patrick, Siparia (AMNH 179954).

Pteronotus davyi fulvus: **Mexico:** Chiapas; 18 mi W Ixhuatan (AMNH 203563–64); Jalisco; 7.5 km W Jamai, Cueva ‘‘Deb’’ (204959–65); Jalisco; Los Masos (AMNH 27294–96); Morelos; Cueva de Tequesquitengo (AMNH 204454–57, 204967–75); Sonora; 5 mi W Alamos (Mine Tunnel at La Adurna) (AMNH 180312); Ocozocoautla; Ocozocoautla (AMNH 171652); San Luis Potos; El Salto (AMNH 177588–611); **El Salvador:** La Union; Tabanco (AMNH 239229).

Pteronotus davyi incae: **Peru:** Cajamarca; Jaen (AMNH 69233); Piura; Huancabamba (AMNH 63721, 64082).

Pteronotus gymnonotus: **Panama:** Canal Zone; Barro Colorada Island, Allee Creek (USNM 498707); Canal Zone; Madden Dam, Chillibrillo Cave (AMNH 89998, USMN 306526, 306529–30); Chilibre (USNH 305177); **Colombia:** Bolivar; Cartagena (USNM 431544); **Venezuela:** Yaracui; Aroa; Bolivar R.R. (AMNH 32083–89, 32091–94).

Pteronotus pristinus: **Cuba:** Las Villas; Cueva de Jaguey, near Trinidad (ROM 59132).

Mormoops blainvillii: **[No data]** (AMNH 213889); **United States:** Puerto Rico; Mona Island (AMNH 72547); Puerto Rico; Trujillo Alto, Cueva de Trujillo Alto (AMNH 72370); **Dominican Republic:** Barahano; Pedernales, Cabo Rio (AMNH 238144); San Cristobal; Cueva La Chepa, 10 km N Bayaguana (USNH 535251); San Rafael; Rancho la Guardia (AMNH 213897); **Jamaica:** St. Catherine; St. Clair (AMNH 246123); St. Elizabeth; Balaclava, Oxford Cave (AMNH 45197–205); Trelawny Parish; Quick Step (USNH 511225–27, 545146); **Cuba:** [No additional information] (AMNH 213889); Oriente; Siboney, Cueva de Los Majaes (AMNH 176149–50); Pinar del Rio; San Vincente, Cueva del Indio (AMNH 176139).

Mormoops megalophylla megalophylla: **Mexico:** Jalisco; Los Masos (AMNH 27298, 27300–03, 27305); Morelos; Tecómen (AMNH 206692–93); Nayarit; Rancho Palo Amarillo (AMNH 25070–71); Oaxaca; 5 mi W Chilltepec (AMNH 190138–39); Oaxaca; Tapamatepec (AMNH 177423–24); Sonora (USNH 314677); Sonora; 15 mi NW Guaumas (AMNH 239230, 239232); Tamaulipas; Acuña; Sierra de Tamaulipas (AMNH 249066).

Mormoops megalophylla intermedia: **Netherland Antilles:** Aruba (AMNH 185613, 185615–17); Curacao (USNH 102225); Curacao; Round Cliff (AMNH 149395–96).

Mormoops megalophylla tumidiceps: **Colombia:** Bolivar; Cartagena (USNM 431641); Santander; San Gil (AMNH 149257, 183315–16); **Trinidad and Tobago:** [No additional information] (AMNH 3173); St. Andrew; Tamaná, Mt. Tamaná (AMNH 175566, 175576); St. George; Port of Spain, Goodwood Park (AMNH 183845).

Macrotus waterhousii: **Mexico:** Jalisco; Bolaño

(AMNH 2003); Morelos; Lago de Tequesquitengo, Cueva del Cerro (USNM 559490–91); Nayarit; Islas Tres Marias; Maria Madre (AMNH 180523); Oaxaca; Tehuantepec; Arroyo Ocotita (AMNH 182158); **Dominican Republic:** Caves near River Charon; E La Romana (AMNH 120975); near San Juan Bay, Rolla Seco (AMNH 91314); **Haiti:** Sud; 1 mi S Duchity (7 km S Beaumont) (AMNH 236657–58); **Cuba:** Maranzos, near Cidra (AMNH 61161); **Jamaica:** Clarendon; Mahoe Gardens, Portland Cave (USMN 511232–33); St. Catherine; Healthshire Hills (AMNH 268068); St. Elizabeth; Balaclava, Oxford Cave (AMNH 45229); St. Elizabeth; Hounslow; Money Cave (AMNH 268071); Trelawny; 1 km E Quick Step (USMN 511230); Trelawny; Windsor (AMNH 45230–31); **Cayman Islands:** Grand Cayman Island; 1 km E Spots (USNM 538120).

Macrotus californicus: **United States:** Arizona (USNH 314679); California; Imperial, 3 mi N Potholes (AMNH 139575–78); **Mexico:** Sonora; Isla Tiburon (USNH 513814, 513816).

Artibeus jamaicensis: **Mexico:** Chiapas; 15 mi SE Mapastepec (by road), 150’ (AMNH 251657–58); Jalisco; 2.3 mi SW (by road) Le Cuesta (AMNH 254662); Oaxaca; Tapanatepec (AMNH 177744); Vera Cruz; 1 mi SE Oja de Agua (AMNH 254669); Yucantan; Chichen Itza (AMNH 91236); Yucatan; Sobre La Cairetera a Tixkokof (AMNH 204983); **Panama:** Canal Zone; rodman (AMNH 213402); **Venezuela:** El Enoatado (AMNH 135159); **Brazil:** Rio Tocantins; Iles do Tavina (AMNH 97036–37); **Bolivia:** La Paz; 6.6 road km downstream Caranaui, Rio Coraica Valley (AMNH 246641, 246644); **Barbados:** 10 mi E Bridge Town, Chancery Lane (AMNH 239927) **United States:** Puerto Rico; Utuado (AMNH 39117–18); St. Croix; Cane Bay (AMNH 214228); **Jamaica:** Cambridge (AMNH 45170); St. Mary, 2 mi W Port Maria (AMNH 219170).

Noctilio leporinus: **Panama:** Canal Zone; Chagres River (AMNH 173912); **Brazil:** Amazonas; Rio Madiera (AMHH 91937); Amazonas; Rio Madiera, Auara Igarapé (AMNH 91960–75); Pará; Fero (AMNH 93803); Pará: R. Tocantins, Ilha do Taiuna (AMNH 96930); **Peru:** Amazonas; Rio Amazonas, Pt. Indiana (AMNH 93932, 93970); Pacso; Oxapampa, San Juan (AMNH 230105, 230108–09); Pasco; Oxapampa, San Pablo (AMNH 230110–12); **Bolivia:** Beni; ca. 23 km W San Javier (AMNH 210598); Cochabamba; Jodoe Santoe (AMNH 38562); **Paraguay:** Boqueron; Pozo Colorado (trans-chaco route, km 250) (AMNH 234277); **Trinidad and Tobago:** North Manzanilla (AMNH 175534); **United States:** Puerto Rico; Humacao, Old Loiza (AMNH 39574, 39587); **St. Kitts-Nevis:** Nelson Spring (AMNH 246993).

Noctilio albiventris: **Colombia:** Amazonas; Leticia (AMNH 207772, 207774); **Brazil:** Amazonas; Rio Madeira, Auarer Igarapé (AMNH 92019–30); Amazonas; Rio Negro, near Manaus (AMNH 79626, 79632); Amazonas; Rio Amazonas, Villa Bella Imperatriz (AMNH 92998); **Peru:** Oxapampa, San Pablo (AMNH 23102); **Bolivia:** Beni (AMNH 210624); Beni; 5 km S Guyarmarin (AMNH 209254); Beni; ca. 23 km W San Javier (AMNH 210595); **Paraguay:** Olempo XVI Feurte Olempo (AMNH 234256–66).

Mystacina robusta: **New Zealand:** Stewart Island (AMNH 160269); Island off SW of Stewart Isl. (AMNH 214243).

Mystacina tubuerculata: **New Zealand:** [No additional data] (MNHN 1983.1464; MVZ 174825); North Island; Omahuta Kauri Forest (MVZ 173919; ROM 80308).

Saccopteryx bilineata: **Mexico:** Ejido Tepextles (AMNH 172063); Oaxaca; Sacatepec; Cotzocon; Mazatlan (AMNH 175300–01, 178776–77); **Costa Rico:** Palmer (Pacific) (AMNH 139449); **Panama:** Canal Zone; Gatun Lake (USNM 514986); Chilibrillo Caves (USNM 306471); **Guyana:** Rupununi Dist.; 15 mi E Dadanawa (USNM 338917); **French Guiana:** Paracou; near Sinnamary (AMNH 267060, 267064, 267377); **Brazil:** Para; Altamira, 52 km SSW, E Bank Rio Xingu (USNM 549311); **Bolivia:** Beni; 5 km NW Grande river mouth (AMNH 210469).

APPENDIX 2: TAXON-CHARACTER MATRIX

The taxon-character matrix presented below corresponds to the character descriptions and coding described in the text. An electronic version of this data matrix (in MacClade format, including character-state labels) is available over the internet at ftp://ftp.amnh.org/pub/mammalogy.

Saccopteryx bilineata

```
11-10   00000   00000   12000   01021   1210-   1-020   01--0   1--00   10???   ??001
01100   ?0000   021?0   00000   00000   00000   00000   00010   00000   10002   01060
00100   00020   -0101   00000   01001   10000   00101   10000   00001   10013   00000
00202   20220   00000   1000?   0????   ?????   ?1000   01000   0011
```

Noctilio albiventris

```
00201   01100   11100   12111   01000   12000   0122-   11--1   01100   21???   ??0??
?????   ?????   ?????   ?0001   10100   02000   00000   10030   00000   02000   02112
01000   01030   -0100   00101   00102   11001   11000   10100   00001   03102   01110
10001   11131   00100   00000   0????   ???0?   01011   0100?   0002
```

Noctilio leporinus

```
00201   01100   11100   12111   01000   12000   0121-   11--1   01100   21010   11012
00113   10100   02000   ?0001   10100   02000   00000   10030   00000   02000   02112
01000   01030   -0100   00101   00102   11001   11000   10100   00001   03102   01110
10001   11131   00100   00000   0????   ???0?   01011   0100?   0002
```

Mystacina robusta

```
00000   00001   23100   10110   10000   0110-   0-22-   10001   01000   20???   ??011
00013   ?2111   002??   ?????   ??000   00003   00000   00000   0????   ??0??   ?0???
00020   01010   -1001   11111   01000   01022   01300   10010   01001   01011   10010
?0000   20001   1????   ?????   ?????   ?????   ????0   0000?   ????
```

Mystacina tuberculata

```
00000   00001   23100   10110   00000   0110-   0-22-   10001   01000   20020   ?????
?????   ?????   ?????   ?1110   10000   00003   00000   00000   01001   11022   10002
00020   0????   ?????   ?????   ?????   ??022   013?0   ??010   01101   ?1011   1?010
?0000   30?01   1????   ?????   ?????   ?????   ?01??   ?????   ????
```

Macrotus waterhousii

```
00001   00000   12100   02110   10110   00010   00111   10100   00000   20???   ??011
20113   ?0101   12?01   01110   10000   00112   20001   02002   02010   01022   10020
02000   00020   -0100   10001   10110   10010   00210   11011   00011   14000   20001
10111   40120   01011   11000   00010   01100   1210?   ?????   0100
```

Macrotus californicus

```
00001   00000   12100   02110   10110   00010   00111   10100   00000   20200   ?00??
?????   ?????   ?????   ?1110   10000   00112   20001   02002   02010   01022   10020
02000   00020   -1100   10001   10110   10010   00210   11011   00011   14000   20001
10111   40120   01011   11000   00010   01100   12102   1110?   ????
```

Artibeus jamaicensis

```
00001   00100   02100   02110   00100   01001   00111   10001   010-1   3-201   0201?
20113   00100   02001   01121   11010   00112   20000   00003   00121   11111   10051
02010   00011   00001   11001   00100   10010   00200   10011   00001   02100   00001
10201   00001   0???1   11??0   ?????   ???01   02103   21112   1110
```

Pteronotus parnellii

```
00001   10000   13100   10111   02111   12010   00121   10010   01100   20210   01211
10110   00110   02010   10130   00011   01110   10110   10010   11011   02032   00112
02001   11021   11011   10101   01012   20111   01201   11101   00100   00100   01101
11201   30210   00011   11000   00100   20011   10101   11000   0002
```

Pteronotus pristinus

```
00001   10001   13100   10???   0??1?   ??0??   ?11??   100?0   01100   20???   ?????
?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????
?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????
?????   ?????   ?????   ?????   ?????   ?????   ?????   ?????   ????
```

APPENDIX 2: *Continued.*

Pteronotus personotus										
00001	10000	33110	10110	00100	12010	01120	10010	01110	10011	1?210
?????	?????	?????	?0130	00011	01113	10110	10110	11011	02022	00142
02001	11021	01111	10101	01011	20111	01200	11101	00100	00100	01101
11201	30210	00???	??010	00101	1001-	-010?	?????	????		
Pteronotus macleayii										
00001	10010	13110	10110	00100	12010	01120	10010	01100	10???	??2??
?????	?????	?????	?0130	00011	01110	10200	10110	11011	02042	00142
02001	11021	01011	10101	01011	20111	01201	11101	00100	00100	01001
?1201	30220	00???	??010	00101	00011	10111	1100?	????		
Pteronotus quadridens										
00001	10010	13110	10110	00100	12010	01120	10010	01100	10???	??2??
?????	?????	?????	?0130	00011	01113	10200	10110	11011	02042	00142
02001	11021	01111	10101	01011	20111	01201	11101	00100	00100	01001
?1201	30210	00???	??010	00101	0001-	-0101	1100?	????		
Pteronotus davyi										
00001	10100	23100	10110	00100	12010	01120	10010	01100	20???	??2??
?????	?1???	????0	10130	00011	01113	10200	10010	11011	02002	00102
12001	01021	01011	10101	01011	20111	11201	11101	00100	00100	01001
11201	30220	00011	11010	00100	0001-	-010?	????0	????		
Pteronotus gymnonotus										
00001	10100	23100	10110	00100	12010	01120	10010	01100	20???	?12??
?????	?????	?????	?0130	00011	01113	10200	10010	11011	02000	00102
12001	01021	01011	10101	01011	20111	11201	11101	00100	00100	01001
11201	30220	00???	??010	00100	00011	1010?	?????	????		
Mormoops blainvillii										
00002	10000	01101	10110	00100	12010	11120	10110	00000	10???	??2??
?????	?????	?????	?1110	00010	12101	01211	11011	20021	02022	10131
02001	01110	-1111	00001	01011	10101	01201	21100	11111	11000	10001
11201	30130	00???	??101	11000	10001	10101	1100?	????		
Mormoops megalophylla										
00002	10000	01101	10110	00100	12010	11120	10110	00000	10101	112??
?????	?1???	????0	11110	00010	12101	01211	11011	20021	02053	10131
02001	01110	-1110	00001	01012	20101	01210	21100	11101	11000	10101
11201	30130	00012	21101	11000	10001	1010?	????1	0002		