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MOLECULAR PHYLOGENETICS OF THE PHYLLOSTOMID BAT GENUS *MICRONYCTERIS* WITH DESCRIPTIONS OF TWO NEW SUBGENERA

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We analyzed DNA sequence variation in the cytochrome-*b* gene and intron 7 of the nuclear fibrinogen, B beta polypeptide gene for 45 specimens of the bat genus *Micronycteris*, including all currently recognized species except *M. sanborni*. Phylogenetic analyses of both data sets supported 4 primary lineages within *Micronycteris*, which we recognize as subgenera: *Leuconycteris* new subgenus (*M. brosseti*), *Micronycteris* Gray (*M. megalotis*, *M. microtis*, *M. matses*, and *M. giovanniae*), *Schizonycteris* new subgenus (*M. minuta*, *M. schimdtorum*, and *M. sanborni*), and *Xenoctenes* Miller (*M. hirsuta*). Although we provisionally recognize the current alpha taxonomy within *Micronycteris*, our results did not support monophyly of *M. microtis* as the name is currently applied. Our results further indicate that cryptic species probably exist within the taxa currently recognized as *M. megalotis* and *M. minuta* and possibly *M. hirsuta*. Additional studies, including thorough geographic sampling and detailed morphological and molecular data sets, are necessary to test our genealogic hypotheses and assess the biodiversity within *Micronycteris*.

Key words: cytochrome *b*, fibrinogen, *Leuconycteris*, *Micronycteris*, *Schizonycteris*, systematics

Little big-eared bats of the genus *Micronycteris* constitute a diverse group of New World leaf-nosed bats (Phyllostomidae). With specializations for gleaning insects (Alonso-Mejía and Medellín 1991; Humphrey et al. 1983; Medellín et al. 1985; Wilson 1971), a primitive condition for phyllostomids, it is a long-held view that *Micronycteris* diversified early in the family's history (Baker et al. 1989; Smith 1976). Approximately 16 species were classified traditionally in 6 or 7 subgenera (*Barticonycteris*, *Glyphonycteris*, *Lampronycteris*, *Micronycteris*, *Neonycteris*, *Trinycteris*, and *Xenoctenes*; Table 1—Koopman 1993; Sanborn 1949; Simmons 1996). However, a series of new morphologic and molecular studies have narrowed the definition of the genus by recognizing generic status for all but 2 of the subgenera (Baker et al. 2000, 2003; Simmons and Voss 1998; Simmons et al. 2002; Wetterer et al. 2000); the 2 exceptions, *Barticonycteris* and *Xenoctenes*, are no longer recognized by most workers and are regarded as junior synonyms of *Glyphonycteris* (Genoways and Williams 1986) and *Micronycteris* (Davis 1976), respectively. The justification for these generic revisions is evident in both molecular and morphological data (Baker et al. 2000, 2003; Simmons and Voss 1998; Simmons et al. 2002; Wetterer et al. 2000).

Based on congruence between mitochondrial and nuclear DNA sequence variation among 43 of the 53 phyllostomid genera, including a representative subset of *Micronycteris* (sensu lato) species, Baker et al. (2003) proposed that *Lampronycteris* and *Micronycteris* (subfamily Micronycterinae) represent a basal group in Phyllostomidae that diverged after the Macrotinae and before the vampires (Desmodontinae), and that *Glyphonycteris* and *Trinycteris* (subfamily Glyphonycterinae) have affinities with Carolliinae. This proposed phylogeny differs markedly from previous hypotheses of little big-eared bats, implying that the primitive life history characteristics of *Micronycteris* (sensu lato) are not proof of monophyly, but have been maintained independently in at least 2 lineages within Phyllostomidae. The status of *Neonycteris*, samples of which were unavailable for the study by Baker et al. (2003), remains defined based solely on morphologic criteria

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TABLE 1.—Taxonomy of genus *Micronycteris* in this study compared with previous publications. Parenthetical taxa are subgenera.

Andersen 1906	Sanborn 1949	Wetterer et al. 2000; Simmons et al. 2002	This study
Micronycteris Gray, 1866	*Micronycteris* Gray, 1866	*Micronycteris* Gray, 1866	*Micronycteris* Gray, 1866
M. megalotis (Gray, 1842)[a]	(*Micronycteris*) Gray, 1866	"dark bellied"	(*Micronycteris*) Gray, 1866
M. m. megalotis (Gray, 1842)	*M.* (*M.*) *megalotis* (Gray, 1842)	*M. megalotis* (Gray, 1842)[a,b]	*M.* (*M.*) *megalotis* (Gray, 1842)[a]
M. m. mexicana Miller, 1898	*M.* (*M.*) *m. megalotis* (Gray, 1842)	*M. microtis* (Gray, 1866)	*M.* (*M.*) *microtis* Miller, 1898
M. microtis Miller, 1898	*M.* (*M.*) *m. mexicana* Miller, 1898	*M. hirsuta* (Peters, 1869)	*M.* (*M.*) *matses* Simmons, Voss, and Fleck, 2002
M. minuta (Gervais, 1896)[c]	*M.* (*M.*) *m. microtis* Miller, 1898	*M. matses* Simmons, Voss, and Fleck, 2002	*M.* (*M.*) *giovanniae* Baker and Fonseca, 2007
M. hirsuta (Peters, 1869)	*M.* (*M.*) *minuta* (Gervais, 1896)[c]	"pale-bellied"	(*Leuconycteris*) new subgenus
Glyphonycteris Thomas, 1896	*M.* (*M.*) *schmidtorum* Sanborn, 1935	*M. minuta* (Gervais, 1856)[c]	*M.* (*L.*) *brosseti* Simmons and Voss, 1998
G. behnii (Peters, 1865)	(*Xenoctenes*) Miller, 1907	*M. schmidtorum* Sanborn, 1935	(*Schizonycteris*) new subgenus
G. sylvestris Thomas, 1896	*M.* (*X.*) *hirsuta* (Peters, 1869)	*M. homezi* Pirlot, 1967	*M.* (*S.*) *minuta* (Gervais, 1856)[c,d]
G. brachyotis (Dobson, 1878)	(*Lampronycteris*) Sanborn, 1949	*M. brosseti* Simmons and Voss, 1998	*M.* (*S.*) *schmidtorum* Sanborn, 1935
	M. (*L.*) *platyceps* Sanborn, 1949	*M. sanborni* Simmons, 1996	*M.* (*S.*) *sanborni* Simmons, 1996
	(*Neonycteris*) Sanborn, 1949	*Lampronycteris* Sanborn, 1949	(*Xenoctenes*) Miller, 1907
	M. (*N.*) *pusilla* Sanborn, 1949	*L. brachyotis* (Dobson, 1878)[e]	*M.* (*X.*) *hirsuta* (Peters, 1869)
	(*Trinycteris*) Sanborn, 1949	*Neonycteris* Sanborn, 1949	*Lampronycteris* Sanborn, 1949
	M. (*T.*) *nicefori* Sanborn, 1949	*N. pusilla* (Sanborn, 1949)	*L. brachyotis* (Dobson, 1878)[e]
	(*Glyphonycteris*) Thomas, 1896	*Trinycteris* Sanborn, 1949	*Neonycteris* Sanborn, 1949
	M. (*G.*) *behnii* (Peters, 1865)	*T. nicefori* Sanborn, 1949	*N. pusilla* (Sanborn, 1949)
	M. (*G.*) *sylvestris* (Thomas, 1896)	*Glyphonycteris* Thomas, 1896	*Trinycteris* Sanborn, 1949
	M. (*G.*) *brachyotis* (Dobson, 1878)	*G. behnii* (Peters, 1865)[f]	*T. nicefori* Sanborn, 1949
		G. sylvestris Thomas, 1896	*Glyphonycteris* Thomas, 1896
		G. daviesi (Hill, 1964)	*G. behnii* (Peters, 1865)[f]
			G. sylvestris Thomas, 1896
			G. daviesi (Hill, 1964)

[a] Includes *elongata* and *scrobiculatum*.
[b] Includes *pygmaeus* and *mexicana*.
[c] Includes *hypoleuca*.
[d] Includes *homezi*.
[e] Includes *platyceps*.
[f] May be a senior synonym of *G. sylvestris*.

and currently is placed near *Glyphonycteris* and *Trinycteris* by Simmons (1996).

The genus *Micronycteris* has undergone considerable taxonomic change (Table 1) and is defined at present by emended diagnosis of the genus by Simmons and Voss (1998). Ten species are currently recognized that are distributed in diverse habitats from Mexico to Paraguay and throughout most of South America (Simmons 2005): 5 dark-bellied species (*giovanniae*, *hirsuta*, *matses*, *megalotis*, and *microtis*), and 5 pale-bellied species (*brosseti*, *homezi*, *minuta*, *sanborni*, and *schmidtorum*). Four of these (*matses*, *brosseti*, *homezi*, and *sanborni*) have been described or elevated to species status in the past decade.

Relationships among these 10 species are largely unknown because of a combination of factors, including insufficient information from the morphological characters examined thus far (e.g., Simmons 1996), insufficient taxonomic sampling in previous molecular studies (e.g., Arnold et al. 1983; Baker et al. 2003), recent recognition for 5 of the 10 species, and limited availability of museum specimens and tissue samples for many species. Although *Micronycteris* is sometimes divided into 2 informal groups based on venter coloration, the monophyly of these groups is doubtful. No formal subgenera or species groups are currently recognized (Simmons 2005). Furthermore, there is conflicting morphological data relating to the validity of 2 currently recognized species, *M. homezi* (Ochoa and Sánchez 2005; Simmons and Voss 1998) and *M. microtis* (Koopman 1993; Sanborn 1949; Simmons 1996), and it is possible that an additional unrecognized species, *M. mexicana* (Simmons 1996), exists.

Our purpose in this study was to address these species-level questions and to help resolve interspecific relationships within *Micronycteris* (sensu stricto) by examining DNA sequences from a mitochondrial gene (cytochrome-*b* [*Cytb*] gene) and nuclear intron (intron 7 of the nuclear fibrinogen, B beta polypeptide gene [*Fgb*-I7]). We chose these independent markers to identify areas of congruence in nuclear and mitochondrial data sets. The *Fgb*-I7 sequence evolves more slowly than the *Cytb* gene and would be expected to provide better resolution for deep branches within the genus (Prychitko and Moore 1997; Wickliffe et al. 2003). We inferred relationships among 45 specimens of *Micronycteris* (sensu stricto), representing all recognized species except *M. sanborni*, for which samples were unavailable. Sequences of *Lampronycteris* and *Desmodus* were used as an outgroup.

Materials and Methods

Specimens examined.—Using sequences generated in our laboratory combined with data from GenBank, we analyzed complete *Cytb* gene sequences (1,140 base pairs) and complete *Fgb*-I7 sequences (approximately 530 base pairs) for 45 individuals of *Micronycteris* (Appendix I).

We used sequences (Appendix I) from *Desmodus* (subfamily Desmodontinae) and *Lampronycteris* (subfamily Micronycterinae) as outgroups for analyses of both *Cytb* and *Fgb*-I7 data, because previous morphological and molecular studies agree that all are outgroups to the remainder of taxa in this study (Baker et al. 2000, 2003; Jones et al. 2002; Simmons 1996; Simmons and Voss 1998; Simmons et al. 2002; Wetterer et al. 2000).

Data generation.—We extracted DNA from liver or skeletal muscle tissue with standard methods (Longmire et al. 1997). Using polymerase chain reaction (PCR), we amplified the entire *Cytb* gene by using a combination of the primers glo7L and glo6H (Hoffmann and Baker 2001) and L14724 and H15915 (Irwin et al. 1991). Reagent concentrations and thermal profiles generally followed Hoffmann and Baker (2001), although in some cases we reduced the annealing temperature from 48°C to 45°C.

We purified double-stranded PCR amplicons by using a QIAquick PCR Purification Kit (Qiagen, Inc., Chatsworth, California) and sequenced both strands by using Big-Dye or dRhodamine chain terminators according to the manufacturer's instructions, followed by electrophoresis on a 310 or 3100-*Avant* Genetic Analyzer (chain terminators and genetic analyzer from Applied Biosystems, Inc., Foster City, California). We used appropriate external primers and a combination of internal primers designed for this study or by Hoffmann and Baker (2001) to sequence each strand entirely. We used Sequencher version 3.1 software (Gene Codes Corp., Ann Arbor, Michigan) or VectorNTI software (Informax Inc., Bethesda, Maryland) to assemble and check resulting, overlapping fragments.

We used PCR to amplify *Fgb*-I7 by using primers and conditions modified from those in Wickliffe et al. (2003), because we were unable to produce amplifications suitable for direct sequencing using their methods. We developed 2 new sets of primers for phyllostomid bats that we sometimes used in a 2-round nested PCR design: BI7L-rod2, 5′-ATG TCC CAG CTG TAA AGG CCA CCC AGT-3′; BI7U-2, 5′-AGG ACA ATG ACA ATT CAC AAC GGC-3′; BI7L-rod3, 5′-CTG TAA AGG CCA CCC AGT AG-3′; BI7U-3, 5′-ACG GCA TGT TCT TCA GCA CC-3′. We used primers BI7L-rod2 and BI7U-2 in the 1st-round PCR and the following conditions and thermal profile: 35-μl reaction, including approximately 150 ng DNA, 0.35 μM each primer, 1.6 mM $MgCl_2$, 0.17 mM deoxynucleoside triphosphates, 1X final buffer concentration, and 0.75 U FailSafe PCR Enzyme Mix (Epicentre Biotechnologies, Inc., Madison, Wisconsin); initial denaturation at 95°C for 2 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 56°C ramped down to 51°C and ramped back up to 56°C (ramping was set to 0.6°C/s, which totaled about 40 s of annealing time), and 72°C for 1 min, followed by 72°C for 15 min; we set the ramping rate between each of the 3 stages of PCR at 1.0°C/s. If necessary, we used 1 μl of resultant PCR product and primers BI7L-rod3 and BI7U-3 in a 2nd-round PCR under the following conditions and thermal profile: 35-μl reaction, 0.35 μM each primer, 1.4 mM $MgCl_2$, 0.17 mM deoxynucleoside triphosphates, 1X final buffer concentration, and 1.2 U Taq DNA polymerase (Promega Corp., Madison, Wisconsin); initial denaturation at 95°C for 2 min, followed by 30 cycles of denaturation at 95°C for 30 s, annealing at 58°C for 30 s, and 72°C for 1 min, followed by 72°C for 15 min; we set the ramping rate between each of the 3 stages of PCR at 1.0°C/s.

We purified, sequenced, and assembled resulting fragments as described above, although with appropriate *Fgb*-I7 external primers and 2 new internal primers (BI7L-int, 5′-ANG ATA GCT TTC CAA TCC C-3′ and BI7U-int2, 5′-AGA AYR CTC YTR CCY TCT GAG-3′). We resolved base calling ambiguities on single strands by choosing the call on the cleanest strand or by using appropriate International Union of Biochemistry ambiguity codes if both strands showed the same ambiguity (i.e., heterozygous sites).

Data analysis.—We performed multiple sequence alignment for both data sets in Clustal W software (Thompson et al. 1994) with default parameters for costs of opening and extending gaps. We viewed alignments in MacClade software (version 4.0—Maddison and Maddison 2002) to ensure there were no insertions–deletions (indels) or stop codons in the *Cytb* sequences and to inspect gap placement in the *Fgb*-I7 sequences. Whereas sequence alignment of *Cytb* sequences was unequivocal, we identified 14 indel events in the *Fgb*-I7 alignment. We coded and analyzed these 14 events either as missing data or as present or absent data (Simmons and Ochoterena 2000). Using the latter method, we appended 14 binary characters to the data matrix, as each indel event regardless of length is treated as an additional character and weighted equally. Otherwise, we coded nucleotides as unordered, discrete characters and multiple states as polymorphisms.

We inferred phylogenetic relationships by Bayesian analysis implemented in MrBayes 3.1.2 software (Huelsenbeck and Ronquist 2001) and by parsimony analyses implemented in PAUP* software (test version 4.0b10—Swofford 2002). According to Modeltest 3.06 software (Posada and Crandall 1998) and MrModeltest 2.2 software (Nylander 2004), the general time reversible (GTR) model with allowance for gamma distribution of rate variation (Γ) and for proportion of invariant sites (I) best fit the *Cytb* data and the GTR + Γ model best fit the *Fgb*-I7 data.

For Bayesian analysis, we ran 2×10^6 generations (until the average standard deviation of the split frequencies was <0.004) with 1 cold and 3 incrementally heated Markov chains, random starting trees for each chain, and trees sampled (saved) every 100 generations. We treated model GTR + Γ + I and GTR + Γ parameters as unknown variables (with uniform priors) to be estimated in each Bayesian analysis (Leaché and Reeder 2002). For analyses including the 14 indel binary characters, we did not correct for ascertainment bias because it is generally unnecessary for analyses of more than 20–30 taxa

(Ronquist et al. 2005). We calculated a 70% majority-rule consensus tree from the sample of stabilized trees in PAUP* software (test version 4.0b10—Swofford 2002) and obtained branch lengths via the "sumt" option in MrBayes software (Huelsenbeck and Ronquist 2001). We assessed clade reliability via posterior probabilities and regarded values $\geq$0.95 as significant.

For parsimony analysis, we treated all characters and substitution types with equal probability and conducted full heuristic searches with 25 random additions, starting trees by simple addition, and tree-bisection-reconnection branch swapping. We assessed clade reliability via bootstrapping with 1,000 iterations for parsimony analyses (Felsenstein 1985).

Conditional combination of Cytb and Fgb-I7.—We assessed combinability of the 2 data sets based on the presence of supported conflicts (Leaché and Reeder 2002; Wiens 1998). The outgroups included 1 individual of *Lampronycteris* and a composite sequence for *Desmodus*, consisting of *Cytb* and *Fgb*-I7 sequences for 2 individuals from the same locality in Honduras. In the combined analysis, the data were partitioned with each gene sequence being analyzed with the same models and parameters (from Modeltest) determined above for each partition.

Results

All *Cytb* sequences were free of indels and premature stop codons. The sequences were based on high-quality chromatograms showing no ambiguities in both the forward and reverse directions. This evidence supports our conclusion that these sequences were of mitochondrial origin (Bensasson et al. 2001; Triant and DeWoody 2007). Regardless of the method of indel coding, there were no supported conflicts ($P \geq 0.95$, bootstrap value $\geq$70%) between analyses of the *Cytb* gene and *Fgb*-I7 (trees not illustrated); therefore, we combined data sets and our phylogenetic conclusions are based on analysis of the combined data. Fig. 1 shows the Bayesian phylogram for the combined analysis with support values for both Bayesian and parsimony analyses.

All analyses provided strong support for 4 major clades within the genus *Micronycteris*. The 4 clades are indicated by Roman numerals in Fig. 1. Mean *Cytb* distances within and between clades are shown in Table 2. Each of these major branches was supported by bootstrap and posterior probabilities of 100% for all analyses of all data sets as well as the combined data. Uncorrected mean *Cytb* genetic distances within and between the 4 clades are shown in Table 2. Major branches within clade IV are labeled A–F and mean *Cytb* distances are shown in Table 3.

Discussion

Simmons and Voss (1998) and Simmons et al. (2002) recognized 2 species groups within *Micronycteris* corresponding to "dark-bellied" (*hirsuta*, *matses*, *megalotis*, and *microtis*) and "pale-bellied" (*brosseti*, *homezi*, *minuta*, *sanborni*, and *schmidtorum*) forms (Table 1). The dark- and pale-bellied groups are not monophyletic in our analyses because of the positions of *M. hirsuta* and *M. brosseti*. The dark-bellied *M. hirsuta* is not included in the clade of other dark-bellied forms, whereas the pale-bellied *M. brosseti* is not included in the clade of other pale-bellied forms. Thus, the present study supports 4 primary clades within *Micronycteris* that are not in strict correspondence with venter coloration. We recognize these clades as subgenera (see "Taxonomic Conclusions").

Status of M. microtis.—Miller (1898) described *M. microtis* from a single specimen collected in Nicaragua. Since then, several generations of taxonomists and field biologists have struggled to find consistent nonoverlapping characters distinguishing *M. microtis* from *M. megalotis*. As suggested by the name, Miller's (1898) original description distinguishes *M. microtis* from *M. megalotis* primarily by ear size. However, Miller's (1898) description also includes differences in pelage color, dentition, skull shape, and ear ridges. Andersen (1906) did not examine Miller's (1898) specimen, but proposed that differences in ear ridges and ear size in the holotype of *M. microtis* may have been an artifact of preservation, and suggested the possibility of dimorphism in pelage color. Despite his reservations, Andersen (1906) retained *M. microtis* as a valid species.

Sanborn's (1949) revision (Table 1) recognized *microtis* as a subspecies of *M. megalotis* occurring in Nicaragua and Panama. Jones and Carter (1976) and Jones et al. (1977) recognized 2 Middle American subspecies of *M. megalotis*: *M. m. mexicana* (Mexico to western Nicaragua and Costa Rica) and *M. m. microtis* (eastern Nicaragua to Panama and northwestern South America). Handley (1976) reported *M. m. microtis* and *M. m. megalotis* as sympatric in Venezuela. Brosset and Charles-Dominique (1990) found both small- and large-eared bats sympatric in French Guiana, occurring in separate roosts within 1 km. They recognized the 2 forms as distinct species and referred the small-eared bats to *M. microtis*. Brosset and Charles-Dominique (1990) reported an ear length of 15 mm in *M. microtis* compared with 20 mm in *M. megalotis*. These measurements compare well with Miller's (1898) description of 20–23 mm in *M. megalotis* and 16 mm in *M. microtis*, although Miller (1898) measured from the meatus, rather than from the notch as is the modern practice. Compared with *M. megalotis*, Brosset and Charles-Dominique's (1990:522) illustrations show the skull of their *M. microtis* to be "less inflated vertically, its profile being less convex" and with zygomatic arches being less flared laterally. In the original description, Miller (1898) also described *M. microtis* as having less flared zygomatic arches, but reported its skull to be more elevated behind the orbits; however, Miller (1898) suggested that these cranial differences might prove to be the result of individual variation. Despite the difference in the profile of the skull, the specimens examined by Brosset and Charles-Dominique (1990) appear to conform reasonably well to Miller's (1898) description of *M. microtis*.

Simmons (1996) reported *M. microtis* sympatric with *M. megalotis* in Colombia, Venezuela, French Guiana, and Brazil. However, Simmons (1996) and Simmons et al. (2002) reported considerable overlap in the ear length of the 2 taxa (ranging from 21.0 to 23.0 mm in *M. megalotis* and from 19.0 to 22.0

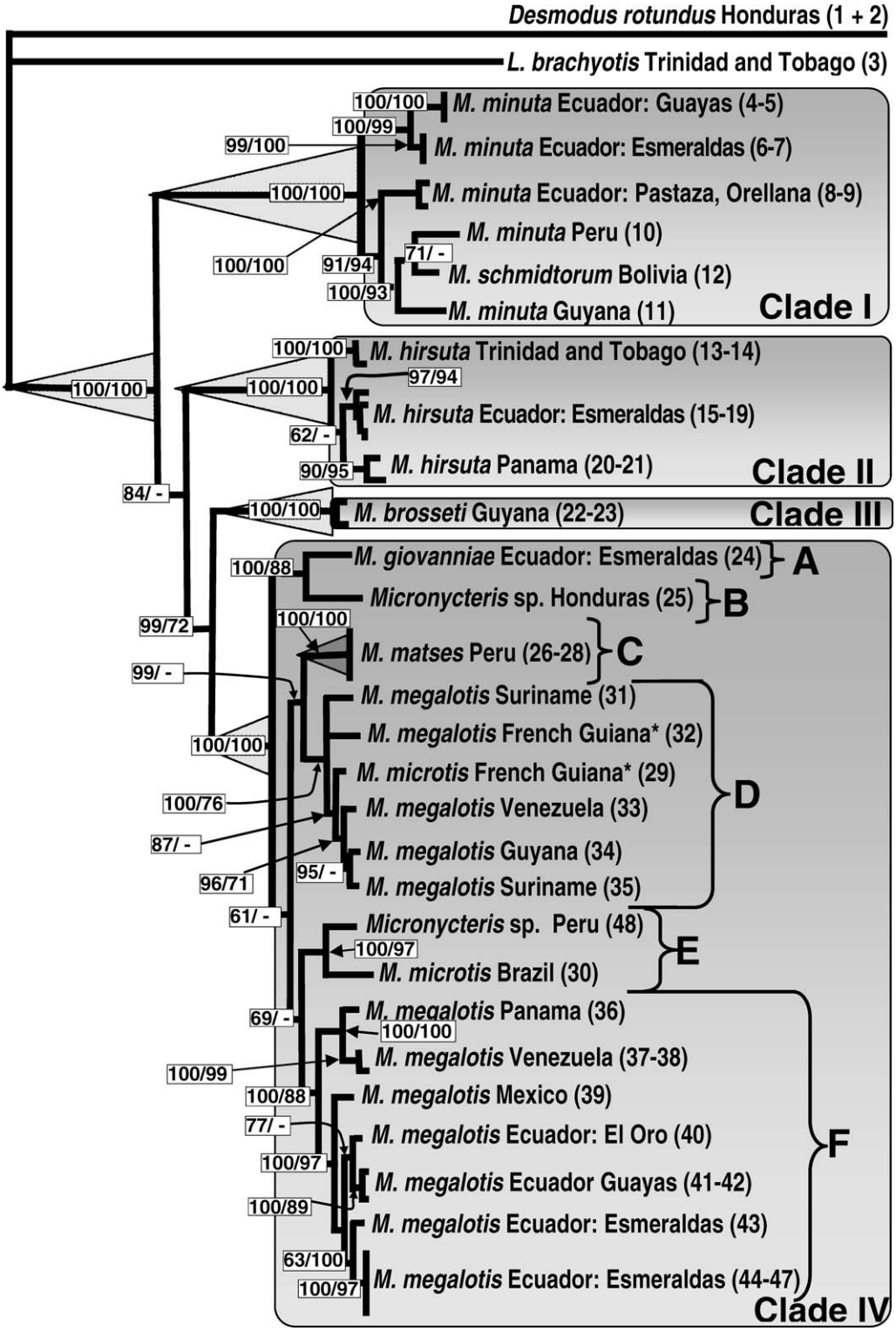

Fig. 1.—Bayesian phylogram from analysis of combined cytochrome-*b* gene and intron 7 of the nuclear fibrinogen, B beta polypeptide gene sequences (~1,670 base pairs) using best-fit models and parameters for each data partition. Numbers in parentheses designate individual specimens listed in Appendix I. We designated *Desmodus* (subfamily Desmodontinae) and *Lampronycteris* (subfamily Micronycterinae) as outgroups. Insertions–deletions, regardless of length, are treated as additional characters. Numbers before the slash are Bayesian posterior probabilities and those after are parsimony bootstrap percentages. Values are shown only for nodes supported by posterior probability or bootstrap percent > 70. Asterisks indicate specimens from Paracou, French Guiana, that Simmons (1996) identified as distinct species. Gray triangles represent clades with strong support in all analyses of both data sets. The letters A–F designate clades within subgenus *Micronycteris* discussed in the text.

Table 2.—Mean genetic distances within and between the 4 major clades of the genus *Micronycteris*. Values are expressed as a percentage and are based on uncorrected genetic distance of cytochrome-*b* sequence data. Values on the diagonal represent mean distances within clades.

	Clade I	Clade II	Clade III	Clade IV
Clade I	5.8			
Clade II	15.9	1.8		
Clade III	13.7	11.3	0.4	
Clade IV	13.1	10.0	9.4	2.4

mm in *M. microtis*). The ears of Simmons' (1996) specimens of *M. microtis* are approximately 3–6 mm larger than those of the holotype and 4–7 mm (26–47%) larger than the ears of bats identified as *M. microtis* by Brosset and Charles-Dominique (1990). Simmons (1996) distinguished the 2 species by differences in the length of hair on the leading edge of the pinna. However, the basis for this distinction is unclear because no previous workers have identified length of ear hair as a diagnostic character for the species and there is no published indication that short ear hair is a character state of the holotype of *M. microtis*. Simmons and Voss (1998) could find no consistent differences in cranial measurements or pelage, and reiterated the utility of ear hair as a diagnostic character.

It is clear that bats with short ear hair occur in sympatry with those having long ear hair. It is less clear to us what evidence supports the proposition that these bats are distinct species. No other morphological character definitively distinguishes the bats. Simmons (1996) and Simmons and Voss (1998) cite sympatry as evidence for the bats being specifically distinct. However, sympatry would also be expected if the ear hair character is a dimorphism within a population or species. The observation of separate roosts by Brosset and Charles-Dominique (1990) does provide evidence suggesting specific status for the bats they collected in French Guiana. However, the connection seems dubious between the short-eared bats of Brosset and Charles-Dominique (1990) and the longer-eared but short ear-haired specimens of Simmons (1996). For these reasons, we are skeptical that Simmons' (1996) specimens of *M. microtis* are specifically distinct from *M. megalotis*. We also remain unconvinced that the bats are conspecific with the holotype of *M. microtis* or specimens of Brosset and Charles-Dominique (1990), all of which have substantially shorter ears.

Our analysis includes specimens of *M. microtis* and *M. megalotis* that were examined for morphological data and identified by Simmons and Voss (1998) and Simmons et al. (2002). Both specimens (AMNH267090 and AMNH267097) were collected from the same locality in French Guiana and appear near each other in the combined analyses (see asterisks in Fig. 1). Despite being identified morphologically as distinct species, the 2 specimens differ genetically by only 0.4% (*Fgb*-I7) and 2.6% (*Cytb*). This level of *Cytb* divergence is lower than most values reported for comparisons of sister species in other mammals, but within the range of variation typically found among populations of a single species (Bradley and Baker 2001).

Table 3.—Mean genetic distances within and between the major branches of clade IV. Values are expressed as a percentage and are based on uncorrected genetic distance of cytochrome-*b* sequence data. Values on the diagonal represent mean genetic distances within clades. Dashes indicate clades represented by a single individual.

	Clade A	Clade B	Clade C	Clade D	Clade E	Clade F
Clade A	—					
Clade B	5.3	—				
Clade C	5.3	6.1	0.2			
Clade D	5.6	5.9	3.2	2.2		
Clade E	6.1	7.1	5.0	5.3	4.4	
Clade F	5.5	6.0	4.3	4.8	5.2	2.4

Our phylogenetic analyses do not support distinct clades of *M. megalotis* and *M. microtis*, and the genetic distances are relatively small between nominal specimens of the 2 species. Of the 1,864 nucleotide positions in the combined analysis, the 2 specimens of *M. microtis* share only 1 fixed difference (a probable homoplasy found in the *Fgb*-I7 sequence) from other members of the genus. Examination of our molecular data therefore controverts the recognition of *M. microtis* as the name is now applied. We considered the possibility that the specimens of *M. microtis* represented in the study may have been misidentified. At our request, the Brazilian voucher of *M. microtis* was examined by personnel of the Royal Ontario Museum, who confirmed its identification based on the criteria of Simmons (1996). Identification is a moot issue for the French Guianan specimen because the bat was collected and identified by Simmons and colleagues. By definition, the specimen can be used to investigate the validity of species boundaries proposed by Simmons and coworkers.

In our view, the morphological characters that have been used to characterize *M. microtis* may represent intraspecies polymorphism. However, pending additional study and resolution of species boundaries, we refrain from making any definitive changes in the taxonomy of the *M. megalotis* complex.

Systematics of M. megalotis and its relatives.—We identify 6 distinct lineages within clade IV. These are identified as clades A–F in Fig. 1. As described by Baker and Bradley (2006), genetic species are groups of "genetically compatible interbreeding natural populations which are genetically isolated from other such groups." Several of the subclades of clade IV are distinguished by >5% genetic divergence in the *Cytb* gene (Table 3) and by the criteria established by Baker and Bradley (2006), are potential genetic species that warrant further study. Clades A and C have been described as *M. giovanniae* and *M. matses*, respectively (Fonseca et al. 2007; Simmons et al. 2002). Compared with other species within clade IV, *M. matses* has somewhat lower genetic distance with other species (Table 3), but the 3–5% divergence values do not preclude species status under the genetic species concept (Baker and Bradley 2006). If these are valid species, then our molecular data also would support recognition of several other species among the specimens identified as *M. megalotis* and *M. microtis*.

Clade B of Fig. 1 consists of a single specimen (TK136752) from Honduras, identified as *Micronycteris* sp. Analyses of the combined data support a sister-group relationship between

this specimen and *M. giovanniae* (clade A). We have compared TK136752 directly with the holotype of *M. giovanniae*, and found important morphological differences between them, with *M. giovanniae* being a substantially larger bat overall. Examination of the morphological data combined with the degree of genetic divergence (Table 3) indicates that the bats represented by clades A and B are probably not conspecific. The type locality of *M. microtis* is in Nicaragua, and it is worth considering that our Honduran specimen may be conspecific with the holotype of *M. microtis*. However, the forearm of TK136752 is 35.05 mm, compared with only 31 mm reported for the holotype of *M. microtis* (Miller 1898). In addition, our specimen has more ear ridges than reported for the holotype of *M. microtis*. Further study will be required to determine if there is an available name that can be applied to this bat.

Clade C (*M. matses*) is well defined and distinct in all analyses. Clade D consists of specimens from a geographically restricted area ranging from French Guiana to eastern Venezuela. Although clades C and D have a relatively low *Cytb* genetic distance (Table 3), the bats are morphologically distinct, and we do not regard them as conspecific. Clade F includes specimens ranging from Mexico through western and central Venezuela to western Ecuador.

Clade E includes 2 specimens, 1 from Brazil identified as *M. microtis*, and another from Peru of uncertain identification. These 2 specimens are not particularly close genetically, but their taxonomic status remains to be resolved.

Systematics of M. minuta and M. schmidtorum.—Our analyses indicate that *M. minuta* is paraphyletic with respect to *M. schmidtorum*. Both data sets agree that the specimens from the western provinces of Ecuador (Guayas and Esmeraldas) form a distinct group, whereas bats from northern South America and the western side of the Andes are allied with *M. schmidtorum*. Based on paraphyly with *M. schmidtorum*, the specimens from western Ecuador appear to represent a distinct species. If the distribution of the western species extends to the north, then *M. hypoleuca* (type locality on the Caribbean coast of Colombia) may be the valid name for this species. Another specimen identified as *M. minuta* (TK82836 from Peru) is associated with *M. schmidtorum* (Fig. 1), and has a *Cytb* genetic distance of only 0.4% from a Peruvian *M. schmidtorum*, suggesting that the 2 bats may be conspecific.

Systematics of M. hirsuta.—Baker et al. (1973) reported different karyotypes in Central American specimens of *M. hirsuta* compared with those from Trinidad and Tobago. They also reported some morphological differences between these chromosome races. It is worth noting that specimens of *M. hirsuta* are clearly differentiated into Central American, Ecuadorian, and Trinidadian clades (Fig. 1).

Current evidence suggests some geographic differentiation of populations based on nuclear (chromosomal), mitochondrial (*Cytb*), and morphological (Baker et al. 1973) markers. If this differentiation is supported by further study, recognition of species or subspecies may be justified based on chromosomal race boundaries (Baker and Bradley 2006). We currently regard the clade as monotypic until we are able to examine additional specimens and data, especially chromosomal data.

Taxonomic Conclusions

Genus *Micronycteris* Gray, 1866

Diagnosis.—The genus is diagnosed by the following 16 characters described by Simmons and Voss (1998:62):

> Dorsal fur bicolored (the hairs brown with white bases); pinnae large, rounded distally, connected by notched band of skin (interauricular band) across crown of head; ventral edge of narial horseshoe defined by thick ridge; chin with pair of dermal pads arranged in a "V" with no central papilla; third metacarpal shortest, fifth longest; first and second phalanges of wing digit III subequal in length; first and second phalanges of wing digit IV either subequal or second phalanx shorter than first; rostrum and anterior orbital region not inflated; basisphenoid pits shallow; dental formula I 2/2, C 1/1, P 2/3, M 3/3 $\times$ 2 = 34; height of upper canine greater than or equal to twice height of inner upper incisor; outer upper incisor in normal position between inner incisor and canine, not excluded from occlusion with lower incisors; P3 not molariform, lingual cingulum and cusp absent; lingual cingulum of P4 with concave outline and raised edge, lingual cusp small or absent; lower incisors bifid; lower premolars aligned in row on mandible, none excluded from toothrow.

Comments.—The genus *Micronycteris* as discussed here follows Simmons and Voss (1998) and combines the subgenera *Micronycteris* and *Xenoctenes* of Sanborn (1949). *Micronycteris* belongs in the family Phyllostomidae Gray, 1825, and subfamily Micronycterinae. The subfamily was 1st defined in Van Den Bussche (1992) for the single genus *Micronycteris* sensu Sanborn (1949; see Table 1), but herein is composed of the more restricted genera *Micronycteris* and *Lampronycteris* (Table 1). Based on our analyses, we recognize 4 subgenera (Table 1). The subgenera correspond to clades I–IV in Fig. 1. Based on *Cytb* analyses, the mean genetic distance between subgenera ranges from 9.4% to 15.9%, whereas the mean genetic distance between individuals within subgenera ranges from 0.4% to 5.8% (Table 2).

Subgenus *Micronycteris* Gray, 1866

Type species.—*Phyllophora megalotis* Gray, 1842.

Included species.—*Micronycteris* (*Micronycteris*) *megalotis*, *M.* (*Micronycteris*) *microtis*, *M.* (*Micronycteris*) *matses*, and *M.* (*Micronycteris*) *giovanniae*. We regard the nominal species *elongata*, *mexicana*, *pygmaeus*, and *scrobiculatum* as junior synonyms of *M.* (*M.*) *megalotis*, although these names would be available for putative cryptic species identified in the *M.* (*M.*) *megalotis* complex.

Diagnosis.—Pinnae connected by low interauricular membrane with shallow notch at the midline; small to medium in overall size (weight generally 5–14 g; forearm 31–40 mm); ventral fur dark; calcar longer than foot; 2nd phalanx of wing digit IV shorter than 1st; mastoid breadth less than zygomatic breadth; diploid number 40; fundamental number 68 (Baker 1967; Fonseca et al. 2007; Gardner 1977; Honeycutt et al. 1980; Patton and Baker 1978; Simmons 1996; Simmons and Voss 1998; Simmons et al. 2002).

Comments.—This subgenus includes all dark-bellied species except *M. hirsuta*. Examination of our data does not support

recognition of *M.* (*M.*) *microtis* as the name is currently applied (e.g., Simmons and Voss 1998), but we defer making a taxonomic change pending additional study. Chromosomal characters of the subgenus are based on karyotypes of *M.* (*M.*) *megalotis* (Patton and Baker 1978) and *M.* (*M.*) *giovanniae* (Fonseca et al. 2007). *M.* (*M.*) *microtis* and *M.* (*M.*) *matses* have not been karyotyped, although Simmons (1996) suggested that (based on locality) the karyotype of *M. megalotis* reported by Baker (1967) was actually that of *M. microtis*.

Subgenus *Leuconycteris*, new subgenus

Etymology.—From Leuconoe, the daughter of Minyas in Greek mythology, who was transformed into a bat. The name also makes apt reference to the pale belly (from the Greek *leuco*) that is unique among the low-banded species of the genus.

Type species.—*Micronycteris brosseti* Simmons and Voss, 1998.

Included species.—*Micronycteris* (*Leuconycteris*) *brosseti*.

Diagnosis.—Pinnae connected by low interauricular membrane with shallow notch at the midline; very small in overall size (weight 4–5 g; forearm 31–34 mm); ventral fur light; calcar longer than foot; 2nd phalanx of wing digit IV shorter than 1st; mastoid breadth less than zygomatic breadth (Simmons and Voss 1998).

Comments.—In the field, this taxon is distinguished by its small size, low interauricular band, and pale belly.

Subgenus *Schizonycteris*, new subgenus

Etymology.—From Greek *schizo* for the prominent split in the interauricular membrane. The subgenus name also acknowledges the original generic name *Schizostoma* Gervais, 1856, which is invalid as a junior homonym. Had it been valid, Gervais' name would have been applicable to this subgenus.

Type species.—*Schizostoma minutum* Gervais, 1856.

Included species.—*Micronycteris* (*Schizonycteris*) *minuta*, *M.* (*Schizonycteris*) *schmidtorum*, and *M.* (*Schizonycteris*) *sanborni*. *M. homezi* is regarded as a synonym of *M.* (*S.*) *minuta*, following Ochoa and Sánchez (2005). The name *Micronycteris hypoleuca* may be applicable to a member of the *M.* (*S.*) *minuta* complex, but we provisionally consider *M. hypoleuca* to be a synonym of *M.* (*S.*) *minuta*.

Diagnosis.—Moderate to high interauricular membrane with moderate to deep midline notch, dividing the membrane into 2 triangular flaps; overall size small (weight < 9 g; forearm < 38 mm); ventral fur white or pale gray or buff, lighter in color than dorsal fur; lower incisors not hypsodont, crown height no more than 2 times the crown width; diploid number 28–38; fundamental number 50–66 (Baker 1973; Gardner 1977; Simmons 1996; Simmons and Voss 1998).

Comments.—This taxon includes all of the "pale bellied" species (Simmons and Voss 1998; Simmons et al. 2002) except *M. brosseti*, which belongs to *Leuconycteris*. The V-shaped notch in the interauricular membrane divides the band into 2 triangular segments (Simmons and Voss 1998:72, figure 30). Karyotypic data have been reported for all species of *Schizonycteris* (Baker 1973; Gardner 1977; Simmons 1996). *M.* (*Schizonycteris*) *schmidtorum* retains some morphological characters that may be primitive for the genus, including a calcar longer than the foot, mastoid breadth less than zygomatic breadth, a 2nd phalanx of wing digit IV shorter than the 1st (Simmons and Voss 1998), and a karyotype similar to that found in *M.* (*M.*) *megalotis* (Baker 1973). The interauricular band in *M.* (*S.*) *schmidtorum* is intermediate in morphology between that seen in other species of *Schizonycteris* and the low band found in the other subgenera. Examination of the molecular data presented in this study and by Baker et al. (2000, 2003) places *M. schmidtorum* as a member *Schizonycteris*. The phylogeny presented by Jones et al. (2002) also provides support for this taxon.

Bayesian analysis of the molecular data indicates that *Schizonycteris* represents the basal lineage within the genus and is sister to the other 3 subgenera (Fig. 1). *Schizonycteris* is characterized by moderate levels of genetic distance among its species (mean of 5.8% for *Cytb*; Table 1), all of which are extremely divergent from other *Micronycteris*. Monophyly of *Schizonycteris* as defined in this study also receives support from studies of morphological data (Simmons 1996), mitochondrial ribosomal (Baker et al. 2003), and nuclear *RAG2* (Baker et al. 2000, 2003) sequence data, and a combination of morphological and molecular data (Jones et al. 2002).

The species *M.* (*S.*) *sanborni* is not included in our molecular analyses, but we place it in this taxon based on previous morphological studies (Simmons 1996).

Subgenus *Xenoctenes* Miller, 1907

Type species.—*Schizostoma hirsutum* Peters, 1869.

Included species.—*Micronycteris* (*Xenoctenes*) *hirsuta*.

Diagnosis.—Moderately high interauricular membrane with a broad notch; overall size large relative to the other subgenera (weight at least 12 g; forearm 41 mm or longer); ventral fur dark; calcar longer than foot; 2nd phalanx of wing digit IV longer than 1st; mastoid breadth less than zygomatic breadth; lower incisors hypsodont, crown height approximately 3 times crown width; diploid number 28–30; fundamental number 32 (Baker et al. 1973; Simmons and Voss 1998).

Comments.—Bats of this subgenus are characterized by large size, hypsodont lower incisors, and a karyotype unique in the genus, with low diploid and fundamental numbers (Baker et al. 1973). Andersen (1906) and Sanborn (1949) reported that *M.* (*X.*) *hirsuta* has a low, unnotched interauricular band. However, Davis (1976) reported that the band is moderately high with a broad notch. According to Davis (1976), D. C. Carter examined the holotype and found a moderately high band with a notch intermediate in depth between *M. megalotis* and *M. minuta*. Davis (1976) and Simmons (1996) regarded *Xenoctenes* as a synonym of subgenus *Micronycteris* (sensu Sanborn 1949). With the recognition of the more restricted genus of Simmons and Voss (1998), *Xenoctenes* can be regarded as valid without producing paraphyly within the genus. In addition to the DNA sequence data, recognition of

Xenoctenes is justified by its larger size, distinct dental characteristics, and unique karyotype.

Resumen

En en presente trabajo analizamos variación en la secuencia de ADN en el gen mitocondrial del citocromo-*b*, y en intrón 7 del polipéptido beta del fibrinogeno dentro del género *Micronycteris*, incluyendo muestras de todas las especies actualemente reconocidas con la excepción de *M. sanborni*. Los resultados de los análisis filogenéticos de los 2 fragmentos estudiados agrupan las especies en 4 linajes, que son reconocidos como subgéneros: *Leuconycteris* nuevo subgénero (*M. brosseti*), *Micronycteris* Gray (*M. megalotis*, *M. microtis*, *M. matses*, y *M. giovanniae*), *Schizonycteris* nuevo subgénero (*M. minuta*, *M. schimdtorum*, y *M. sanborni*), y *Xenoctenes* Miller (*M. hirsuta*). Nuestros resultados no apoyan la monofilia de *M. microtis* como se reconoce actualmente, a pesar de lo cual reconocemos provisionalmente la taxonomía alfa dentro de *Micronycteris*. Nuestros resultados tambien indican la probable existencia de especies cripticas dentro de lo que hoy se reconoce como *M. megalotis* y *M. minuta*, y posiblemente *M. hirsuta*. Estudios adicionales con una representación geográfica mas exhaustiva y un muestro mas detallado de la variación morfológica y genética serán necesarios para evaluar nuestras hipótesis genealógicas, y estimar la biodiversidad dentro de *Micronycteris*.

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APPENDIX I

Specimens examined.—Numbers associated with each specimen are enclosed in parentheses. The 1st number identifies the specimen in Fig. 1. The 2nd number is the University of New Mexico (NK) or Texas Tech University (TK) tissue number. The 3rd number identifies the museum voucher. The 4th and 5th numbers are GenBank accession numbers for the *Cytb* gene and *Fgb*-I7, respectively. As a matter of curatorial routine, genetic samples borrowed by Texas Tech University are assigned a TK number in addition to any identifying numbers given by the lending institution. This practice simplifies record keeping and ensures that borrowed samples are

properly accounted for and can be easily cross-referenced with loan records, voucher specimens, and with the collection of the lending institution. It does not imply that the tissues or DNA samples are accessioned into the Texas Tech collection.

Collections housing voucher specimens are identified by the following acronyms: AMNH = American Museum of Natural History, New York; CM = Carnegie Museum of Natural History, Pittsburgh; DGR = Division of Genomic Resources, Museum of Southwestern Biology, University of New Mexico, Albuquerque; KU = University of Kansas Natural History Museum, Lawrence; MSB = Museum of Southwestern Biology, University of New Mexico, Albuquerque; QCAZ = Museo de Zoología, Pontifica Universidad Católica del Ecuador, Quito; ROM = Royal Ontario Museum, Toronto; TTU = Natural Science Research Laboratory, Texas Tech University, Lubbock; USNM = United States National Museum, Smithsonian Institution, Washington. TTU specimens without a voucher number have not yet been catalogued.

Desmodus rotundus.—HONDURAS: Atlantida: Lancetilla Botanical Garden (UTM: 16-451344 17-40863). (1: TK40368; TTU61104; DQ077398; no *Fgb*-I7 data) (2: TK101831; TTU84488; no *Cytb* data; DQ077430).

Lampronycteris brachyotis.—TRINIDAD AND TOBAGO: Trinidad: County Mayaro: 1 mile S, 2 miles W Guayaguayare. (3: TK25239; CM97174; AY380748; DQ077431).

Micronycteris brosseti.—GUYANA: Potaro-Siparuni: Inokrame Reserve. (22: TK82751; KU155162; AY380770; DQ077454) (23: TK87252; KU155163; AY380771; DQ077455).

Micronycteris hirsuta.—ECUADOR: Esmeraldas: E San Lorenzo (toward Lita), Finca San Jose, 144 m, UTM 17 764596E 0117145N. (15: TK104677; TTU85449; DQ077410; DQ077448). (16: TK104680; TTU85452; DQ077412; DQ077449). Mataje, Navy Base, 1°20′45.6″N, 78°43′0.1″W. (17: TK135971; TTU; DQ077415; DQ077453). S San Lorenzo, La Chiquita Experimental Station, 30 min walk in. (18: TK104656; TTU85428; DQ077414; DQ077451) (19: TK104660; TTU85432; DQ077413; DQ077450). PANAMA: Veraguas: Cerro Hoya, Rio Portobelo, 7°14.473′N, 80°36.719′S. (20: NK101614; MSB94371; AY380768; DQ077444) (21: NK101615; MSB94372; AY380769; DQ077445). TRINIDAD AND TOBAGO: Trinidad: County St. George: 4 miles N Simla Research Center. (13: TK25041; CM97177; AY380751; DQ077447). County Mayaro: 1 mile S, 2 miles W Guayaguayare. (14: TK25229; TTU43943; DQ077408; DQ077446).

Micronycteris matses.—PERU: Loreto: Rio Galvez, Nuevo San Juan. (26: TK82756; AMNH272814; DQ077417; DQ077457. Paratype) (27: TK82833; AMNH273043; DQ077418; DQ077458. Paratype) (28: TK82834; AMNH273095; DQ077419; DQ077459. Paratype).

Micronycteris megalotis.—ECUADOR: El Oro: Puyango, Bosque Petrificado—Sector Quebrada de los Sabalos, 3°52′46.2″S, 80°5′34.3″W. (40: TK135244; TTU; DQ077427; DQ077478). Guayas: Bosque Protector Cerro Blanco, 2°10′47.6″S, 80°01′17.7″W. (41: TK134837; TTU; DQ077428; DQ077479). Guayas: Isla Puna, 2°44′40.6″S, 79°54′53.6″W. (42: TK134960; TTU; DQ077429; DQ077480). Esmeraldas: S San Lorenzo, La Chiquita Experimental Station. (43: TK104517; TTU85289; DQ077426; DQ077477). Esmeraldas: E San Lorenzo, La Guarapera banana farm and pasture. (44: TK104617; TTU85389; DQ077422; DQ077473). Esmeraldas: S San Lorenzo, La Chiquita Experimental Station, 30 min walk in. (45: TK104663; TTU85435; DQ077424; DQ077476) (46: TK104664; TTU85436; DQ077425; DQ077475). Esmeraldas: Terrenos aledanos de la Comuna San Francisco de Bogota, 1°05′36.8″N, 78°42′21.5″W. (47: TK135636; TTU; DQ077423; DQ077474). FRENCH GUIANA: Paracou, near Sinnamary. (32: TK18785; AMNH267090; AY380761; DQ077465). GUYANA: Potaro-Siparuni: 40 km SSW of Kurupukary, Inokrame Reserve, Gorge Camp, 4°22′N, 58°43′W. (34: TK16375; ROM108745; AY380757; DQ077462). MEXICO: Chiapas: 8.2 miles SE, 2.5 miles E Tonala, Rio Ocuilapa. (39: TK20558; TTU36534; AY380764; DQ077472). PANAMA: Canal Zone: Gamboa, 9°6′N, 79°4′W. (36: TK16372; ROM104195; AY380765; DQ077468). SURINAME: Nickerie (now Sipaliwini): Kayserberg Airstrip. (31: TK17071; CM68390; AY380758; DQ077464). Marowijne: Perica. (35: TK17606; CM76768; AY380759; DQ077466). VENEZUELA: Bolivar: 18 km NE El Manteco. (33: TK19040; CM78295; AY380773; DQ077467). Guarico: 45 km S Calabozo. (37: TK15175; TTU33276; AY380763; DQ077421). Barinas: 8 km by road SW Santa Barbara. (38: TK19407; CM78291; DQ077431; DQ077469).

Micronycteris microtis.—BRAZIL: Sao Paulo: Caetetus Ecological Station, 22°23′S, 49°40′W. (30: TK16377; ROM111099; AY380755; DQ077463). FRENCH GUIANA: Paracou, near Sinnamary. (29: TK18782; AMNH267097; AY380756; DQ077461).

Micronycteris minuta.—ECUADOR: Guayas: Bosque Protector Cerro Blanco: 2°25′38.2″S, 80°1′17.7″W. (4: TK134785; TTU; DQ077400; DQ077434). Bosque Protector Cerro Blanco, 2°10′50.8″S, 80°1′54.3″W. (5: TK134860; TTU; DQ077401; DQ077435). Esmeraldas: Terrenos aledanos de la Comuna San Francisco de Bogota, 1°4′21.3″N, 78°42′41.4″W. (6: TK135801; TTU; DQ077402; DQ077436) (7: TK135798; TTU; DQ077403; DQ077437). Orellana: 30 km S Pompeya Sur, Parque Nacional Yasuni, 0°37′S, 76°28′W. (8: TK16371; ROM104067; AY380752; DQ077438). Pastaza: Puyo, Finca El Pigual. (9: TK104053; TTU84825; DQ077404; DQ077439). GUYANA: East Berbice-Corentyne: Dubulay Ranch, 5°40′91″N, 57°51′52″W, elevation 41 m. (11: TK86643; USNM582262; AY380754; DQ077441. This specimen is nominally *M. homezi*). PERU: Loreto: Rio Galvez, Nuevo San Juan. (10: TK82836; AMNH273172; DQ077405; DQ077440).

Micronycteris schmidtorum.—BOLIVIA: Santa Cruz: National Park Noel Kempff Mercado. (12: NK22684; DGR4582; DQ077406; DQ077442).

Micronycteris sp.—HONDURAS: Colon: Trujillo, Parque Nacional Caprio y Calentua. (25: TK136752; TTU; DQ077420; DQ077460). PERU: Loreto: Rio Galvez, Nuevo San Juan. (48: TK82837; AMNH273169; DQ077407; DQ077443).

Micronycteris giovanniae.—EQUADOR: Esmeraldas: E San Lorenzo (toward Lita), Finca San Jose, 1°3′32.1″N, 78°37′20.7″W. (24: TK104673; QCAZ7200; AY380750; DQ077456. Holotype).