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A New Species of *Micronycteris* (Chiroptera: Phyllostomidae) from Northeastern Brazil, with Comments on Phylogenetic Relationships

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ABSTRACT

Micronycteris is a diverse group of small to medium-sized Neotropical phyllostomid bats. Five species are recognized in the nominate subgenus: *hirsuta, megalotis, microtis, minuta,* and *schmidtorum.* In this contribution I describe and name a new species from cerrado and caatinga habitats in northeastern Brazil, and discuss external and craniodental characters that distinguish species in the subgenus *Micronycteris.* A data set of potentially informative morphological characters is described and analyzed, additional data from karyotypic, immunological, and allozyme studies are discussed, and a hypothesis of relationships within the genus *Micronycteris* is presented. The new species from Brazil appears to be closely related to *minuta* and *schmidtorum.* The subgenus *Micronycteris* (including *Xenoctenes*) and the subgenus *Glyphonycteris* (*M. sylvestris* + *M. daviesi*) are each monophyletic. *M. nicefori* (subgenus *Trinycteris*) and *M. pusilla* (subgenus *Neonycteris*) are closely related to *Glyphonycteris. M. brachyotis* (subgenus *Lampronycteris*) apparently occupies the most basal branch within the genus *Micronycteris.*

INTRODUCTION

Micronycteris comprises a diverse group of small to medium-sized Neotropical phyllostomid bats thought to be specialized for gleaning insects, though some may also feed on fruit (Wilson, 1971; Humphrey et al., 1983; Medellin et al., 1985; Alonso-Mejía and Medellín, 1991). While many species of *Micronycteris* are widely distributed, these bats are captured infrequently and most species are uncommon in museum collections. Monophyly of *Micronycteris* is supported by data from G-banded chromosomes (Patton and Baker, 1978); analyses of allozymes, morphological data, and albumin immunological distances have been inconclusive (Honeycutt, 1981; Arnold et al., 1983; personal obs.). Although most authors place *Micronycteris* in the subfamily Phyllostominae (Koopman, 1993, 1994), Van Den Bussche (1992) recently named a new subfamily for the genus, Micronycterinae.

The most recent revision of *Micronycteris* (Sanborn, 1949) recognized six subgenera and nine species. Hill (1964) subsequently described a new genus and species, *Barticonycteris daviesi,* that most workers now place in *Micronycteris* either in the subgenus *Barticonycteris* or *Glyphonycteris* (table 1; Handley, 1976; Genoways and Williams, 1986; Koopman and Cockrum, 1967; Koopman, 1993, 1994). *Micronycteris microtis,* considered by Sanborn to be a subspecies of *megalotis,* has been collected in sympatry with *megalotis* in Colombia, Venezuela, French Guiana, and Brazil (Handley, 1976; Brosset and Charles-Dominique, 1990; Appendix 1) and thus represents a distinct species. *Micronycteris mexicana,* long considered a subspecies of *megalotis,* may be either a distinct species or a subspecies of *microtis.*[2] *Micronycteris hirsuta,* placed in its own subgenus (*Xenoctenes*) by Sanborn, shares derived features with bats of the subgenus *Micronycteris* (see below). On this basis, Davis (1976) suggested that *Xenoctenes* be considered a junior synonym of the subgenus *Micronycteris.*

Sanborn (1949) divided *Micronycteris* into subgenera based on size, ear shape, presence or absence of a band of skin between the ears, proportions of various wing elements, and

[2] A preliminary study of species limits in *Micronycteris* suggests that *megalotis* is confined to South America, while *microtis,* sensu stricto, ranges from Brazil to at least western Nicaragua. *M. mexicana,* which ranges from Costa Rica and western Nicaragua to Mexico, was considered by Miller (1899) and subsequent authors to represent a subspecies of *megalotis.* However, *mexicana* lacks an important synapomorphy of *megalotis,* i.e., long hair on the leading edge of the pinna. It now seems likely that *mexicana* either represents a distinct species or is a subspecies of *microtis.* I know of no discrete characters that distinguish *microtis* and *mexicana* in the area where their geographic ranges supposedly approach one another (Costa Rica/Nicaragua/Honduras). Measurements of *mexicana* mostly fall outside the range of variation for *microtis,* sensu stricto, but there is at least some overlap in all of the measurements used in this study. Pending further examination of the problem, it therefore seems most reasonable to consider *mexicana* to be a subspecies of *microtis.*

shape and proportions of P3 and P4. Members of the nominate subgenus (i.e., *megalotis, microtis, minuta,* and *schmidtorum*) were characterized by Sanborn (1949) as sharing small size (forearm 31.0–37.5 mm, skull 17.0–20.0 mm); large, rounded ears connected by a high, notched band of skin; wings in which the third metacarpal is shortest and the fifth longest; and a large P3 about equal in size to P4. Significantly, *Micronycteris hirsuta* shares most of these features, including the derived band of skin between the ears (Davis, 1976). *Micronycteris hirsuta* differs from *megalotis* and other species of the subgenus *Micronycteris* principally in incisor morphology and body size (see below), both of which are apparently autapomorphic. I therefore agree with Davis' conclusion that *hirsuta* should be considered a member of the subgenus *Micronycteris.* Accordingly, five species are currently recognized in this subgenus: *hirsuta, megalotis, microtis, minuta,* and *schmidtorum* (table 1). *Micronycteris minuta* has a pale gray or tan venter, a deep notch in the band between the ears, and a calcar that is distinctly shorter than the foot. *Micronycteris schmidtorum* also has a pale venter, but the notch between the ears is only moderately deep and the calcar is longer than the foot. *Micronycteris megalotis* and *microtis* both have a dark venter, a very shallow notch in the ear band, and a calcar that is longer than the foot. Although some craniodental measurements may serve to diagnose these species where they occur in sympatry, they are most easily distinguished on the basis of the ears, which have much longer fur along the leading edge in *megalotis. Micronycteris hirsuta* resembles *megalotis* and *microtis* in general appearance, but is significantly larger (forearm 39–46 mm; Koopman, 1994) and has a unique dentition in which both upper and lower incisors have unusually high crowns. For detailed descriptions and figures of these species, see Sanborn (1935, 1949), Davis (1976), Genoways and Williams (1986), Alonso-Mejía and Medellín (1991), and Brosset and Charles-Dominique (1990).

In 1977 and 1978 several small *Micronycteris* were collected by M. R. Willig and A. L. Gardner at localities in Ceará and Pernambuco in northeastern Brazil. Mares et al. (1981) referred some of these specimens to "*Micronycteris* sp." and others to *minuta,* and a few years later Willig (1983) reported that the collection also contained specimens of *megalotis.* Ascorra et al. (1991) reexamined this material and identified five specimens (CM 98908, 98909, 98910; USNM 555702, 555703) as *schmidtorum* based on color of the venter, length of the calcar and uropatagium, and depth of the notch in the band between the ears. In the course of surveying morphological variation in *Micronycteris* I noticed that one of the specimens referred to *schmidtorum* by Ascorra et al. (1991) differs from other individuals of that species. Closer examination of this specimen and others previously identified as *minuta* revealed that they represent an undescribed species that differs significantly from *schmidtorum, minuta,* and other members of the subgenus *Micronycteris.* Accordingly, a new taxon is named and described below on the basis of this material.

METHODS

All observations reported here are based on adult individuals with closed epiphyses. External and craniodental measurements are in millimeters; body mass (weight) in grams. The first five measurements listed below were taken from skin tags or other records made by the collector of each specimen; I measured the other dimensions using digital calipers. Measurements are defined as follows:

Weight: Body mass in grams.

Total length: Distance between the tip of the snout and the tip of the last caudal vertebra.

Tail length: Distance between posteriormost point on the pelvis and the tip of the last caudal vertebra.

Hind foot length: Distance from the anterior edge of the base of the calcar to the tip of the claw of the longest toe on the hind foot.

Ear length: Distance between the ear notch and the tip of the ear.

Forearm length: Distance from the elbow (measured from the tip of olecranon process) to the distal end of the forearm including carpals. This measurement is made with the wing at least partially folded.

Thumb length: Distance from the proximal end of the metacarpal of digit 1 to the tip of the claw of the thumb.

Tibia length: Distance from the proximal end of the tibia to the posterior base of the calcar.

Condyloincisive length: Distance between the posteriormost point on the occipital condyles and

TABLE 1
Contents and Classifications of the Genus *Micronycteris* Gray

Koopman (1994)	This paper[a]
Genus *Micronycteris*	Genus *Micronycteris*
Subgenus *Micronycteris*	Subgenus *Micronycteris*
Micronycteris megalotis	*Micronycteris hirsuta*[b]
M. megalotis megalotis	*Micronycteris megalotis*[c]
M. megalotis microtis	*Micronycteris microtis*[d]
M. megalotis mexicana	*M. microtis microtis*, new combination
Micronycteris minuta	*M. microtis mexicana*, new combination[e]
Micronycteris schmidtorum	*Micronycteris minuta*[f]
Subgenus *Xenoctenes*	*Micronycteris sanborni*, new species
Micronycteris hirsuta	*Micronycteris schmidtorum*
Subgenus *Trinycteris*	Subgenus *Trinycteris*
Micronycteris nicefori	*Micronycteris nicefori*
Subgenus *Neonycteris*	Subgenus *Neonycteris*
Micronycteris pusilla	*Micronycteris pusilla*
Subgenus *Lampronycteris*	Subgenus *Lampronycteris*
Micronycteris brachyotis	*Micronycteris brachyotis*[g]
Subgenus *Glyphonycteris*	Subgenus *Glyphonycteris*
Micronycteris behnii	*Micronycteris behnii*[h]
Micronycteris sylvestris	*Micronycteris sylvestris*
Subgenus *Barticonycteris*	*Mironycteris daviesi*[i]
Micronycteris daviesi	

[a] The status of two names associated with the genus *Micronycteris* has yet to be resolved. *Phyllostoma scrobiculatum* Wagner, 1855 (collected by Natterer in "Brazil") was considered by Andersen (1906) to be a junior synonym of *Micronycteris megalotis*, the only species of small, dark *Micronycteris* known from South America at the time. Measurements of the holotype of *scrobiculatum* provided by Carter and Dolan (1978) fall within the range of variation of both *megalotis* and *microtis*, and morphology of the interauricular band is likewise similar. I have not seen the holotype of *scrobiculatum* and thus cannot determine if this name is a synonym of *megalotis* or *microtis*, or whether it is a valid species. Another problematic taxon, *Micronycteris megalotis homezi* Pirlot, 1967, was named based on three specimens collected in the western Venezuelan state of Zulia. These specimens (including the holotype) were destroyed along with the rest of Pirlot's collection sometime during the 1970s (Pirlot, phone conversation with T. Griffiths). The published description of *homezi* is incomplete, but several features described by Pirlot (e.g., pale venter, deep notch in ear membrane) suggest that *homezi* is not related to *megalotis*. It is not clear from the type description if *homezi* represents a distinct species or is synonymous with *minuta, schmidtorum*, or *sanborni*.

[b] *M. hirsuta* is placed in the subgenus *Micronycteris* (rather than *Xenoctenes*) based on Davis (1976) and observations made in the current study (see "Phylogenetic Relationships within *Micronycteris*" in text).

[c] *M. megalotis* includes *Phyllostoma elongata* Gray, 1842. I examined the holotype of *elongata* (BMNH 42.8.17.8, skin and partial skull) and found that it corresponds with *megalotis* in all respects. The type locality of *elongata* ("Brazil") is within the known geographic range of *megalotis*. Both Andersen (1906) and Sanborn (1949) considered *elongata* to be a junior synonym of *megalotis*; I agree with their assessment.

[d] *M. microtis* is recognized as a species distinct from *megalotis* because these two taxa occur sympatrically in Colombia, Venezuela, French Guiana, and Brazil (Handley, 1976; Brosset and Charles-Dominique, 1990; personal obs.).

[e] Morphological comparisons indicate that *mexicana* may represent a distinct species or may be a subspecies of *microtis*; it is not a subspecies of *megalotis*. See footnote 2 (page 2) for further discussion. *M. microtis mexicana* includes *Macrotus pygmaeus* Rehn, 1904. I examined the holotype of *pygmaeus* (AMNH 12756/11043, skin and skull) and found that it corresponds with *mexicana* in all respects. The type locality of *pygmaeus* (Mexico: "Yucatan") is within the known geographic range of *mexicana*. Goodwin (1953) considered *pygmaeus* to be a junior synonym of *mexicana*; I agree with his assessment.

[f] *M. minuta* includes *Micronycteris hypoleuca* J. A. Allen, 1900. I examined and measured the holotype of *hypoleuca* (AMNH 15131; skin only) and found that it corresponds with *minuta* in all respects. The type locality of *hypoleuca* (Colombia: Magalena, Bonda) falls well within the known geographic range of *minuta*. Both Andersen (1906) and Sanborn (1949) considered *hypoleuca* to be a junior synonym of *minuta*; I agree with their assessment.

[g] *M. brachyotis* includes *Micronycteris platyceps* Sanborn, 1935; see Goodwin and Greenhall (1961).

[h] *M. behnii* may be a senior synonym of *M. sylvestris*, but this has yet to be resolved. The two species are currently

the anteriormost point on the upper incisors. This measurement was preferred over other possible measures of skull length (e.g., greatest length of skull, condylobasilar length) because it was found to be consistently repeatable and maximized the number of specimens from which measurements could be taken.

Zygomatic breadth: Greatest breadth across the outer edges of the zygomatic arches.

Braincase breadth: Greatest breadth of the globular part of the braincase.

Interorbital breadth: Least breadth across the postorbital constriction.

Maxillary toothrow length: Greatest crown length of the maxillary toothrow, measured from the anteriormost edge of the canine to the posteriormost edge of M3.

I combined measurements of males and females for the purpose of species comparisons because no consistent size differences are apparent between males and females in any species in the subgenus *Micronycteris*. Statistical testing for sexual dimorphism in *Micronycteris* is difficult because most collections from a single locality consist of only a few specimens. Willig (1983) suggested that there might be slight dimorphism in craniodental measurements in *megalotis*, but his sample was small (N = 14) and heterogeneous (containing individuals from two localities 40 km apart in different vegetation zones). I analyzed a large single-locality series of *Micronycteris* (nine males and eight females of *microtis*) collected in lowland rainforest within a 3 km radius at Paracou in French Guiana (AMNH 266024–025, 266027, 266029–030, 266038, 267097, 267866–870, 267872–873; MNHN 1995.805–807). Two-tailed Student's *t*-tests for sexual differences in 13 external and craniodental dimensions (see above) indicated no significant sexual dimorphism in this sample.

A phylogenetic analysis of relationships within *Micronycteris* was conducted based on characters identified in the course of species comparisons. Monophyly of *Micronycteris* was assumed based on the results of Patton and Baker's (1978) chromosome analysis. To test monophyly of the nominate subgenus, I included all species currently referred to *Micronycteris* in the analysis with the exception of *behnii* (which may be a senior synonym of *sylvestris*; see table 1). A hypothetical ancestor was constructed to root the tree(s).[3]

[3] Choice of an outgroup for studies of *Micronycteris* is difficult because there is little agreement concerning interrelationships of "phyllostomine" phyllostomids (Smith, 1976; Honeycutt, 1981; Arnold et al., 1983; Baker et al., 1989; Van Den Bussche, 1991; Peffley and Simmons, 1993). On the basis of morphological comparisons, Smith (1976) suggested that *Micronycteris* belongs in a clade with *Macrotus, Lonchorhina,* and *Macrophyllum.* Alternatively, a close relationship between *Micronycteris* and *Vampyrum* has been indicated by immunological data (Honeycutt, 1981; Honeycutt and Sarich, 1987), while bootstrap analyses of rDNA restriction sites placed *Micronycteris* in a clade with *Tonatia, Lonchorhina,* and *Phyllostomus* (Van Den Bussche, 1991). Baker et al. (1989) placed *Micronycteris* incertae sedis within Phyllostomidae, implying that the sister group of *Micronycteris* might be either (1) desmodontines; (2) *Macrotus*; (3) a clade containing *Vampyrum, Chrotopterus,* and *Trachops*; or (4) a much larger clade comprising the remaining genera of "phyllostomines" plus all of the other phyllostomid genera. Resolution of relationships of *Micronycteris* within Phyllostomidae will require analyses of taxa and data far beyond the scope of this paper. Accordingly, I chose to construct a hypothetical ancestor to root the tree(s) in the current study, attributing to this taxon only those character states that appear to vary little among "phyllostomines."

←

distinguished on the basis of size (forearm 37–44 mm in sylvestris, 45–47 mm in *behnii*) and the degree of grooving on the upper incisors (prominent in *sylvestris,* somewhat less prominent in *behnii*; Anderson, 1906; Koopman, 1994). Only three specimens have been referred to *behnii*: the holotype (ZMB 5154), and two specimens in the British Museum (BMNH 69.5.13.3, 69.5.13.4) that Anderson referred to *behnii* in his 1906 revision. I examined the latter specimens (both in alcohol, one with skull cleaned), and found that they fall within the range of variation of *sylvestris* in all measurable dimensions. The forearms of both specimens are broken; Anderson (1906) reconstructed their length as 45 mm, but I estimate the actual length to be closer to 40–42 mm. The degree of grooving of the upper incisors also falls within the range I have observed in *sylvestris.* Unfortunately, I have not yet seen the holotype of *behnii,* which Peters (1865) described as having a forearm length of 47 mm.

[i] *M. daviesi* is placed in *Glyphonycteris* (rather than *Barticonycteris*) following Genoways and Williams (1986). A close relationship between *sylvestris* and *daviesi* is indicated on the basis of albumin immunological data, allozymes, and morphology (see "Phylogenetic Relationships within *Micronycteris*" in text).

Character states were recorded in a taxon-character matrix using MacClade version 3.0 (Maddison and Maddison, 1992), and phylogenetic analyses were conducted using PAUP version 3.1.1 (Swofford, 1993). 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 ten steps longer) were identified in subsequent branch-and-bound analyses. A decay analysis was conducted as suggested by Bremer (1988) to investigate the number of additional steps required to collapse various clades. A branch-and-bound bootstrap analysis with 1000 replicates was additionally used to evaluate relative support for various groupings.

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

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
CBF	Colección Boliviana de Fauna, Instituto de Ecología, Museo Nacional de Historia Natural, La Paz
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
MNHN	Museum National d'Histoire Naturelle, Paris
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima
TTU	The Museum, Texas Tech University, Lubbock
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMB	Zoologisches Museum der Humboldt Universität zu Berlin, Berlin

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE

Genus *Micronycteris* Gray, 1866

Subgenus *Micronycteris* Gray

Micronycteris sanborni, new species

Figures 1, 2A, 3A, 4A, 5A, 6

TYPE MATERIAL: The holotype of *Micronycteris sanborni* (USNM 555702) is an adult female skin and skull collected by A. L. Gardner on 26 March 1978 at Sitio Luanda, Itaitera, 4 km S of Crato in the Brazilian state of Ceará (original field number ALG 13745). The skin is well preserved with the exception of the fourth toe on the right hind foot, which is missing the distal phalanges. At the time that I examined and measured the holotype, the skull was essentially complete although a small segment was missing from the right zygomatic arch (fig. 1). An accident during photography subsequently damaged the skull, but the key diagnostic features (see below) are still preserved. The mandibles are undamaged. The karyotype of USNM 555702 is illustrated in figure 6.

Paratypes include one additional specimen from Ceará (CM 98913) and four from two nearby localities in Pernambuco (CM 98914, 98915, 98916, 98917). These specimens, also skins and skulls, were collected by Michael Willig in 1977. An unknown number of additional specimens may be present in the Museu de Zoologia, Universidade de São Paulo, which received half of the collections made by Willig and his colleagues (Mares et al., 1981).

DISTRIBUTION: Currently known only from the region of the Chapada do Araripe plateau in northeastern Brazil. Specimens have been collected at two localities in Ceará and two in Pernambuco (see Appendix 1), sites located within 50 km of one another along the Ceará/Pernambuco border (Mares et al., 1981). See "Natural History" below for a discussion of local habitats.

ETYMOLOGY: *Micronycteris sanborni* is named in honor of Colin Campbell Sanborn in recognition of his important contributions to systematics of Neotropical bats. His 1949 revision of *Micronycteris* still stands as the primary reference on the genus, providing the groundwork for all subsequent systematic work including this contribution.

DIAGNOSIS: A small *Micronycteris* with white ventral fur that extends anteriorly onto throat and chin; thin mustache of white hairs on upper lip; small patch of white fur on ventral surface of uropatagium at base of tail; dorsal hairs bicolored, brown with white bases, white base comprises $^2/_3$–$^4/_5$ of each hair; long, white hairs sparsely distributed on inside of anteromedial half of pinna; fur on outside of medial third of pinna short ($\leq$ 3

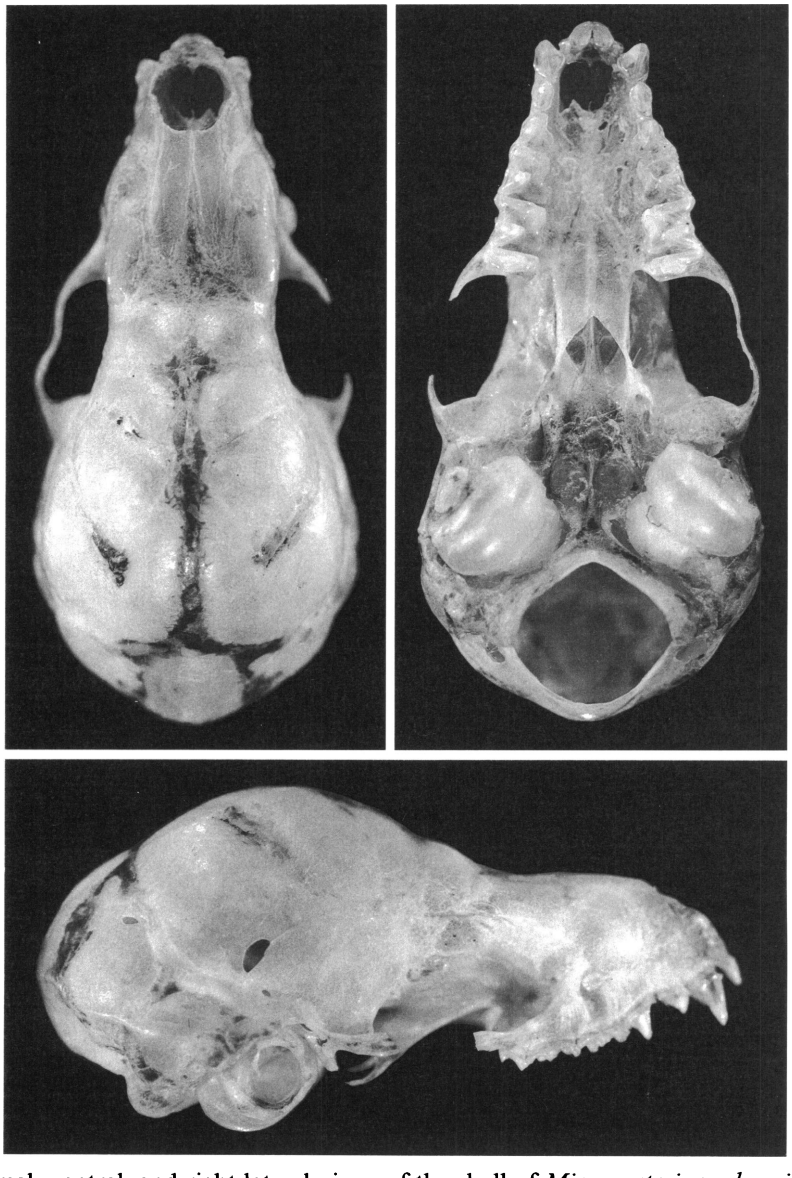

Fig. 1. Dorsal, ventral, and right lateral views of the skull of *Micronycteris sanborni,* n sp. (USNM 555702, the holotype). See table 2 for measurements.

mm) and dense; pinnae large with rounded tips; high band of skin present between ears, deeply notched in middle, resultant flaps triangular in appearance; ventral edge of horseshoe of noseleaf defined by thick ridge; thumb relatively small; third metacarpal shortest, fifth longest; length of second phalanx equals length of first phalanx in digits III and IV of wing; calcar approximately the same length as the foot; rostrum and anterior orbital region not inflated; mastoid breadth greater than zygomatic breadth; basisphenoid pits shallow; dental formula I $^2/_2$, C $^1/_1$, P $^2/_3$, M $^3/_3$ × 2 = 34; crown height of upper incisors reduced; gap present between outer upper incisor and canine; P3 smaller than P4 in both height and anteroposterior length; P4 with large lingual heel and poorly developed lin-

TABLE 2
Comparative Measurements[a] of Members of the Subgenus *Micronycteris*

	M. sanborni, n. sp.	*M. minuta*	*M. schmidtorum*
Sex	4 females, 2 males	38 females, 29 males	9 females, 16 males
Weight	6.3 (5.5–8.0) 6	7.3 (6.5–8.5) 11	6.2 (5.0–7.4) 8
Total length	57.5 (55.5–65.0) 6	59.9 (55.0–69.0) 28	61.1 (54.5–67.0) 21
Tail length	12.5 (12.0–14.0) 6	11.2 (9.0–14.0) 28	13.1 (11.0–17.0) 21
Hind foot length	8.7 (8.0–9.0) 6	11.8 (9.0–13.0) 35	9.7 (8.0–11.0) 24
Ear length	20.2 (19.0–21.0) 6	21.1 (19.5–23.0) 23	19.2 (16.0–21.0) 17
Forearm length	33.6 (32.0–34.0) 6	35.4 (33.0–36.8) 33	35.3 (33.0–37.8) 25
Thumb length	7.1 (7.0–7.3) 6	8.5 (7.7–9.1) 37	10.2 (9.3–11.1) 17
Tibia length	13.1 (12.6–14.0) 6	14.3 (13.3–15.2) 12	16.1 (14.0–17.7) 16
Condyloincisive length	15.16 (14.91–15.39) 6	16.64 (15.62–17.54) 39	17.56 (16.34–18.32) 23
Zygomatic breadth	8.02 (7.88–8.19) 5	8.54 (8.02–9.00) 26	9.36 (8.72–9.87) 23
Braincase breadth	7.41 (7.32–7.48) 6	7.59 (7.23–8.04) 40	7.88 (7.42–8.24) 22
Interorbital breadth	3.92 (3.70–4.07) 6	4.12 (3.84–4.37) 43	4.12 (3.98–4.29) 23
Maxillary toothrow length	5.76 (5.64–5.92) 6	6.65 (6.37–6.94) 45	7.51 (7.10–7.97) 23

gual cusp; M1 and M2 subequal; gap present between posterior edge of cingulum of M2 hypocone and anterolingual edge of M3; lower incisors small and bilobed; crown height of p2 less than or equal to its length; p3 tiny, much smaller than p2 and p4; coronoid process low, upper margin of the ascending ramus with shallow slope ($\approx 16°$); karyotype 2N = 28, FN = 50.

DESCRIPTION AND COMPARISONS: *Micronycteris sanborni* can be distinguished unambiguously from other members of the genus on the basis of both craniodental and external characters. Like other members of the nominate subgenus, *sanborni* has bicolored dorsal fur, large rounded ears connected by a notched band of skin, and wings in which the third metacarpal is shortest and the fifth longest. By contrast, *sylvestris, behnii, daviesi, brachyotis, nicefori,* and *pusilla* (members of other subgenera) have different patterns of fur coloration, different metacarpal formulae, and lack an interauricular band (Sanborn, 1949; Hill, 1964). The ears in *sylvestris, behnii, daviesi, brachyotis, nicefori* also have a different shape—the outer margin of the distal portion of the pinna is concave rather than convex, so the ears appear pointed rather than rounded. Thus, close comparisons are required only with other members of the subgenus *Micronycteris.*

Micronycteris sanborni is relatively small, resembling *megalotis, microtis, minuta,* and *schmidtorum* in body size (table 2). Measurements of *sanborni* fall within the low end of the range of variation of other species in many dimensions (table 2; see table 2 for all comparative measurements). However, *sanborni* is smaller than any measured specimens of *minuta* in thumb length, condyloincisive length, and length of the maxillary toothrow. Hind foot length and forearm length overlap only slightly in these species, with *sanborni* being the smaller of the two. Similarly, *sanborni* is smaller than *schmidtorum* in thumb length, tibia length, condyloincisive length, zygomatic breadth, and length of the maxillary toothrow. *Micronycteris sanborni* is smaller than *megalotis* in thumb length, condyloincisive length, and length of the maxillary toothrow, and is smaller than *microtis* in thumb length and length of the maxillary toothrow. *Micronycteris sanborni* is smaller than *hirsuta* in all dimensions except tail length. When all of the species are considered simultaneously, two measurements—thumb length and length of the maxillary toothrow—unambiguously distinguish *sanborni* from all other members of the subgenus *Micronycteris.*

The entire dorsal pelage of *sanborni* is composed of bicolored hairs with bright white bases and brown tips. The white base comprises approximately $\frac{2}{3}$–$\frac{4}{5}$ of each hair. Other species in the subgenus also have bicolored dorsal fur. In *schmidtorum, hirsuta, microtis* and *megalotis,* hairs on the anterior part of the back have white bases that comprise $\frac{1}{4}$–

TABLE 2
(*Extended*)

M. megalotis	*M. microtis microtis*	*M. microtis mexicana*	*M. hirsuta*
12 females, 18 males	19 females, 22 males	21 females, 25 males	11 females, 18 males
5.5 (5.0–6.3) 9	5.6 (5.0–6.5) 17	6.9 (5.7–9.0) 6	13.1 (10.3–18.0) 18
59.4 (55.0–66.0) 19	57.5 (51.0–63.0) 29	62.2 (54.5–67.0) 17	70.8 (65.0–81.0) 17
13.4 (10.0–16.0) 19	12.4 (8.0–17.0) 29	12.6 (11.0–14.0) 17	14.7 (11.0–19.0) 16
9.2 (7.4–10.0) 19	10.3 (8.7–12.0) 23	10.3 (9.0–12.0) 21	13.6 (10.0–18.0) 18
22.1 (20.5–23.0) 14	20.1 (19.0–21.0) 17	21.1 (18.0–23.0) 17	24.5 (24.0–25.5) 16
34.2 (31.9–36.0) 19	33.4 (30.4–35.5) 35	35.5 (33.8–37.8) 37	43.6 (41.0–46.0) 28
8.8 (8.1–9.7) 28	8.5 (7.8–9.2) 37	9.2 (7.8–10.0) 40	12.2 (11.2–13.7) 21
13.4 (12.1–14.8) 15	13.2 (12.0–14.5) 31	13.7 (12.6–14.6) 28	19.3 (18.4–20.3) 15
15.97 (15.54–16.94) 16	15.87 (15.31–16.50) 30	17.06 (16.32–17.55) 29	20.90 (19.89–21.52) 15
8.64 (8.08–9.19) 19	8.62 (8.09–9.19) 29	9.29 (9.01–9.59) 22	11.62 (11.24–12.05) 16
7.92 (7.12–8.30) 20	7.42 (7.14–7.66) 31	7.72 (7.26–8.15) 32	8.67 (8.43–8.91) 16
3.82 (3.54–4.12) 25	3.97 (3.67–4.18) 37	4.06 (3.83–4.35) 39	4.95 (4.72–5.16) 17
6.69 (6.32–7.08) 25	6.66 (6.34–7.25) 38	7.17 (6.74–7.59) 44	9.15 (8.97–9.52) 18

[a] Summary statistics (mean, observed range, and sample size) of measurements for each species (see Appendix 1 for a list of the specimens measured). Weight is given in grams, all other measurements are recorded in millimeters. See text for a description of measurement methods.

½ of each hair; in *minuta,* only ½–⅔ of each hair is white. Coloration of hair on the posterior part of the body is more variable. The fur in this region is either unicolored brown (*hirsuta,* some *schmidtorum*), white just at the base (some *schmidtorum,* some *minuta*), or is bicolored with the white base comprising ⅓–½ of each hair (*megalotis, microtis,* most *minuta,* some *schmidtorum*). Thin, unicolored brown hairs are found scattered throughout the dorsal pelage of a few adult specimens in every species, usually in younger individuals (as judged by tooth wear).

The ventral fur of *sanborni* is white. This stands in sharp contrast to *megalotis, microtis,* and *hirsuta,* all of which have brown underparts. Although *schmidtorum* and *minuta* have pale underparts, the ventral fur in those taxa is usually a pale gray or buff that rarely approaches the true white seen in *sanborni.* The white ventral fur in *sanborni* continues anteriorly onto the throat and chin, and posteriorly onto the base of the ventral surface of the uropatagium. The fur on the uropatagium forms a small, roughly triangular patch whose apex is directed toward the tip of the tail. This fur patch extends approximately ⅔ of the distance from tail base to tip (approximately 8 mm). A similar fur patch is present in *hirsuta,* but it is proportionately smaller and consists of brown rather than white fur. *Micronycteris schmidtorum* lacks a distinct fur patch on the uropatagium, although the proximal portion of the legs are densely furred and these hairs often cover the base of the tail. The uropatagium and base of the tail are naked in *minuta, megalotis,* and *microtis.*

Like other members of the nominate subgenus, *sanborni* has a pair of dermal pads arranged in a V-shaped pattern on the apex of the chin, and the ventral edge of the horseshoe of the noseleaf is defined by a thick ridge. Although most of the facial pelage is brown, a thin mustache of white hairs is present on the upper lip. Long, thin white hairs are also sparsely distributed on the inside of the medial half of the pinnae. In contrast, *minuta* has only a few white hairs on the upper lip, and other members of the subgenus lack them entirely. No other species of *Micronycteris* has white hairs on the inside of the pinnae.

The external surface of the pinna is largely naked in *sanborni,* as in other species of *Micronycteris.* However, the anterior third of the external surface (i.e., the leading edge) is covered with short (≤3 mm), dense fur in *sanborni.* Many of the hairs on the base of the ears are bicolored like those of the dorsum. A similar pattern is seen in *minuta, microtis,* and *hirsuta.* Both *megalotis* and *schmidtorum* have much longer fur on the ears (5–8 mm).

A high, deeply notched band of skin extends between the anterior external surfaces

of the pinnae in *sanborni*. The notch effectively divides the band into two flaps, each of which is roughly triangular in shape. Each flap originates from the basal 1/6 of the pinna, expands dorsally as it approaches the midline, then steeply descends to terminate at the midline. The shape and height of these flaps and the depth of the intervening notch is similar to the condition seen in *minuta*. In contrast, the interauricular band in *megalotis, microtis,* and *hirsuta* has a more horizontal profile and a very shallow notch. The interauricular band in *schmidtorum* has a moderately deep notch that is roughly intermediate between the condition seen in *sanborni/minuta* and that seen in *megalotis/microtis/hirsuta*. All other species of *Micronycteris* lack an interauricular band.

Like other members of the nominate subgenus, *sanborni* has a metacarpal formula of 3 < 4 < 5. The length of the first phalanx equals the length of the second phalanx in both digits III and IV of the wing in *sanborni* as in *minuta*. In contrast, the second phalanx of digit IV is shorter than the first phalanx in *hirsuta, megalotis, microtis,* and *schmidtorum*. Morphology of digit III is similar in all members of the subgenus.

The relative proportions of the calcar and hind foot vary among species of *Micronycteris*. The calcar is approximately the same length as the hind foot in *sanborni* although the calcar may appear slightly longer or shorter depending on preparation methods (e.g., the placement of pins and degree of spreading of the uropatagium). The calcar is distinctly shorter than the hindfoot in *minuta,* and is markedly longer than the hindfoot in *hirsuta, megalotis, microtis,* and *schmidtorum*.

Morphology of the skull is remarkably similar in all members of the subgenus *Micronycteris*. The rostrum is long and narrow with no antorbital inflation, the braincase is globular, and there is little or no development of a sagittal crest (fig. 1). However, the relative breadth of the mastoid and zygomatic regions varies significantly among species. The maximum breadth of the mastoid region exceeds the maximum breadth of the zygoma in *sanborni* and *minuta,* whereas the reverse is true in *hirsuta, schmidtorum, megalotis,* and *microtis*. The condition in *sanborni* and *minuta* appears to be the result of relative enlargement of the mastoid region because proportions of the zygomatic arches (as compared to the rostrum and braincase) are similar in all members of the subgenus.

With the exception of slight differences in relative width (which may be explained by difference in the dentition), the palate is essentially similar in all members of the subgenus *Micronycteris* including *sanborni*. The postpalatal extension is roughly parallel-sided and has a V-shaped posterior margin (fig. 1). The basisphenoid pits are relatively shallow and are separated by a low medial ridge.

Like other members of the nominate subgenus, *sanborni* has a dental formula of I 2/2, C 1/1, P 2/3, M 3/3 × 2 = 34. Crown height of the upper incisors is somewhat reduced in *sanborni,* and 12 appears particularly small in comparison with the canine (figs. 2, 3). This reduction is accentuated by the presence of a gap between the outer upper incisor and canine, a feature absent in other species of *Micronycteris* (fig. 3). This gap is present in all available specimens of *sanborni* but varies in width, with the holotype (fig. 3A) exhibiting maximum development of this feature. The upper canine of some specimens of *sanborni* is slightly smaller and somewhat more pyramidal than in other members of the subgenus *Micronycteris* (figs. 2, 3).

The premolar dentition also differs in *sanborni*: P3 is distinctly smaller than P4, and P4 has an unusually large posterolingual cingulum or heel (figs. 2, 4). P3 and P4 are subequal in anteroposterior length in all members of the nominate subgenus.[4] However,

[4] Sanborn (1949: 216) used proportions of P3 and P4 to help distinguish subgenera, noting that "P3 large, about equal to P4" characterized his subgenus *Micronycteris* (*megalotis, microtis, minuta,* and *schmidtorum*) and subgenus *Xenoctenes* (= *hirsuta*). However, this generalization does not hold up on closer inspection. In all of these species, the anteroposterior length of P3 is similar to that of P4, but in *minuta* and *sanborni* the height of P3 is significantly less than that of P4. Another species, *nicefori* (= *Trinycteris*) was described by Sanborn (1949: 216) as having "P3 smaller than P4," but the premolar dentition in that form differs significantly from that of *sanborni, minuta,* and other members of the subgenus *Micronycteris*. P3 in *nicefori* is a long, low tooth with the main cusp located over the anterior root. In contrast, this tooth is shorter anteroposteriorly, has a relatively higher crown, and the main cusp is located between the two roots in all members of the nominate subgenus. P4 in *nicefori* has an unusually large anterobasal cusp, and

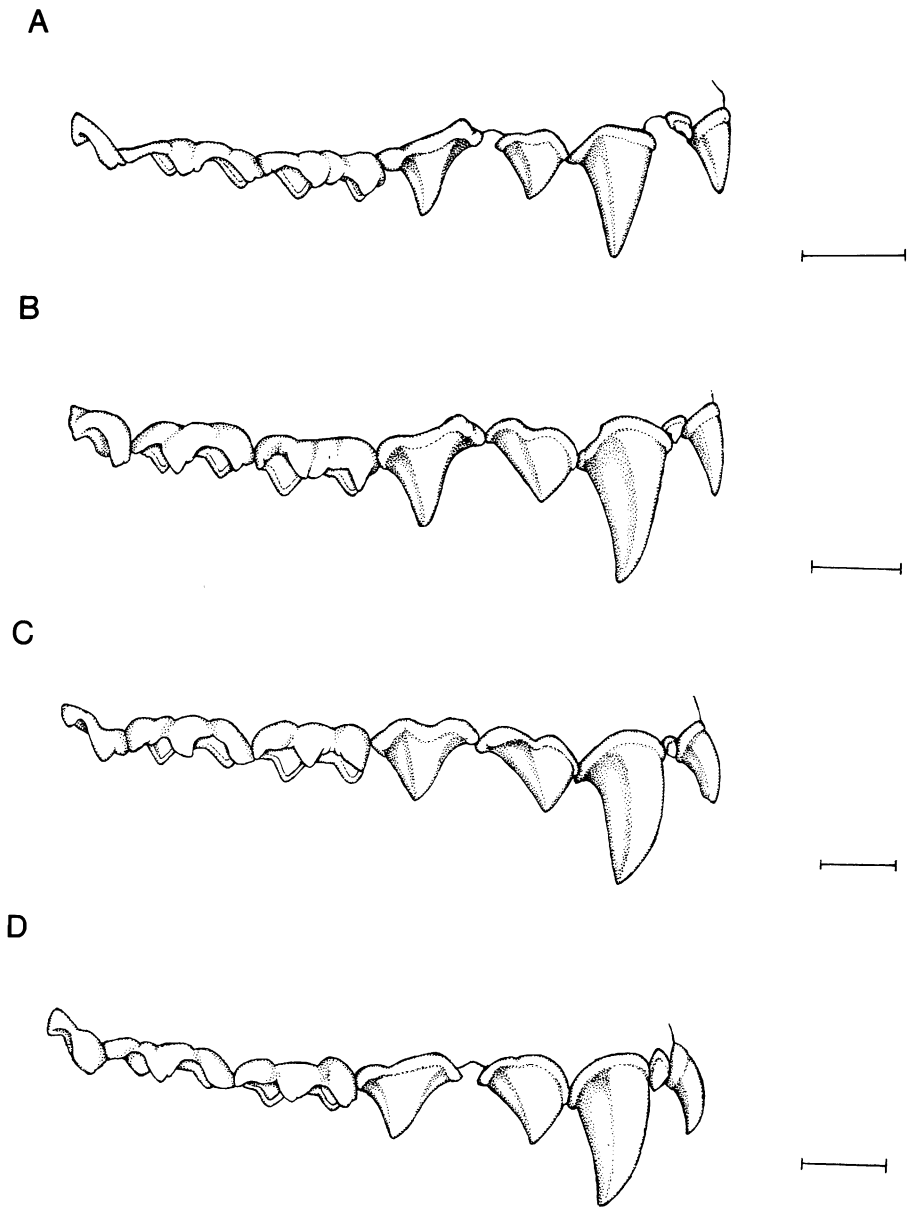

Fig. 2. Lateral view of the upper dentition in **(A)** *Micronycteris sanborni,* n. sp. (USNM 555702, the holotype), **(B)** *M. minuta* (AMNH 267098), **(C)** *M. schmidtorum* (AMNH 256821), and **(D)** *M. megalotis* (AMNH 266020). Exposed roots of some teeth have been omitted to facilitate visual comparisons of crown morphology.

←

the large main cusp is recurved. In contrast, P4 in members of the subgenus *Micronycteris* has a poorly developed anterobasal cusp, and the main cusp is not significantly recurved.

height of P3 is significantly less than that of P4 in *sanborni* and *minuta.* Development of the posterolingual heel and lingual cusp on P4 varies among species (fig. 4). The heel is quite small in *minuta,* somewhat larger in *hirsuta, schmidtorum, megalotis,* and *microtis,* and reaches its largest relative propor-

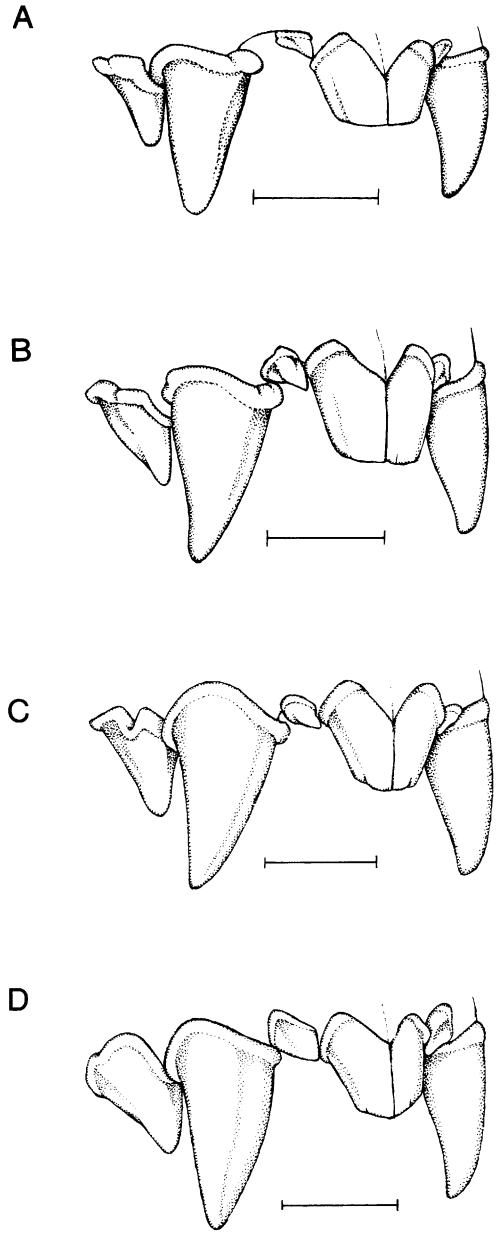

Fig. 3. Oblique view of the anterior upper dentition in **(A)** *Micronycteris sanborni,* n. sp. (USNM 555702, the holotype), **(B)** *M. minuta* (AMNH 267098), **(C)** *M. schmidtorum* (AMNH 256821), and **(D)** *M. megalotis* (AMNH 266020). Exposed roots of some teeth have been omitted to facilitate visual comparisons of crown morphology.

tions in *sanborni.* The lingual cusp, formed from the raised lingual edge of the tooth, is poorly developed and lacks a sharp point in *sanborni.* This cusp is formed in the same manner and shows a similar degree of development in most other members of the subgenus *Micronycteris,* although there is some variation both between and within species. The lingual cusp tends to be somewhat better-developed in *megalotis* and *microtis,* where it is pointed and often marked by a small but distinct wear facet. However, some individuals of both of these species lack the lingual cusp entirely. The lingual cusp is usually absent in *schmidtorum,* although a poorly developed cusp may be present in some individuals.

Size of the P4 heel is correlated with size of the lingual region of M1. The lingual portion of M1 (particularly the cingulum of the hypocone) is relatively large in *sanborni,* resulting in an almost square tooth that has dimensions similar to M2. In other species of the subgenus, the lingual portion of M1 is proportionally narrower, the occlusal outline of the tooth is more rectangular, and the width of M1 is significantly less than the width of M2 (fig. 4). In most species of *Micronycteris,* the cingulum of the hypocone of M2 extends posteriorly as far as or beyond the metacrista, appearing to contact or nearly contact the anterolingual margin of M3 when these teeth are seen in occlusal view (fig. 4). In contrast, in *sanborni* the hypoconular region of M2 extends more lingually than posteriorly resulting in a large gap between the lingual regions of M2 and M3.

The lower dentition of *sanborni* is much like that of other species of *Micronycteris.* The lower incisors are small and bilobed. The lower canine of *sanborni* is somewhat smaller than that of other members of the subgenus, but there is otherwise little difference in morphology (fig. 5). Crown height of p2 is less than its length in most individuals of *sanborni,* though these proportions vary somewhat with tooth wear. In both *sanborni* and *minuta,* p3 is a tiny tooth that is much smaller than p2 and p4. In comparison, p3 is only slightly reduced in *schmidtorum* and *hirsuta*; p2, p3, and p4 are approximately the same size in *megalotis* and *microtis.* The lower mo-

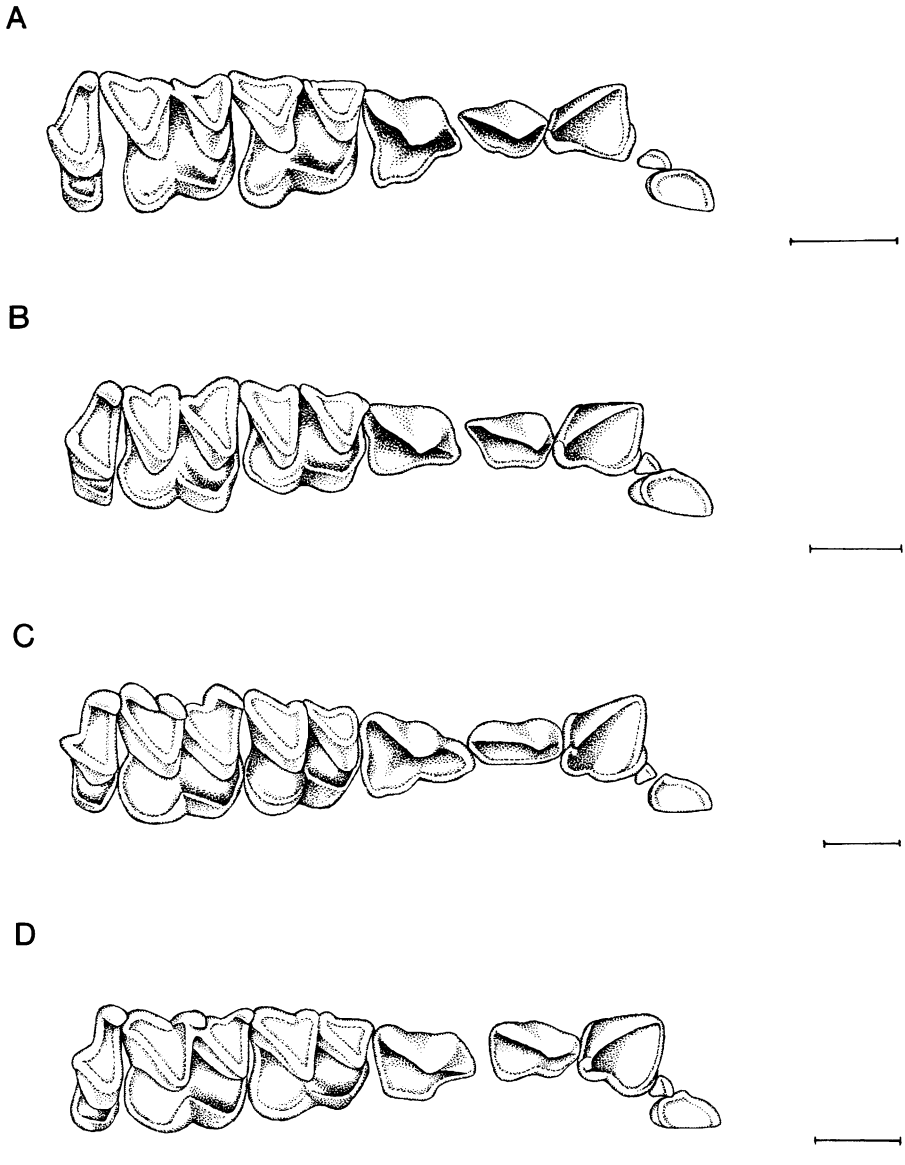

Fig. 4. Occlusal view of the upper dentition in **(A)** *Micronycteris sanborni,* n. sp. (USNM 555702, the holotype), **(B)** *M. minuta* (AMNH 267098), **(C)** *M. schmidtorum* (AMNH 256821), and **(D)** *M. megalotis* (AMNH 266020).

lar dentition is similar in all members of the nominate subgenus.

Shape of the posterior lower jaw varies among species of *Micronycteris.* The coronoid process in *sanborni* and *minuta* is comparatively low and the upper margin of the ascending ramus has a shallow slope (16–18°; fig. 5). In contrast, the coronoid process is somewhat higher and the upper border of the ascending ramus has a steeper slope (25–30°) in *schmidtorum, hirsuta, megalotis,* and *microtis.*

KARYOTYPE: The standard karyotype of the female holotype (prepared by A. L. Gardner)

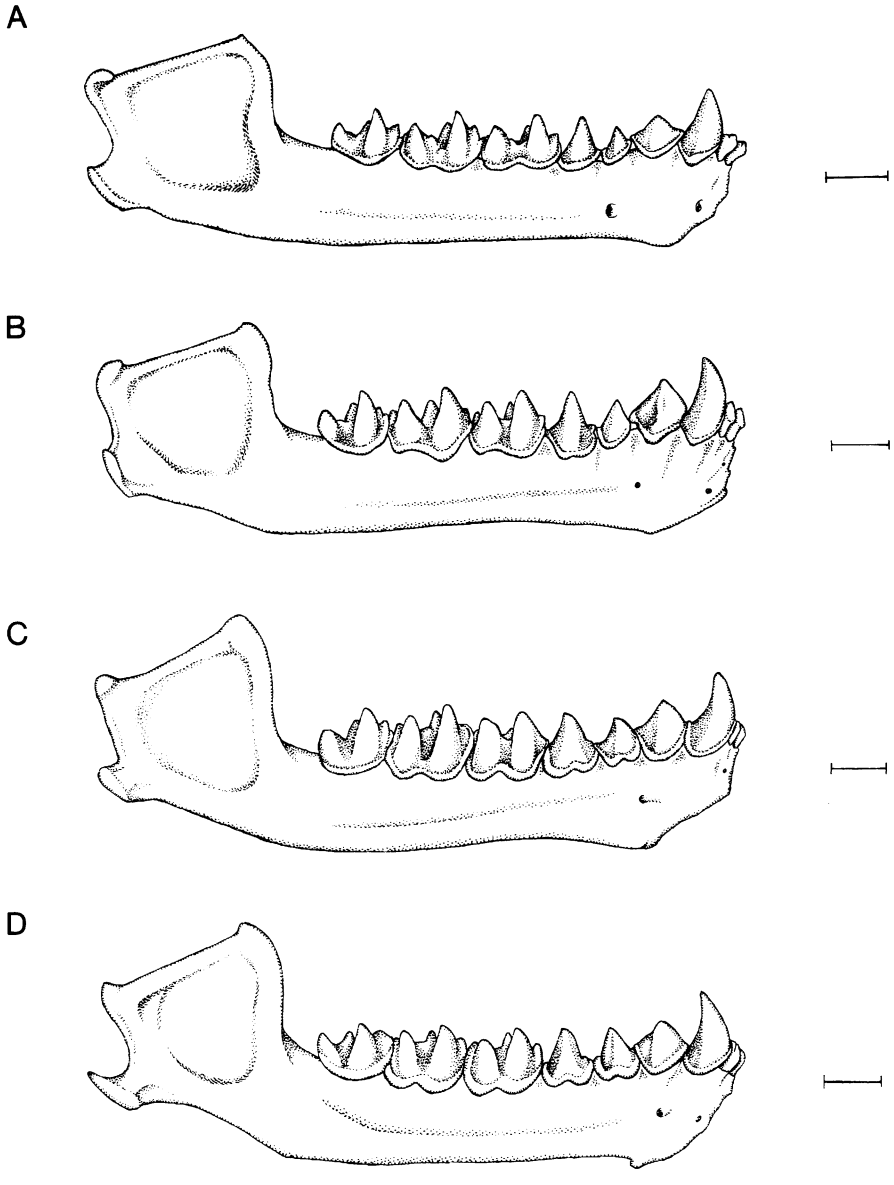

Fig. 5. Lateral view of the lower jaw and dentition in **(A)** *Micronycteris sanborni,* n. sp. (USNM 555702, the holotype), **(B)** *M. minuta* (AMNH 267098), **(C)** *M. schmidtorum* (AMNH 256821), and **(D)** *M. megalotis* (AMNH 266020). Exposed roots of some teeth have been omitted to facilitate visual comparisons of crown morphology.

includes five pairs of metacentric chromosomes, seven pairs of submetacentric chromosomes, and one pair of small telocentric chromosomes (2N = 28, FN = 50); the two large submetacentrics are assumed to represent the X-chromosomes (fig. 6). As thus reconstructed, the karyotype of *sanborni* appears identical to the karyotype of *minuta* (2N = 28, FN = 50) published by Patton and Baker (1978), although the homologies of different arms cannot be assessed because G- or C-band data are not available for *sanborni.*

Fig. 6. Photograph of mitotic metaphase chromosomes of the female holotype (USNM 555702) of *Micronycteris sanborni,* n. sp. (above) and the reconstructed karyotype (below). The autosomal complement consists of five metacentric pairs, seven submetacentric pairs, and a single pair of small telocentric elements. Two large submetacentrics are assummed to represent the X-chromosomes. As depicted, the standard karyotype is 2N = 28, FN = 50.

All other species of the subgenus *Micronycteris* have karyotypes that differ from those of *minuta* and *sanborni*. *M. megalotis* and *microtis* have identical diploid and fundamental numbers[5] (2N = 40, FN = 68), while *schmidtorum* (2N = 38, FN = 66) and *hirsuta* (2N = 28–30, FN = 32) have unique karyotypes (Gardner, 1977; Patton and Baker, 1978; Honeycutt et al., 1980).

NATURAL HISTORY

Little can be deduced about the natural history of *Micronycteris sanborni* other than aspects of its habitat. The type locality is located in the cerrado vegetation zone of northeastern Brazil. Willig (1983: 13) described the habitat of the Crato study area as follows:

> Physiognomically, the Cerrado on the Chapada [plateau] do Araripe is an open tree and shrub woodland with a pervasive grass component. Small trees (3–5 m) and shrubs (0.5–3 m) form approximately half the vegetation cover, and various grass species occupy the remaining area. Taller trees, rarely exceeding a height of 15 m are scattered throughout the area. As a result, the canopy is open, irregular and undulating in profile, with numerous areas lacking woody plants . . . [Some sections], for the most part bordering the windward side of the Chapada do Araripe, differ substantially from Cerrado vegetation in plant density, physiognomony, and species importance. Stands with very little grass, few shrubs, and numerous trees are . . . referred to as Cerradão. Larger trees compose Cerradão habitats and form a closed canopy between 12 and 17 m high. . . . The understory may vary from quite dense to sparse; however, in either situation, small shrubs (~1 m) and grasses are rare.

The presence of cerradão vegetation on the windward side of the Chapada do Araripe—and more mesic "humid forest" on hillsides at the base of the plateau—is apparently the result of orographic rainfall produced by adiabatic cooling of rising air currents (Mares et al., 1981; Willig, 1983).

According to Gardner (personal commun.) the holotype of *sanborni* was collected in a ground-level mist net set adjacent to a dam in a small canyon cut into the slope of the northern (windward) margin of the Chapada do Araripe. There is more moisture in the canyon than on the plateau above, a difference reflected in the presence of more mesic vegetation in the canyon. No other specimens of *Micronycteris* were captured at the type locality. However, another specimen of *sanborni* (CM 98913) was collected on the Chapada do Araripe near the town of Nova Olinda in Ceará, and other specimens possibly referable to this species[6] have been captured in both cerrado and cerradão habitats on the plateau (Mares et al., 1981).

Specimens of *sanborni* have also been collected in caatinga habitats in the vicinity of Exu in Pernambuco. "Caatinga" subsumes a variety of vegetation assemblages comprised of xeric-adapted plants. Many caatinga plants are deciduous, and cacti and euphorbs form a significant component of the flora (Mares et al., 1981; Willig, 1983). Four types of caatinga habitats were described by Mares et al. (1981) and Willig (1983): caatinga baixa, caatinga alta, serrotes, and lajeiros. Caatinga

[5] A specimen of "*megalotis*" karyotyped by Baker (1967) and discussed by Hsu et al. (1968) and Gardner (1977) is a male collected in Chiapas, Mexico. Based on its geographic origin, this specimen almost certainly represents *M. microtis mexicana* rather than *megalotis* (see footnote 2). Specimens identified as *megalotis* from Trinidad (TTU 23759 [karyotype TK 8463]) and Surinam (CM 63575) have karyotypes with the same diploid and fundamental number (Patton and Baker, 1978; Honeycutt et al., 1980). I reexamined these specimens and found the published identifications to be correct. Thus *megalotis* and *microtis* apparently have very similar (if not identical) karyotypes.

[6] Mares et al. (1981) indicated that "*Micronycteris* sp." and *minuta* are rare components of cerrado, cerradão, and caatinga habitats in the Chapada do Araripe region. Willig (1983) later concluded that all of the specimens referred to *minuta* by Mares et al. (1981) are actually *megalotis*, and that those referred to *Micronycteris* sp. actually represent *minuta*. I have seen all of the voucher specimens deposited at the Carnegie Museum (see Appendix 1), and I agree with Willig's identification of the *megalotis* (CM 98911, 98912). However, at least two of Willig's *minuta* specimens represent *schmidtorum* (CM 98908, 98909; Ascorra et al., 1991; personal obs.), while four others form the type series for *sanborni* (USNM 555702; CM 98913, 98914, 98915). None of the Carnegie Museum specimens from Ceará and Pernambuco represent *minuta*. On this basis, it seems likely that the remainder of the "*Micronycteris* sp." collection—presumably housed in the Museu de Zoologia, Universidade de São Paulo—also consists of *sanborni* and *schmidtorum*.

baixa, or low caatinga, is the predominant habitat at lower elevations in the Exu region (Willig, 1983). Plant species composition varies from site to site, but the vegetation is typically dense. Large cacti are common, and trees are xerophytic with most reaching heights of 3 to 5 m (Mares et al., 1981; Willig, 1983). Caatinga alta is dominated by larger trees (10–12 m), which typically lose their leaves synchronously during the dry season and form a closed canopy during the wet season (Mares et al., 1981; Willig, 1983). The understory of caatinga alta is less dense than in caatinga baixa habitats, but there is considerable variation from locality to locality. Caatinga alta habitats are generally restricted to higher elevations, hillsides, and the gentle valleys associated with serrotes (Mares et al., 1981; Willig, 1983). Serrotes are small granitic mountains (sometimes termed "brejos") that are common in the Exu region (Willig, 1983). These topographic features, which receive some orographic rainfall, apparently harbor the most mesic components of the caatinga flora and may remain green for extended periods during the dry season (Willig, 1983). The vegetation of serrotes often contains a mixture of caatinga alta flora and more mesic plants such as palm trees (Mares et al., 1981; Willig, 1983). Lajeiros are low granite outcrops (<15 m high) that are distributed throughout areas dominated by caatinga baixa (Mares et al., 1981; Willig, 1983). Lajeiros range from small, unbroken rock faces to fissured and boulder-strewn outcrops of several hectares (Willig, 1983). Depressions and crevices in the rock apparently often fill with water during the wet season and moisture persists for a variable length of time in the dry season (Mares et al., 1981). The vegetation associated with lajeiros includes cacti and small shrubs that grow in fissures in the rock. A list of the most common tree, shrub, and grass species for each cerrado and caatinga habitat type was provided by Mares et al. (1981).

No specimens of *Micronycteris* have been captured in caatinga baixa (Mares et al., 1981), perhaps because the density of the vegetation precludes gleaning. This hypothesis is supported by the absence of other putative gleaners known from the region (e.g., *Tonatia bidens, Tonatia brasiliensis, Mimon crenulatum*) from the fauna of this particular habitat (Mares et al., 1981). Mares et al. (1981: 104) reported that "*Micronycteris* sp." (see footnote 6) was "rare in the Caatingas where it is usually captured near serrotes or lajeiros." At least 4 specimens collected in the caatinga represent *sanborni* (CM 98914, 98915, 98916, 98917). It is possible that *sanborni* and other *Micronycteris* species selectively utilize the more mesic areas within caatinga and cerrado regions—stream courses, relatively moist serrotes, etc. Unfortunately, there are not enough data available to test this or any other hypothesis concerning distribution patterns of *Micronycteris* in northeastern Brazil. Over 5000 bats were captured by Willig and his colleagues in Ceará and Pernambuco, but this sample included only 26 specimens of *Micronycteris* (Mares et al., 1981; Willig, 1983). This suggests that all species of *Micronycteris* are uncommon in the area. However, it should be noted that net capture frequencies may underestimate the relative abundance of these elusive bats. This seems to be the case in French Guiana, where collecting at roost sites suggests higher population densities for species in the subgenus *Micronycteris* than do mist-net surveys (Simmons and Voss, in prep.).

Three species in the genus *Micronycteris* appear to be actually or potentially sympatric in northeastern Brazil: *sanborni, schmidtorum,* and *megalotis.* Despite the published accounts of Mares et al. (1981) and Willig (1983), *minuta* does not appear to occur in the area (see footnote 6). Of the three species present in northeastern Brazil, only *sanborni* and *megalotis* have been shown to occur in sympatry at the same collecting locality (i.e., Fazenda Pomonha, 21 km SSW of Exu, Pernambuco). However, Fazenda Pomonha is only 15 km from a site where *schmidtorum* has been collected (Fazenda Alto de Ferreira, 5 km SW of Exu), suggesting that all three species of *Micronycteris* probably are sympatric in the area. Multiple species of *Micronycteris* are known to occur at localities elsewhere (e.g., Paracou, French Guiana; Appendix 1), but uncovering such patterns requires intense collecting at single sites. More data will be necessary before we can effectively evaluate patterns of *Micronycteris* species diversity and distribution in various cerrado and caatinga habitats.

Reproductive patterns in *sanborni* are

largely unknown although some information is available on general timing of parturition. Two females captured at a locality in Pernambuco in mid-December (CM 98915, 98916) were both pregnant with large fetuses; another individual captured at the same locality in late April (CM 98914) was not pregnant. The holotype of *sanborni* (USNM 555702), a female collected in Ceará in mid-March, was not pregnant at the time of capture. According to Willig (1985), the wet season in northeastern Brazil begins in November or December and extends until April or May. In this context, it seems likely that *sanborni* follows a pattern similar to that seen in other species of cerrado and caatingas bats, many of which give birth in the wet season and wean their young around the beginning of the following dry season (Willig, 1985).

PHYLOGENETIC RELATIONSHIPS WITHIN *MICRONYCTERIS*

The preceding species comparisons provide a rich source of characters for analyses of relationships within the genus *Micronycteris*. In order to test monophyly of the nominate subgenus, all species currently referred to the genus *Micronycteris* (with the exception of *behnii*) were included in the analysis, and a hypothetical ancestral taxon was constructed to root the tree (see footnote 3 on page 5). Comparisons of the species in question resulted in identification of 22 morphological characters of potential phylogenetic significance.

Morphological Characters

The characters listed below are based on features discussed in "Description and Comparisons" above. A taxon-character matrix summarizing the data is given in table 4, and a list of the specimens examined is provided in Appendix 1.

Character 1: *Dorsal fur unicolored, dark brown or gray (0); or bicolored, hairs with white bases and dark tips (1); or tricolored, hairs with dark bases, a pale medial band, and dark tips (2).* All members of the subgenus *Micronycteris* have bicolored dorsal fur. In contrast, *brachyotis* and *daviesi* have unicolored dorsal fur, and *nicefori* and *sylvestris* have tricolored fur. I was not able to determine the color pattern of the fur in *pusilla* because the only available specimens have been preserved in alcohol for over 60 years. The ancestral condition cannot be reconstructed because there is too much variation

TABLE 3
Key to Species of the Subgenus *Micronycteris*[a]

1. Forearm greater than 39 mm; notch in ear band shallow; I1 with high crown, tapers to blunt point; lower incisors with very high crowns, compressed laterally between canines; karyotype 2N = 28–30, FN = 32 ..... *M. hirsuta*
1′. Forearm less than 39 mm; notch in ear band shallow to deep; spatulate I1 with moderately high crown; lower incisors with low crowns, not laterally compressed 2
2. Ventral fur color much paler than dorsal fur color; notch in ear band moderate or deep; crown height of P3 less than P2 and P4; calcar either equal to or shorter than foot 3
2′. Ventral fur approximately the same color as dorsal fur; notch in ear band shallow; P2, P3, and P4 approximately the same height; calcar longer than foot; karyotype 2N = 40, FN = 68 5
3. Notch in ear band moderately deep; coronoid process high with relatively steep posterior slope along upper margin; calcar longer than foot; thumb longer than 9.2 mm; karyotype 2N = 38, FN = 66 ..... *M. schmidtorum*
3′. Notch in ear band very deep; coronoid process low with relatively shallow posterior slope along upper margin; calcar either equal to or shorter than foot; thumb shorter than 9.2 mm; karyotype 2N = 28, FN = 50 4
4. No gap between I2 and canine; calcar shorter than foot; thumb longer than 7.5 mm ..... *M. minuta*
4′. Gap between I2 and canine; length of calcar equal to that of foot; thumb shorter than 7.5 mm ..... *M. sanborni*
5. Long fur on leading edge of ear (4–8 mm) ..... *M. megalotis*
5′. Short fur on leading edge of ear (≤3 mm) ..... *M. microtis*

[a] All members of the subgenus *Micronycteris* share the following: (1) V-shaped pair of pads on chin; (2) bicolored dorsal fur (brown with white base); (3) large, rounded ears connected by a notched band of skin; (4) metacarpal formula $3 < 4 < 5$; (5) first and second phalanges of digit III of wing subequal in length; and (6) bifid lower incisors.

TABLE 4
Taxon-Character Data Matrix of Morphological Characters[a]

Ancestor	??0?0	?????	?0?00	???00	??
M. brachyotis	00010	?1312	11000	11000	10
M. nicefori	20010	?0212	20100	10210	10
M. pusilla	?0000	?1212	21100	10010	11
M. sylvestris	20010	?0112	21101	21111	11
M. daviesi	00010	?0112	21101	21011	11
M. megalotis	10101	01000	00000	01000	00
M. microtis	10001	01000	00000	01000	00
M. hirsuta	10001	01000	00000	01100	00
M. schmidtorum	11101	11000	00000	01100	00
M. minuta	11001	21001	20010	00200	01
M. sanborni	11001	21001	00010	00200	01

[a] See text for character descriptions.

among potential outgroups (i.e., other "phyllostomines" sensu Koopman, 1993, 1994).

Character 2: *Ventral fur dark, either gray, brown, or yellow-brown (0); or pale, either white, tan, or pale gray (1).* The ventral fur is dark in *pusilla, brachyotis, sylvestris, nicefori, hirsuta, megalotis,* and *microtis.* It is pale in *schmidtorum, minuta,* and *sanborni.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 3: *Fur on external surface of leading edge of pinna short, ≤ 4 mm (0); or long, 5–8 mm (1).* The fur on the leading edge of the pinna is short in *pusilla, brachyotis, sylvestris, nicefori, hirsuta, microtis, minuta,* and *sanborni.* In contrast, the fur on the leading edge of the ear is long in *megalotis* and *schmidtorum.* Comparisons with other "phyllostomines" suggest that the former condition (short fur) is primitive.

Character 4: *Pinna rounded distally, with no concavity on posterior border near tip (0); or pointed, with concavity on posterior border near tip (1). Micronycteris pusilla* and all members of the subgenus *Micronycteris* have rounded ears. In contrast, *brachyotis, sylvestris, daviesi,* and *nicefori* have pointed ears. The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 5: *Interauricular band absent (0); or present (1).* All members of the subgenus *Micronycteris* have a band of skin between the ears. This structure is absent in *pusilla, brachyotis, sylvestris, daviesi,* and *nicefori.* Comparisons with other "phyllostomines" indicates that absence of an interauricular band is the primitive condition.

Character 6: *Notch in interauricular band shallow (0); moderate (1); or deep (2).* The notch in the interauricular band between the ears is relatively shallow in *hirsuta, megalotis,* and *microtis.* In contrast, the notch is of moderate depth in *schmidtorum,* and is relatively deep in *minuta* and *sanborni.* Transformation in this character is specified as ordered (0 ↔ 1 ↔ 2). Taxa that lack an interauricular band (see character 5) were scored "?" for this character.

Character 7: *Ventral margin of noseleaf confluent with upper lip, boundary between horseshoe and lip not defined by ridge or free flap of skin (0); or ventral margin of horseshoe defined by thick ridge of skin (1).* The ventral portion of the horseshoe grades gradually into the upper lip in *sylvestris, daviesi,* and *nicefori.* No thick ridge or free flap of skin marks the boundary between the horseshoe and lip in these forms. In contrast, the ventral margin of the horseshoe is defined by a thick ridge of skin that clearly delineates the boundary between horseshoe and lip in *pusilla, brachyotis,* and all members of the subgenus *Micronycteris.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 8: *Metacarpal formula 3 < 4 < 5 (0); or 4 < 3 < 5 (1); or 4 < 5 < 3 (2); or 5 < 4 = 3 (3).* All members of the subgenus *Micronycteris* have a metacarpal formula of 3 < 4 < 5. The metacarpal formula is 4 < 3 < 5 in *sylvestris* and *daviesi,* and 4 < 5 < 3 in *pusilla* and *nicefori.* The metacarpal for-

mula in *brachyotis* is 5 < 4 = 3. The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups. No transformation series was specified for this character.

Character 9: *Second phalanx of digit III of wing longer than first phalanx (0); or the same length as first phalanx (1).* The second phalanx of digit III of the wing is longer than the first phalanx in *pusilla, brachyotis, sylvestris, daviesi, nicefori,* and *sylvestris.* The second phalanx is about the same length as the first phalanx in all members of the subgenus *Micronycteris.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 10: *Second phalanx of digit IV of wing longer than first phalanx (0); or the same length as first phalanx (1); or shorter than the first phalanx (2).* The second phalanx of digit IV is longer than the first in *pusilla, brachyotis, sylvestris, daviesi,* and *nicefori.* In contrast, the second phalanx is shorter than the first phalanx in *hirsuta, megalotis, microtis,* and *schmidtorum,* and these two elements are the same length in *minuta* and *sanborni.* Transformation in this character is specified as ordered (0 ↔ 1 ↔ 2). The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 11: *Calcar length equal to or greater than hind foot length (0); or less than hind foot length (1).* The calcar is the same length or longer than the hind foot[7] in *brachyotis, hirsuta, megalotis, microtis, schmidtorum,* and *sanborni.* In contrast, the calcar is markedly shorter than the hindfoot in *pusilla, sylvestris, daviesi, nicefori,* and *minuta.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 12: *Rostrum and anterior orbital region not inflated, dorsum of rostrum convex (0); or inflated, dorsum of rostrum flat or concave (1).* The rostrum and anterior orbital region is not inflated in *nicefori* or members of the subgenus *Micronycteris.* In contrast, inflation is present in *pusilla, brachyotis, sylvestris,* and *daviesi.* Comparisons with other "phyllostomines" indicate that the former condition (absence of inflation) is primitive.

Character 13: *Basisphenoid pits shallow (0); or deep (1).* The basisphenoid pits are relatively shallow in *brachyotis* and all members of the subgenus *Micronycteris.* In contrast, they are quite deep in *pusilla, sylvestris, daviesi,* and *nicefori.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 14: *Mastoid breadth less than zygomatic breadth (0); or greater than zygomatic breadth (1).* Breadth of the skull measured across the mastoid region is less than breadth measured across the zygoma in *pusilla, brachyotis, sylvestris, daviesi, nicefori, hirsuta, megalotis, microtis,* and *schmidtorum.* In contrast, mastoid breadth is greater than zygomatic breadth in *minuta* and *sanborni.* Comparisons with other "phyllostomines" indicate that the former condition (mastoid breadth < zygomatic breadth) is primitive.

Character 15: *P3 not molariform, lingual cingulum and cusp absent (0); or P3 molariform, well-developed lingual cingulum and cusp present (1).* P3 in *brachyotis, pusilla, nicefori,* and all members of the subgenus *Micronycteris* is a nonmolariform, bladelike tooth that lacks a lingual cingulum and cusp. In contrast, P3 in *sylvestris* and *daviesi* is a molariform tooth with a well-developed lingual cingulum and cusp. Comparisons with other "phyllostomines" indicate that the former condition (P3 not molariform) is primitive.

Character 16: *Lingual cingulum of P4 with concave outline and raised edge, lingual cusp small or absent (0); or lingual cingulum with convex outline and raised edge, lingual cusp small or absent (1); or lingual cingulum with convex outline, edge not raised, lingual cusp well-developed (2).* The P4 of all members of the subgenus *Micronycteris* has a lingual cingulum with a concave outline (in occlusal view) and a raised lingual edge. The lingual cusp in these taxa is either minute (comprised of an enlargement of the raised lingual edge) or absent. Morphology of the edge and cusp is similar in *pusilla, brachyotis,* and *nicefori,* but the outline of the tooth is different, with the lingual cingulum convex rather than con-

[7] Two potentially distinct character states ("calcar and hind foot similar in length" and "calcar longer than hind foot") are combined in the scoring used for this character because there is apparently significant within-species variation in *brachyotis* (Sanborn, 1949; personal obs.).

cave in outline. In contrast, *sylvestris* and *daviesi* have a P4 lingual cingulum that has a similar convex outline but lacks the raised edge. Instead, both species have a well-developed lingual cusp that is located more centrally on the cingulum. Transformation in this character is specified as ordered (0 ↔ 1 ↔ 2). The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 17: *Height of P3 less than P4 (0); or P3 and P4 subequal (1).* The crown height of P3 is distinctly less than that of P4 in *pusilla, nicefori, minuta,* and *sanborni.* P3 and P4 are subequal in *brachyotis, sylvestris, daviesi, hirsuta, megalotis, microtis,* and *schmidtorum.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 18: *Lower third premolar (p3) much smaller than p2 and p4 (0); or p3 slightly smaller than p2 and p4 (1); or p3 subequal with p2 and p4 (2).* The lower third premolar (p3) is much smaller than p2 and p4 in *nicefori, minuta,* and *sanborni.* Alternatively, p3 is slightly smaller (in both anteroposterior length and crown height) than p2 and p4 in *sylvestris, hirsuta,* and *schmidtorum.* The lower premolars are subequal in *pusilla, brachyotis, daviesi, megalotis,* and *microtis.* Transformation in this character is specified as ordered (0 ↔ 1 ↔ 2). The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 19: *Upper canine ≥ twice the height of the inner incisor (0); or much less than twice the height of the inner incisor (1).* The upper canine is roughly twice the height of the canine in *brachyotis* and in all members of the subgenus *Micronycteris.* In contrast, relative height of the canine is reduced (canine height ≤1⅓ height of inner incisor) in *pusilla, sylvestris, daviesi,* and *nicefori.* Comparisons with other "phyllostomines" indicate that the former condition (longer canines) is primitive.

Character 20: *Outer upper incisor in normal position between inner incisor and canine, not excluded from occlusion with lower incisors (0); or outer incisor absent or moved dorsally and excluded from occlusion by close apposition of inner incisor and canine (1).* The outer upper incisor is located in an occlusal position between the inner incisor and canine in *pusilla, brachyotis, nicefori,* and all members of the subgenus *Micronycteris.* In contrast, the canine and enlarged inner incisor are closely apposed in *sylvestris* and *daviesi,* leaving no room in the occlusal toothrow for the outer incisor. In *sylvestris* the outer incisor is small but still present, located in an unusual dorsal position between the root of the inner incisor and canine. The outer upper incisor is absent in *daviesi.* Comparisons with other "phyllostomines" indicate that the former condition (outer upper incisor in "normal" occlusal position) is primitive.

Character 21: *Lower incisors trifid (0); or bifid (1). Micronycteris pusilla, brachyotis, sylvestris, daviesi,* and *nicefori* have trifid lower incisors. In contrast, all members of the subgenus *Micronycteris* have bifid lower incisors. The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Character 22: *Coronoid process high, with relatively steep slope along upper margin from anterior to posterior (0); or low, with little slope along dorsal margin (1).* The ascending ramus of the coronoid process is relatively high with a steep posterior slope (25–30°) in *brachyotis, nicefori, hirsuta, megalotis, microtis,* and *schmidtorum.* In contrast, the ascending ramus is low and has a relatively shallow slope (15–20°) in *pusilla, sylvestris, daviesi, minuta,* and *sanborni.* The ancestral condition cannot be reconstructed because there is too much variation among potential outgroups.

Results of Phylogenetic Analysis of Morphological Data

A branch-and-bound analysis of the morphological data matrix given in table 4 resulted in five equally parsimonious trees (each with 42 steps, CI = 0.690, RI = 0.812); a strict consensus of these trees is shown in figure 7. These results suggest that (1) the subgenus *Micronycteris* is monophyletic; (2) *hirsuta, schmidtorum, minuta,* and *sanborni* form a clade within which *hirsuta* occupies the most basal branch; and (3) *minuta* and *sanborni* are sister taxa. Other perceived relationships include a sister-group relationship between *sylvestris* and *daviesi* (supporting monophyly of the subgenus *Glyphonycteris* as defined in table 1), and existence of a clade containing

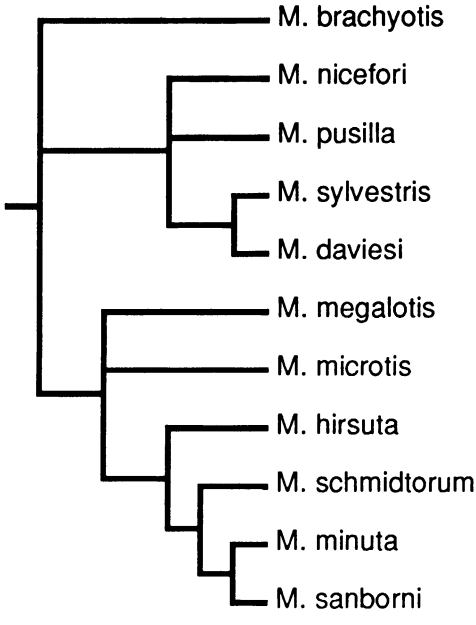

Fig. 7. Results of branch and bound analysis of 22 morphological characters (see text and table 4 for data). The tree shown here is a strict consensus of five equally parsimonious trees, each with 42 steps (CI = 0.690; RI = 0.812). Trees were rooted using a hypothetical ancestor (omitted from this figure) which was scored only for those characters that show little or no variation among putative sister groups; see text for discussion.

Glyphonycteris, nicefori, and *pusilla.* Relationships between the latter clade, *brachyotis,* and the subgenus *Micronycteris* could not be resolved.

Interpretations of character evolution are hampered because polarity cannot be unambiguously established for many characters. However, some conclusions are possible. The clade containing *sanborni* and *minuta* is one of the most strongly supported groupings. This clade is unequivocally diagnosed by six synapomorphies: presence of a deep notch in the ear band, first and second phalanges of digit IV of the wing equal in length, mastoid breadth > zygomatic breadth, height of P3 < height of P4, p3 much smaller than p4, and a low coronoid process. A close relationship between *schmidtorum* and the clade containing *sanborni* + *minuta* is supported by two derived features: pale ventral fur, and presence of at least a moderately deep notch in the ear band. *Micronycteris hirsuta* is linked with the *schmidtorum* + *sanborni* + *minuta* clade on the basis of only one derived feature: slight reduction in the size of P3 relative to P4.

The subgenus *Micronycteris* is diagnosed by seven features: bicolored dorsal fur, presence of a skin band between the ears, metacarpal formula 3 < 4 < 5, first and second phalanges of digit III of the wing subequal in length, second phalanx of digit IV shorter or equal to first phalanx, calcar equal to or longer than the foot (secondarily modified in *minuta*), and bifid lower incisors. Of these features, only presence of the skin band between the ears is unambiguously derived within phyllostomids; some of the other features may turn out to be plesiomorphic when monophyly and relationships of the genus *Micronycteris* are addressed in future studies.

The other major clade identified in the current analysis contains *nicefori* + *pusilla* + *sylvestris* + *daviesi.* This group is diagnosed by three features: calcar shorter than the foot, deep basisphenoid pits, and reduction of the upper canines. Of these, only the reduced canines are clearly derived within phyllostomids. Interpretation of calcar length and basisphenoid pit depth must await further resolution of relationships among "phyllostomine" phyllostomids.

Monophyly of *Glyphonycteris* (containing *sylvestris* + *daviesi*) is supported in the current analysis. Four features diagnose this subgenus: metacarpal formula of 4 < 3 < 5, molariform P3 with lingual cusp, P4 with a convex lingual outline and large lingual cusp, and exclusion of 12 from the occlusal toothrow. Although none of these features occurs in other members of the genus *Micronycteris,* only the molariform P3 and exclusion of 12 from the occlusal toothrow are clearly derived within phyllostomids. As with many other characters, interpretation of metacarpal formulae and P4 morphology must await further resolution of "phyllostomine" relationships.

Previous Studies and Other Data Sets

Relationships among species of *Micronycteris* have been addressed previously in studies of morphology (Andersen, 1906), karyotypes (Gardner, 1977; Patton and Baker,

1978; Arnold et al., 1983), albumin immunological distances (Honeycutt, 1981), and allozymes (Arnold et al., 1983). In the earliest published phylogeny of *Micronycteris,* Andersen (1906: 63) diagramed "probable interrelationships" of the included species based on morphological comparisons. Andersen (1906) recognized two major lineages, one leading to *Glyphonycteris* (defined by him as containing *brachyotis, behnii,* and *sylvestris*) and the other leading to *Micronycteris* (*hirsuta, megalotis,* and *minuta*). Within *Micronycteris,* Andersen (1906) indicated that *megalotis* and *minuta* are closely related to each other, with *hirsuta* a more distant relative. This hypothesis differs from the conclusions of the current study principally in the placement of *hirsuta.* Andersen (1906) commented that he separated *hirsuta* from the other *Micronycteris* species because it lacks their small incisors and because the interauricular band was significantly lower in *hirsuta* than in *megalotis* and *minuta.* The latter observation has been shown to be incorrect (Davis, 1976; personal obs.), a mistake that probably resulted from the poor preservation of specimens available to Andersen. With respect to the incisor dentition, it now seems clear that the condition in *hirsuta* is autapomorphic, while the smaller incisors seen in other *Micronycteris* species are plesiomorphic (Davis, 1976).

Chromosomal data have been discussed by several authors, but enormous variation in karyotypes among species of *Micronycteris* has hampered phylogenetic interpretation of these data. Gardner (1977) considered diploid number, fundamental number, and chromosome structure in five species of *Micronycteris* and concluded that *megalotis,*[5] *schmidtorum,* and *minuta* are chromosomally distinct from *nicefori* and *hirsuta. Micronycteris schmidtorum* (2N = 38, FN = 66), *megalotis* (2N = 40, FN = 68), and *microtis* (2N = 40, FN = 68) have similar karyotypes consistent with a possible close relationship (Gardner, 1977; Honeycutt et al., 1980). The karyotype of *hirsuta* (2N = 28–30, FN = 32) is unique in the genus (Gardner, 1977; Honeycutt et al., 1980). *Micronycteris minuta* (2N = 28, FN = 50) and *nicefori* (2N = 28, FN = 52) have karyotypes with similar diploid and fundamental numbers, but Gardner (1977) concluded that these must have evolved independently because the autosomes of *minuta* are mainly metacentrics while those of *nicefori* are predominantly submetacentrics and subtelocentrics. Since Gardner's (1977) review, *daviesi* (2N = 28, FN = 52) has been shown to have a karyotype nearly identical to that of *nicefori* (Honeycutt et al., 1980), and *sanborni* (2N = 28, FN = 50) has been shown to have a karyotype like that of *minuta* (fig. 6). *Micronycteris sylvestris* exhibits yet another unique karyotype (2N = 22, FN = 36 or 40; Honeycutt et al., 1980). *Micronycteris brachyotis* (2N = 32, FN = 60) has a karyotype somewhat similar to that of *nicefori* (Patton and Baker, 1978).

Data from G- and C-banded chromosomes provide additional insights (Patton and Baker, 1978; Baker and Bickham, 1980; Arnold et al., 1983). Two chromosomal synapomorphies—a terminal translocation (25/26-13) and a Robertsonian fusion (22/14)—are shared by *brachyotis, nicefori,* and *minuta,* an observation supporting monophyly of the genus *Micronycteris* (Patton and Baker, 1978). *Micronycteris brachyotis* and *nicefori* have karyotypes that have apparently undergone few chromosomal changes from the proposed primitive karyotype of the genus (Patton and Baker, 1978; Arnold et al., 1983). In contrast, "the karyotypes of *M. minuta* and *M. megalotis* . . . are so chromosomally unique that apparently most or all of the elements of their karyotypes cannot be parsimoniously related to the karyotypes of each other or any other phyllostomatoid" (Patton and Baker, 1978: 460). None of the derived chromosomes seen in *minuta* and *megalotis* can be matched with putative homologues in the other species (Patton and Baker, 1978; Baker and Bickham, 1980). Baker and Bickham (1980) estimated that a minimum of 14 or 15 independent rearrangements are required to account for the respective differences that distinguish these two species from the hypothesized primitive karyotype for the genus. This degree of differentiation, termed "karyotypic megaevolution" by Baker and Bickham (1980: 249), has apparently also been observed in *hirsuta* although the data have not been published (Arnold et al., 1983). Banded karyotypes are not available for other species of *Micronycteris.*

Phylogenetic interpretation of the karyotypic data currently available for *Micronycteris* is problematic because of the high degree of difference between species and the lack of G- and C-banding data for many taxa. However, some conclusions may be drawn in the context of the phylogenetic hypothesis presented in figure 7. First of all, the karyotype of *sanborni* and *minuta* (2N = 28, FN = 50) appears to represent a synapomorphy diagnosing this clade. In contrast, the karyotype shared by *megalotis* and *microtis* (2N = 40, FN = 68) may be primitive for the subgenus *Micronycteris* or may represent a synapomorphy uniting *megalotis* and *microtis* to the exclusion of other taxa. The karyotype shared by *nicefori* and *daviesi* (2N = 28, FN = 52) is most likely primitive for the clade containing *nicefori* + *Glyphonycteris*. Finally, the observation that karyotypic megaevolution appears limited to the subgenus *Micronycteris* suggests that this clade may differ from other lineages in terms of intrinsic mutation rates, meiotic constraints on chromosomal heterozygotes, and/or deme structure (Baker and Bickman, 1980).

In his Ph.D. dissertation, Honeycutt (1981) examined albumin immunological differences among seven species of *Micronycteris* in the context of a larger study of phyllostomid relationships. A very close relationship between *sylvestris* and *daviesi* was indicated in a set of reciprocal immunological comparisons aimed at establishing relationships among phyllostomid subfamilies; these results were later published by Honeycutt and Sarich (1987). Honeycutt (1981) also described unidirectional comparisons involving albumins from *megalotis, schmidtorum, minuta, hirsuta,* and *nicefori,* combined antisera from *sylvestris* and *daviesi,* antisera from *Vampyrum,* and combined antisera from a series of outgroups (*Macrotus, Desmodus, Glossophaga,* and *Carollia*). Honeycutt (1981: 70) noted in a summary of phylogenetic results that "all the *Micronycteris* species form a monophyletic group," a statement later cited by Arnold et al. (1983). However, this conclusion is not supported by data: Honeycutt's (1981: table 7) immunological comparisons suggest that *minuta* may be more closely related to *Vampyrum* than to *Micronycteris sylvestris* and *daviesi.* These data must be considered preliminary, as they are the result of unidirectional comparisons and remain unpublished. However, it seems clear that albumin immunological data do not unambiguously support monophyly of *Micronycteris* as implied by Arnold et al. (1983). The only relationship unambiguously supported by immunological data is a close relationship between *sylvestris* and *daviesi,* a conclusion also supported by morphological data in the current study.

Arnold et al. (1983) analyzed patterns of allozyme variation at 21 presumptive loci in eight species of *Micronycteris* using *Vampyrum spectrum* and *Rhinophylla pumilio* as outgroups. The cladogram that Arnold et al. (1983) constructed from their data (redrawn in fig. 8A) differs significantly from previous hypotheses and results of the current study. Most notably, Arnold et al. (1983) concluded that the subgenus *Micronycteris* is not monophyletic because a clade comprising *nicefori, sylvestris,* and *daviesi* was found to nest within the smallest clade containing *minuta* and other members of the subgenus *Micronycteris* (fig. 8A).

Unfortunately, the data and methods employed by Arnold et al. (1983) are problematic. A significant amount of intraspecific polymorphism is apparent in the data: 14 out of 21 loci were polymorphic in at least one species, and every species represented by multiple individuals was shown to be polymorphic for at least four loci (Appendix 2, table 5; Arnold et al., 1983). Despite this high degree of variability, half the species included in the study were represented by only a single individual. None of the clades identified by Arnold et al. (1983) were supported by more than two derived allozymes, so increased sampling of individuals within *Micronycteris* species might significantly alter perceived relationships. Single-specimen sampling of the outgroups is also troubling because consideration of additional individuals would likely increase the number of allozymes interpreted as primitive. Finally, lack of an exhaustive parsimony analysis leaves open the possibility that equally or more parsimonious explanations exist for the allozyme data.

To investigate the latter possibility, I reanalyzed the data of Arnold et al. (1983) using the step-matrix method described by Mabee and Humphries (1993) as modified by Mardulyn and Pasteels (1994). The data, meth-

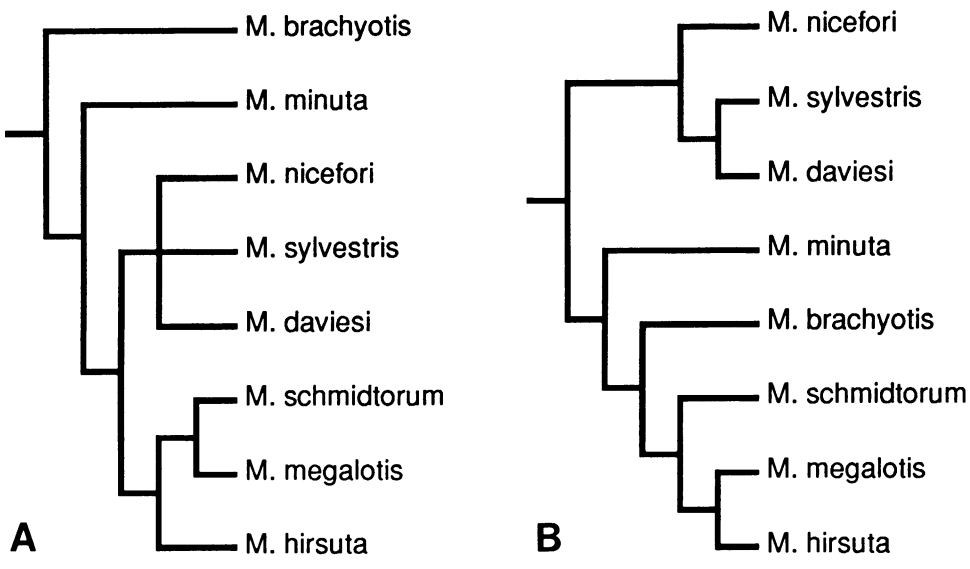

Fig. 8. Results of analyses of allozyme data; see text, Appendix 2, and tables 5 and 6 for discussion and data. **(A)** Cladogram published by Arnold et al. (1983) based on their analysis of allozyme variation at 21 presumptive isozyme loci **(B)** The single most parsimonious tree that resulted from a reanalysis of the allozyme data of Arnold et al. (1983) using the step matrix method of Mabee and Humphries (1993) as modified by Mardulyn and Pasteels (1994). Trees in both analyses were rooted using a composite outgroup consisting of *Rhinophylla pumilio* and *Vampyrum spectrum* (omitted from these figures). In the context of the recoded data set (see Appendix 2), the tree shown in B requires 179 steps, while the tree shown in A requires 184 steps.

ods, and results of this analysis are described in Appendix 2. A branch-and-bound analysis of the recoded allozyme data resulted in discovery of a single most parsimonious tree (179 steps; fig. 8B) that differs significantly from the cladogram published by Arnold et al. (1983). The revised allozyme tree (fig. 8B) is congruent with that derived from morphological data (fig. 7) with respect to the relationships of *nicefori, sylvestris,* and *daviesi.* These three taxa form a clade relative to other *Micronycteris* species in both trees, and monophyly of *Glyphonycteris* (*sylvestris* + *daviesi*) is also supported. In contrast, the revised allozyme tree differs significantly in terms of placement of *brachyotis* (which nests inside the subgenus *Micronycteris*) and relative relationships of *minuta, schmidtorum, megalotis,* and *hirsuta.* However, an allozyme tree congruent with the results of the morphological analysis is only one step (0.6%) longer than the most parsimonious allozyme tree (Appendix 2). This difference is trivial, so the allozyme data cannot be considered incongruent with the morphology-based hypothesis of *Micronycteris* interrelationships (fig. 7).

Results of "Total Evidence" Analysis

As a final step in the current study, I conducted a "total evidence" analysis of a combined data set[8] that included the morphological characters previously described (table 4), the recoded allozyme data (Appendix 2, table 5), and a single multistate character describing the karyotype of each species (2N and FN, see discussion above). A branch-and-bound analysis of this data set identified three equally parsimonious trees (228 steps, CI = 0.729; RI = 0.817); a strict consensus of these is shown in figure 9A. Results of this analysis support all of the relationships postulated on the basis of morphology alone (fig. 7), but provide improved resolution at two key

[8] The complete data set used in this analysis—including character coding and weighting schemes—is available in MacClade format from the author upon request.

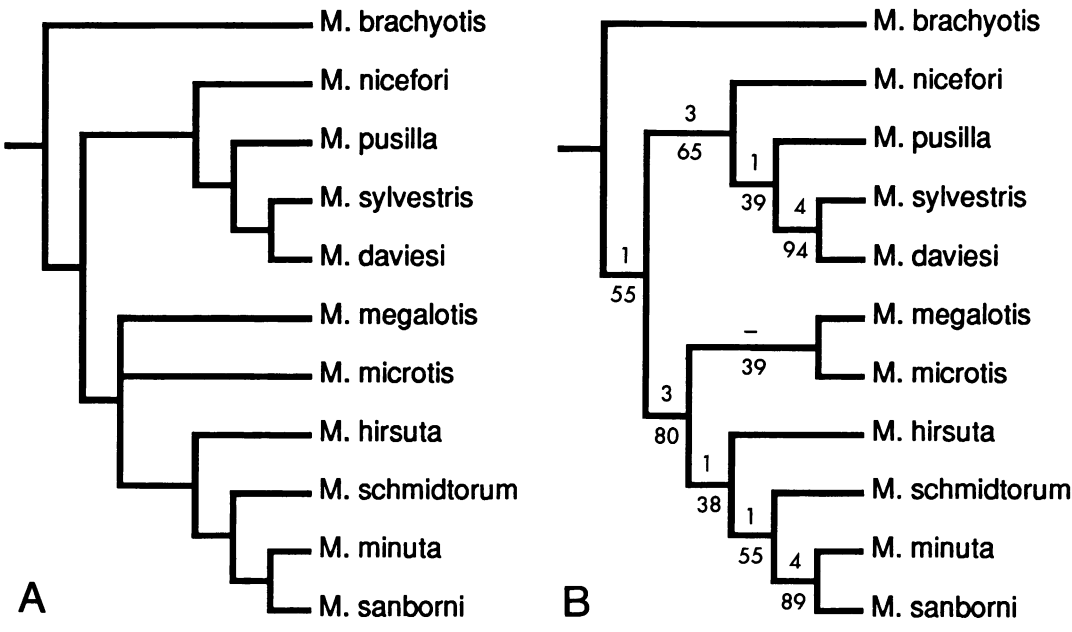

Fig. 9. Results of "total evidence" analysis of a combined data set including morphological characters (table 4), recoded allozyme data (Appendix 2, table 5), and a single unordered multistate character describing the karyotype of each species (2N and FN); see text for discussion. **(A)** A strict consensus of 3 equally parsimonious trees, each of which required 228 steps (CI = 0.729; RI = 0.817). **(B)** Results of a decay analysis and a branch-and-bound bootstrap analysis with 1000 replicates. The tree depicted is a bootstrap majority-rule consensus tree. Numbers given below internal branches indicate the percentage of bootstrap replicates in which each clade appeared; The numbers given above branches indicate the minimum number of additional steps (beyond that required by the shortest trees) required to collapse each clade (this measure applies only to clades identified in the strict consensus tree shown in **A**).

points: *brachyotis* appears as the sister group of a large clade including all of the other species of *Micronycteris,* and *pusilla* is unambiguously placed as the sister group of the subgenus *Glyphonycteris.* The allozyme and karyotypic data also provide additional support for clades previously recognized in the morphological analyses. The subgenus *Micronycteris* is diagnosed by one unique allozyme (Got-1[d]), while two unique allozymes apparently diagnose *Glyphonycteris* (Alb[b], Got-1[b]), the clade comprising *nicefori* + *pusilla* + *Glyphonycteris* (Ldh-2[c], Idh2[d]), and the clade comprising *hirsuta* + *schmidtorum* + *minuta* + *sanborni* (Ldh-2[e], Pgm2[b]; see Appendix 2 and table 5 for explanation of abbreviations). Derived karyotypes diagnose *minuta* + *sanborni* (2N = 28, FN = 50) and the clade comprising *nicefori* + *pusilla* + *Glyphonycteris* (2N = 28, FN = 52). Despite inclusion of the karyotype data, *megalotis* and *microtis* retained their relatively unresolved position at the base of the subgenus *Micronycteris* in the strict consensus tree (fig. 9A).

Decay analysis and a branch-and-bound bootstrap analysis with 1000 replicates were used to evaluate relative support for various groupings in the total evidence tree; results of these analyses are shown in figure 9B. Strong levels of support were found for monophyly of the subgenus *Glyphonycteris* (bootstrap value = 94%, minimum four additional steps to collapse clade), the subgenus *Micronycteris* (bootstrap value = 80%, minimum three additional steps to collapse clade), and the clade comprising *minuta* + *sanborni* (bootstrap value = 89%, minimum four additional steps to collapse clade). Moderate support was found for the clade comprising *nicefori* + *pusilla* + *Glyphonycteris* (bootstrap value = 65%, minimum three addi-

tional steps to collapse clade). Weak support was found for the clade comprising *schmidtorum* + *minuta* + *sanborni* (bootstrap value = 55%, minimum one additional step to collapse clade) and for a larger clade containing all species of *Micronycteris* to the exclusion of *brachyotis* (bootstrap value = 55%, minimum one additional step to collapse clade). Support was very weak for the clade comprising *pusilla* + *Glyphonycteris* (bootstrap value = 39%, minimum one additional step to collapse clade) and the clade comprising *hirsuta* + *schmidtorum* + *minuta* + *sanborni* (bootstrap value = 38%, minimum one additional step to collapse clade). The bootstrap analysis also found very weak support for a clade comprising *megalotis* + *microtis* (bootstrap value = 39%). This clade was not resolved in the strict consensus tree (fig. 9A), but appeared in two of the three most parsimonious trees from which the consensus tree was constructed.

Results of these analyses indicate relatively high levels of uncertainty concerning relationships in several parts of the total-evidence tree. Examination of character transformations suggests that this uncertainty results largely from missing data. Only 25 out of 41 characters were scored in the "hypothetical ancestor" taxon due to uncertainty concerning outgroup relationships (see footnote 3 on page 5). Missing data were also a problem for ingroup taxa: no allozyme data were available for *microtis* and *sanborni,* and both allozyme and karyotype data were lacking for *pusilla.* Future studies may provide better resolution and greater support for recognized clades if more complete character data (perhaps from new sources such as nucleotide sequences or satellite DNA) and multiple outgroup taxa (e.g., "phyllostomine" species) are included in phylogenetic analyses. Identification of sister taxa of the genus *Micronycteris* will be critical for further resolution of relationships within the group.

CONCLUSIONS

The genus *Micronycteris* contains a diverse array of small-and medium-sized phyllostomids which chromosomal data suggest form a monophyletic group (Patton and Baker, 1978). The nominate subgenus comprises six species: *megalotis, microtis, hirsuta, schmidtorum, minuta,* and a new species, *Micronycteris sanborni.* Monophyly of the subgenus *Micronycteris* (as thus defined) is supported by both morphological and allozyme data.

Micronycteris sanborni is known only from Ceará and Pernambuco in northeastern Brazil, where it apparently inhabits a variety of cerrado and caatinga habitats. It is a small bat that resembles *minuta* in many respects, but these species can be distinguished easily on the basis of both external and craniodental features. Autapomorphies of *sanborni* include presence of white hairs on the inside of the pinnae, a patch of white fur on the ventral surface of the uropatagium at the base of the tail, a calcar that is approximately the same length as the hind foot, presence of a gap between outer upper incisor and upper canine, and first and second molars that are approximately subequal in occlusal dimensions. Measurements of length of the thumb and maxillary toothrow are also smaller than in any other species in the subgenus.

Micronycteris sanborni, schmidtorum, and *megalotis* all occur in the region around the Chapada do Araripe in northeastern Brazil, but little is known about details of distribution and habitat preference. Strict sympatry (i.e., occurrence at the same collecting locality) has been documented for *sanborni* and *megalotis* in caatinga habitats south of Exu in Pernambuco. Differences in moisture and vegetation type and structure may be significant in structuring bat communities in northeastern Brazil, but there is not enough data on *Micronycteris* in this region to test hypotheses concerning distribution patterns or habitat preferences.

A phylogenetic analysis of interrelationships among species of *Micronycteris* indicates that *sanborni* and *minuta* are sister taxa, and that *schmidtorum* is probably the sister group of this clade. A sister-group relationship between *hirsuta* and the *schmidtorum* + *minuta* + *sanborni* clade was indicated in strict consensus trees based on both morphology and total evidence, but support for this grouping is weak. Relative relationships of *megalotis* and *microtis* could not be resolved, but a bootstrap analysis of the total evidence data set indicated some support for a sister-group relationship between these taxa.

Among other species of *Micronycteris,* monophyly of the subgenus *Glyphonycteris* (*sylvestris* + *daviesi*) is strongly supported by multiple data sets. A sister-group relationship between *pusilla* and *Glyphonycteris* was indicated in the total evidence analysis, but character support for this grouping is weak. Morphological, allozyme, and total evidence data sets all support an association between *nicefori* and the *pusilla* + *Glyphonycteris* clade. Finally, analysis of the total evidence data set indicated that *brachyotis* may be the sister taxon of a clade containing the other ten species of *Micronycteris.*

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APPENDIX 1

Specimens Examined

The following list summarizes the taxa and specimens examined in the current study. Specimens measured for table 2 are indicated with an asterix.

Micronycteris brachyotis: **Mexico:** Oaxaca, Mazahuito, 18 mi S Matías Romero (AMNH 185856); **Belize:** Cayo District, cave 1 km NW Augustine (FMNH 58144, 58145); **Guatemala:** Petén, Chuntuquí (USNM 245153); Petén, Tikal National Park (USNM 58565); **Nicaragua:** Chinandega, Volcán de Chinandega (AMNH 28336); **Costa Rica:** Guanacaste, Palo Verde Wildlife Refuge - OTS (USNM 566435); Guanacaste, Refugio Rafael Rodriguez, Hacienda Palo Verde (USNM 562750, 563261, 563262, 563263, 563264, 563265, 563266); **Panama:** Colón, Barro Colorado Island (USNM 498708, 544879, 544880); Los Santos, Los Palmitas, near Jobero (USNM 323059, 323060); Panamá, Cerro Azul (USNM 306546); Veraguas, Isla Cébaco (USNM 360146); **Colombia:** Bolívar, Cartagena (USNM 431754); **Venezuela:** Carabobo, 19 km NW of Urama, KM 40 (USNM 371406); Bolívar, 28 km SE El Manteco (USNM 385286); **Trinidad and Tobago:** St. George Parish, Port of Spain, La Fontaine Cave (FMNH 83416); St. George Parish, San Raphael Ward, Guanapeu (FMNH 61941, 61942, 61943); St. Patrick Parish, Siparia Ward, Penal Rock Road, Motor Ranch Trace (AMNH 175626, 175627, 175628, 175629, 175630, 175631, 175632, 175633, 175634); **Brazil:** Pará, Belém, "Sta. A, IAN" (USNM 361501); Pará, Rio Tapajós, Igarapé Bravo (AMNH 94601); Pará, Utinga, Canal da Mariana (USNM 447723, 447724, 447725).

Micronycteris daviesi: **Panama:** Bocas del Toro, Sibube (USNM 335104); San Blas, Armila, Quebrada Venado (USNM 335105); **Ecuador:** Pichincha, Río Palenque Science Center, 47 km S (by road) Santo Domingo (USNM 528475); **Peru:** Pasco, Oxapampa, San Juán (USNM 364265, 364266, 364267); **Guyana:** Forest Reserve, 24 mi S of Bartica on Potaro Road (BMNH 64.767 [holotype]); **French Guiana:** Paracou, near Sinnamary (AMNH 267855, 267856); **Brazil:** Pará, Belém (USNM 460089); **Bolivia:** La Paz, Iturralde, 25 km W Ixiamas en Camino a Alto Madidi (CBF 2908).

Micronycteris hirsuta: **Costa Rica:** Puntarenas, Palmar (AMNH *139441, *139442); **Colombia:** Cauca, Río Saijá (FMNH *90328, *90329); Antioquia, La Frijolera (AMNH *36783); Magdalena, 2 km W Río Don Diego (AMNH 255705);

Magdalena, Bonda (AMNH *14573); **Peru:** Pasco, Oxapampa, San Juán (AMNH *230114, *230115, *230116); Madre de Dios, Left bank of Río Palotoa, 12 km from mouth (FMNH *138857); **Trinidad and Tobago:** "Brickfield" (FMNH *62034); Caroni Parish, Cunupia Ward, Regis Road near Village of Cunupia (AMNH 175615); Fort Reid, Waller Field (AMNH 175609); St. George Parish, Port of Spain, 21 Queens Park (AMNH 76287); St. George Parish, St. Ann's Ward, Old Santa Cruz Road (FMNH *54979); St. Patrick Parish, Cedros Ward, Granville (AMNH 175606, 176623); St. Patrick Parish, Charuma Ward, St. John (AMNH *179958); St. Patrick Parish, La Brea Ward, La Brea, Granys Trace (AMNH *179957, *182698); St. Patrick Parish, Siparia Ward, Fyzabad, Leaseholds (AMNH *179955, *180032, *180033); **French Guiana:** Paracou, near Sinnamary (AMNH *267093, *267094, *267096, *267857, *267858, *267860; MNHN *1995.800, *1995.801, *1995.802); **Brazil:** Pará, Rio Tapajós, Aramanaí (AMNH *94534, *94560).

Micronycteris megalotis: **Colombia:** Cundinamarca, Mesitas del Colegio (AMNH *207775, *207776, *207778); **Peru:** Huánuco, Puerto Márquez, near Montealegre (AMNH *67234, *67235); Junín, Tarma, 2 km NW of San Ramón (AMNH *230117); Loreto, Río Amazonas, Puerto Indiana (AMNH *73497, *73500); Loreto, Río Yavarí, Quebrada Esperanza (FMNH *89097, *89098, *89099); Napo, San José Abajo (AMNH *68009, *68010, *68011, *68012, *68013); **Trinidad and Tobago:** St. George Parish, Maracas (TTU *23759); **Surinam:** Brokopondo, 1.5 km W Rudi Kappelvliegveld (CM *63575); **French Guiana:** Paracou, near Sinnamary (AMNH *266020, *267090, *267091, *267092, *267862, *267864; MNHN *1995.803); **Brazil** [no additional information] (BMNH *not registered [holotype]; BMNH 42.8.17.8 [holotype of *Phyllostoma elongata* Gray, 1842]); Pernambuco, Fazenda Pomonha, 21 km SSW Exu (CM *98912); Pernambuco, Serrote Gamba, 19 km SSW Exu (CM *98911); Pará, Rio Tocantins, Ilha do Taiuna (AMNH *97206, *97219).

Micronycteris microtis mexicana: **Mexico:** Jalisco, Plantinar (USNM *52105 [holotype]); Oaxaca, 0.5 mi W of Chiltepec (AMNH *189597; *189598; *189599); Oaxaca, 17 mi N of Matías Romero (AMNH *185857, *185858, *185859, *185860, *185861); Oaxaca, Ixcuintepec (AMNH *167464); Oaxaca, Juquila, Puerto Escondido to S. Pedro Mixtepec (AMNH *205268); Oaxaca, Tehuantepec, Cerro San Pedro (AMNH *143978, *167031, *167033); Oaxaca, Tehuantepec, Limón (AMNH *213760); Oaxaca, Tehuantepec, Oscuranos (AMNH *167044); Oaxaca, Tehuantepec, San Antonio (AMNH *171595); San Luis Potosí, El Salto (AMNH *177732, *177733, *177734, *177735, *177736, *177737); San Luis Potosí, Rancho Nuevo, 27 km W Cuidad Valles (AMNH *254608, *254609); Tamaulipas, Pana Ayuctle, 5 mi NW of Gomez Farias (AMNH *147948); Veracruz, 24 mi S of Veracruz (AMNH *203567); Veracruz, Tezonapa (AMNH *243855, *243856, *243857, *243858, *243859); Yucatán, Izamal (AMNH 12756/11043 [holotype of *Macrotus pygmaeus*]); **Belize:** Toledo District, 0.6 km NW of Quebrada-de-Oro at Bladen Branch River (AMNH *256820); Toledo District, Jacinto Village, Cueva Creek (AMNH *256845); **Honduras:** La Paz, Humuya (AMNH *126764); Tegucigalpa, La Flor, Archaga (AMNH *126213, *126214, *126215, *126216, *126218, *126219, *127582, *127583, *127584); Tegucigalpa, Sabana Grande, San Marcos (AMNH *126765).

Micronycteris microtis microtis: **Nicaragua:** "Río Coco" (= Río Segovia; AMNH *29419, *29420, *29421, *29422, *29423, *29424, *29499); Río San Juán, Greytown (= San Juán del Norte; USNM *16366/23364 [holotype]); **Costa Rica:** Talamanca, Río Sicaola (AMNH *25966, *25967, *25968, *25970, *25971); **Panama:** Darién, Cituro (AMNH *38146, *38147, *38149); Panamá, Farfan Beach (AMNH *99344); **Colombia:** Cundinamarca, Mesitas del Colegio (AMNH *207778); **French Guiana:** Paracou, near Sinnamary (AMNH *266024, *266025, *266027, *266029, *266030, *266038, *267097, *267866, *267867, *267868, *267869, *267870, *267872, *267873; MNHN *1995.805, *1995.806, *1995.807, 1995.809, 1995.810, 1995.811, 1995.812); **Brazil:** Amazonas, Yucali (= Iucali), Rio Negro (AMNH *79423); Amazonas, Rio Waupes (= Rio Uaupes), Tahulpunta (= Taúa; AMNH *78648, *78649); Pará, Rio Tocantins, Ilha do Taiuna (AMNH *94554, *97218)

Micronycteris minuta: **Colombia:** Magdalena, Bonda (AMNH *15131 [holotype of *M. hypoleuca*]); Putumayo, Río Mecaya (FMNH *72158, *72160, *72161, *72162, *72285); **Ecuador:** Napo, San Jose de Payamino (FMNH *124666, *124667, *124668); "Oriente," San José (AMNH *64004, *64005, *64006, *64007, *64008); **Peru:** Cuzco, Río Mapitunari, 12°39'S, 73°42'W (AMNH *283221); Loreto, Boca Curaray (AMNH *71614, *71615, *71616, *71617, *71618, *71621, *71628, *71629, *71630, *71631); Madre de Dios, Hacienda Amazonia (FMNH *138856); Madre de Dios, Manu, Pakitza (MUSM *6797, *6798, *6799, *6800, *6801, *6802); Pasco, Oxapampa, San Pablo (AMNH *230119, *230120); **Trinidad and Tobago:** Caroni Parish, Montserrat Ward, Freeport, Arena Road (AMNH *175597); Mayaro Parish, Piexrville (AMNH *183295); St. Andrew Parish, Valencia Ward, Cumaca (AMNH *175592, *175593); St. Patrick Parish, La Brea Ward, Point

Fortin, Lot 10, Parrylands (AMNH *183168, *183169); St. Patrick Parish, Siparia Ward, Rochard-Douglas Road (AMNH *175595); **French Guiana:** Paracou, near Sinnamary (AMNH *267098, 267412, 267413, 267415, *267874, *267875; MNHN 1995.813, 1995.814); **Brazil:** Amazonas, Rio Madeira, Rosarinho (AMMH *92408, *92409, *92410, *92411, *92689, *92690, *92691, *92692, *92693, *92694, *92695, *92696, *92697, *92698, *92846); Mato Grosso do Sul, Rio Paraguai, Fazenda Acurizal (AMNH *237910, *244471); Pará, Lago Jauari, livramento Rio Amazonas (FMNH *42431, *42432); Pará, Belém, Mocambo (FMNH *126207, *126208); Pará, Belém, Utinga (FMNH *126206).

Micronycteris nicefori: **Belize:** Toledo District, 1.8 km NNW Quebrada de Oro at Bladen Branch River (AMNH 256822); Toledo District, Aguacate, hill 0.4 km NE of village (FMNH 108761); **Panama:** Colón, Fort Gulick (AMNH 184557, 184558, 184559); **Colombia:** Cundinamarca, Sasaima (FMNH 72278); Norte de Santander; Cúcuta (FMNH 64266 [holotype]); Norte de Santander, Puente Osprina, Río Zulia, 10 km W of Cúcuta (AMNH 149200); **Trinidad and Tobago:** [no additional information] (AMNH 256307); St. Patrick Parish, Erin Ward, Buenos Ayres (AMNH 179984, 179985, 179986); St. Patrick Parish, Siparia Ward, Alta Garcia Trace (AMNH 175643, 175644, 175645); St. Patrick Parish, Siparia Ward, Fyzabad (AMNH 179962); Scotland Bay (FMNH 83130); **Guyana:** Mazaruni-Potaro District, Forest Reserve, 24 mi S of Bartica on Potaro Road (BMNH 65.611); **French Guiana:** Paracou, near Sinnamary (AMNH 266017, 266019, 267410, 267876, 267877, 267878; MNHN 1995.815, 1995.816, 1995.817); **Brazil:** Pará, Belém, Mocambo/Embrapa (FMNH 126210); **Brazil:** Rondonia (USNM 554574).

Micronycteris pusilla: **Brazil:** Amazonas, Rio Waupes (= Rio Uaupes), Tahulpunta (= Tauá; (AMNH 78830 [holotype], 78831).

Micronycteris sanborni: **Brazil:** Ceará, Sitio Luanda, Itaitera, 4 km S of Crato (USNM *555702 [holotype]); Ceará, 4 km SE Novo Olinda, KM 19 on Route CE96 (CM 98913* [paratype]); Pernambuco, Serrote das Lajes, 17 km S of Exu (CM 98917* [paratype]); Pernambuco, 21 km SSW Exu, Fazenda Pomonha (CM 98914*, 98915*, 98916* [paratypes]).

Micronycteris schmidtorum: **Belize:** Corozal District, Patchakan Village (FMNH *108762, *108763); Orange Walk District, Albion, 1.3 km W San Antonio, Río Hondo (FMNH *106766); Toledo District, 1.8 km NNW Quebrada de Oro at Bladen Branch River (AMNH *256821); **Guatemala:** Izabal, Bobas (FMNH *41559 [holotype], *41960); Santa Rosa, 2 km N Chiquimulilla (AMNH *243753); **Hondurus:** Copan (FMNH *47583); **Colombia:** Vichada, Maipures, Río Orinoco (BMNH 99.9.11.24); **Peru:** Madre de Dios, Manu, Pakitza (MUSM *6803); **Venezuela:** Lara, Tocuyo, Río Tocuyo (AMNH *130715, *130716, *130717, *130718, *130719, *130720, *130725); **French Guiana:** Paracou, near Sinnamary (AMNH *267853; MNHN *1995.818); **Brazil:** Pará, Belém, Mocambo/Embrapa (FMNH *126204; *126205); Pernambuco, Estação Ecológica do Tapacura, São Lourenço da Mata (USNM *555703); Pernambuco, Fazenda Alto do Ferreira, 5 km SW Exu (CM *98908, *98909); Pernambuco, Fazenda Cantarena, 4.5 km NNE Exu (CM *98910).

Micronycteris sylvestris: **Costa Rica:** Guanacaste, Hacienda Miravalles (BMNH 96.10.1.2 [holotype]); **Panama:** Colón, Ft. Sherman (USNM 396399); Darién, Jaqué (USNM 362394); San Blas, Armila, Quebrada Venado (USNM 335101); **Colombia:** Bolívar, Socorré, upper Rio Sinú (FMNH 69408, 69409, 69410); **Peru:** Puno, Río Cosñipata (BMNH 69.5.13.3, 69.5.13.4); Cuzco, Cordillera Vilcambamba, W side (AMNH 214316); **Venezuela:** Territorio Federal de Amazonas, Río Manapiare, San Juan, 163 km ESE Pto. Ayacucho (USNM 407260); Territorio Federal de Amazonas, 108 km SSE Esmeralda, Río Mavaca (USNM 388734); Monagas, Cueva del Guácharo, 3 km N of Caripe (USNM 534240); **Trinidad and Tobago:** St. Patrick Parish, La Brea Ward, Point Fortin, Salazar Trace (AMNH 183297, 183846, 183299, 207061); **French Guiana:** Paracou, near Sinnamary (AMNH 267879); **Brazil:** São Paulo, Iporanga, Região do Alambari (AMNH 245656).

APPENDIX 2

Reanalysis of Allozyme Data from Arnold et al. (1983)

As described in the text, Arnold et al. (1983) surveyed allozyme variation at 21 presumptive loci in eight species of *Micronycteris* and two outgroups; their data are given in table 5. To construct a phylogeny based on these data, Arnold et al. (1983) first compared the allozymes of each species of *Micronycteris* with those of the outgroups, *Rhinophylla pumilio* and *Vampyrum spectrum.* Any allozyme shared by one or both of the outgroups and one or more species of *Micronycteris* was interpreted as plesiomorphic. A cladogram was then constructed manually based on patterns

TABLE 5
Allozyme Data from Arnold et al. (1983)

Species (sample size)	Isozyme[a]																			
	Mdh-1	Mdh-2	Ldh-1	Ldh-2	Idh-1	Idh-2	Pep-1	Pep-2	Alb	Mpi	Pgm-1	Pgm-2	Pgi-1	Pgi-2	6-Pdg	Got-1	Got-2	a-Gpd	Lap	Est	Adh
R. pumilio (1)	a	b	f	b	c	c	a	h	a	h	f	d	i	d	j	c	a	f	a	g	b
V. spectrum (1)	a	b	c	b	d	c	d	i	g	i	e	d	h	h	c	c	d	b	b	a	b
M. brachyotis (1)	b	a	f	a	c	a	g	f	e	c	c	a	c	c	i	c	a	f	a	f	g
M. nicefori (6)	a	b	b,d	c	c	d	b,c	f	c,e	i,k	d,g	c	i	d	k	a	c	a,c,f	a	b	c
M. sylvestris (2)	a	b	a	c	b	d	e	c	b	d,e,g	d	c	a	d	a,b	b	a,b	f	a	c,e	a
M. daveisi (1)	a	b	d	c	b	d	c	e	b	f	a	c	f	g	g	b	c	f	a	d	d
M. megalotis (3)	a	b	e	d	b	c	i	e	d	a,b,c	d	c	e,g	f	d,e,h	d	c	e	a	j,k,l	e
M. hirsuta (3)	a	b	f	e	b	b,c	f	a,b	d	j,k	d	b	b	e	f	d	c	f	a	i	h,i
M. schmidtorum (1)	a	b	f	e	b	c	i	d	e	g	e	b	e	b	i	d	c	f	a	m	i
M. minuta (5)	a	b,c	f	e	a	c	h,i	g	e,f	i,l,m	b,h	b	d	a,e	c,i	e,f	c	d,g	a	h	f

[a] Isozymes surveyed are abbreviated as follows: maltate dehydrogenase-1, 2 (Mdh-1, 2); lactate dehydrogenase-1, 2 (Ldh-1, 2); isocitrate dehydrogenase-1, 2 (Idh-1, 2); peptidase-1 (Pep-1, substrate = leucyl glycyl glycine); peptidase-2 (Pep-2, substrate = glycyl-L-leucine); albumin (Alb); mannose-6-phosphate isomerase (Mpi); phosphoglucomutase-1, 2 (Pgm-1, 2); phosphoglucose isomerase-1, 2 (Pgi-1, 2); 6-phosphogluconate dehydrogenase (6-Pgd); glutamate oxalate transaminase-1, 2 (Got-1, 2); a-glycerophosphate dehydrogenase (a-Gpd), leucine aminopeptidase (Lap), esterase (Est), alcohol dehydrogenase (Adh). Letters (a, b, etc.) represent decreasing migration toward the anode.

TABLE 6
Step Matrix for Isozyme Alb[a]

	a	b	c,e	d	e	e,f	g	c,e,f	c	f
a	0	2	3	2	2	3	2	4	2	2
b	2	0	3	2	2	3	2	4	2	2
c,e	3	3	0	3	1	2	3	1	1	2
d	2	2	3	0	2	3	2	4	2	2
e	2	2	1	2	0	1	2	2	2	2
e,f	3	3	2	3	1	0	3	1	3	1
g	2	2	3	2	2	3	0	4	2	2
*c,e,f	4	4	1	4	2	1	4	0	2	2
*c	2	2	1	2	2	3	2	2	0	2
*f	2	2	2	2	2	1	2	2	2	0

[a] Data from Arnold et al. (1983); see table 5 and text for discussion. States marked with an asterisk indicate combinations of alleles that were not observed in any species, but that might have been present in ancestors of two or more taxa. These hypothetical ancestral states were constructed following the methods of Mardulyn and Pasteels (1994).

of distribution of relatively derived allozymes (fig. 8A; Arnold et al., 1983). Monophyly of *Micronycteris* was assumed and a rigorous parsimony analysis was not conducted.

In order to evaluate the results of Arnold et al. (1983) prior to comparison with my morphological analysis, I reanalyzed their allozyme data (table 5) using the step matrix method of Mabee and Humphries (1993) as modified by Mardulyn and Pasteels (1994). These methods have the advantage of taking all homology information into account in searching for most parsimonious trees (Mardulyn and Pasteels, 1994). The technique involves assigning a separate character state to every unique combination of allozymes found at a given locus, reconstructing additional combinations that might have been present at ancestral nodes, and then constructing a step matrix to assign a cost (in terms of number of evolutionary steps) required for every possible transformation between states (Maybee and Humphries, 1993; Mardulyn and Pasteels, 1994). Each gain or loss of an allozyme is interpreted as requiring one evolutionary step. For example, transformation from **a** to **b** requires two steps (loss of **a** and gain of **b**), while transformation from **a** to **a,b** requires only one step (gain of **b**). A sample step matrix for the Alb isozyme is given in table 6; the complete coded allozyme data set and step matrices are available upon request. In the course of coding the data I noted that three isozymes (Mdh-1, Lap, and Est) are not phylogenetically informative with respect to species interrelationships; accordingly, these were omitted from the data set.

The recoded allozyme data set was analyzed using the branch-and-bound option of PAUP (Swofford, 1993). Monophyly of *Micronycteris* was assumed, and trees were rooted using a hypothetical ancestor scored with the conditions seen in the outgroups (*Rhinophylla* and *Vampyrum*). Analysis of the recoded allozyme data resulted in a single most parsimonious tree (179 steps; fig. 8B) that differs significantly from the cladogram published by Arnold et al. (1993). Comparisons indicate that the tree of Arnold et al. (1983) is five steps (3%) longer than the most parsimonious tree given the data coding methods used.

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