MORPHOLOGICAL AND MOLECULAR VARIATION WITHIN LITTLE BIG-EARED BATS OF THE GENUS *MICRONYCTERIS* (PHYLLOSTOMIDAE: MICRONYCTERINAE) FROM SAN LORENZO, ECUADOR

VARIACIÓN MORFOLÓGICA Y MOLECULAR EN EL GÉNERO *MICRONYCTERIS* (PHYLLOSTOMIDAE: MICRONYCTERINAE) DE SAN LORENZO, ECUADOR

René M. Fonseca¹, Steven R. Hoofer, Calvin A. Porter, Chrissy A. Cline, Deidre A. Parish, Federico G. Hoffmann, and Robert J. Baker²

DEDICATION AND ENCOMIUM: The following statement is by Robert Baker.

I first became aware of the significance of Oliver Pearson’s work through the classic paper “Reproduction of the Lump-Nosed Bat (Corynorhinus rafinesquei) in California” (Pearson, O.P., M. R. Koford, and A. K. Pearson. 1952 J. Mammal. 33: 273-320), which impressed me as a standard for scientific research. At the mammal meetings, I had the pleasure of interacting with Professor Pearson and his wife Anita and they always were happy discussing mammalogy, South American research, or a wide array of other topics of interest such as how to keep the birds from eating the fruit from the trees in your yard. It was in Pittsburgh at the Pymatuning Symposium on Mammalian Biology in South America that I became fascinated with his class and style in presentations of papers. I would ask my students that attended the mammal meetings to sit with me and listen to Dr. Pearson present his work because he had such control over the English language and word order that many of his sentences were poetic. My response to such papers was usually something like “Wow! I wish I could present a paper like that.” In that way, he was a mentor to many of my graduate students. I always admired both his science and his dedication to field work. Paynie brought class to our beloved science. The world is a lesser place in his absence.

There are seven authors on this paper, including two South American students of mammalogy (René Fonseca and Federico Hoffmann). Whereas Robert Baker is the only author who had the privilege of personally meeting Dr. Pearson, all authors are aware of Dr. Pearson’s incredible contribution to understanding the mammalian fauna of South America and enthusiastically dedicate our work to Dr. Pearson.

¹ Deceased
² Author for correspondence.

ABSTRACT

The genus *Micronycteris* has undergone several taxonomic changes in recent years. The most recent morphological review of *Micronycteris* recognizes 9 species, including 4 dark-bellied species (*hirsuta, matses, megalotis, microtis*), and 5 pale-bellied species (*brosseti, homezi, minuta, sanborni, schmidtorum*). Specimens of *Micronycteris* from Ecuador are poorly represented in museum collections, and some important areas within the country have few voucher specimens. Only 3 species (*hirsuta, megalotis, and minuta*) have been recorded in Ecuador. We collected a small series (N = 10) of dark-bellied specimens of *Micronycteris* during the Sowell Expedition 2001 to northwest Ecuador. In this paper we assess the morphological and molecular interspecific variation within the genus, comparing our series to other *Micronycteris* found in Ecuador and other Latin American countries. In Ecuador we distinguish 3 morphotypes among dark-bellied forms. With one exception, our specimens except are referable either to *M. megalotis* or *M. hirsuta*. The one exception is unlike any other recognized species of *Micronycteris*. We provide a set of characters useful to distinguish dark-bellied species of *Micronycteris* in Ecuador and describe a new species.

Key words: Phyllostomidae, genetic species concept, *Micronycteris, M. giovanniae, M. megalotis, M. matses, M. hirsuta*, cytochrome-b, karyotypes, morphometrics

RESUMEN

El género *Micronycteris* ha sufrido varios cambios taxonómicos en los últimos años. La revisión morfológica más reciente reconoce 9 especies, incluyendo 4 con vientre oscuro (*hirsuta, matses, megalotis, microtis*), y 5 con vientre pálido (*brosseti, homezi, minuta, sanborni, schmidtorum*). Los ejemplares de Ecuador están pobremente representados en colecciones de museo, y algunas áreas importantes de ese país están representadas por pocos ejemplares. Sólo 3 especies (*hirsuta, megalotis, y minuta*) han sido registradas en Ecuador. Colectamos una pequeña serie (N=10) de especímenes de vientre oscuro de *Micronycteris* durante la Expedición Sowell del 2001 al noroeste de Ecuador. En este trabajo evaluamos la variación morfológica y molecular interespecífica dentro del género, comparando nuestra serie con otros *Micronycteris* encontrados en Ecuador y otros países latinoamericanos. En Ecuador, distinguimos 3 morfotipos entre las formas de vientre oscuro. Con una única excepción, nuestros ejemplares son asignables a *M. megalotis* o a *M. hirsuta*. El ejemplar excepcional no se parece a ninguna especie reconocida de *Micronycteris*. Proveemos un conjunto de caracteres útiles para distinguir a las especies de vientre oscuro de *Micronycteris* en Ecuador y describimos una nueva especie.

INTRODUCTION

The genus *Micronycteris* Gray comprises a group of morphologically diverse phyllostomid bats that has undergone several taxonomic changes in recent years. Based on morphological analyses several authors have suggested that *Micronycteris* (sensu Sanborn, 1949) is not monophyletic (Simmons, 1996; Simmons and Voss, 1998; Wetterer et al., 2000). The subgenera *Glyphonycteris*, *Lampronycteris*, *Micronycteris*, *Neonycteris*, and *Trinycteris* were then elevated to generic level (Wetterer et al., 2000), and these conclusions have been supported by molecular data (Baker et al., 2000, 2003a). Additionally, *Micronycteris* traditionally is placed in the subfamily Phyllostominae (Koopman, 1993) according to morphological similarities with other members of this taxon. However, Baker et al. (2003a) provided strong evidence for placing *Micronycteris* and *Lampronycteris* in the subfamily Micronycterinae, and *Glyphonycteris* and *Trinycteris* in a distantly related subfamily Glyphonycterinae. They were unable to sample *Neonycteris*, and its status is defined based on morphological differences with related taxa (Wetterer et al., 2000).

*Micronycteris* is more narrowly defined today than it has been traditionally based on Sanborn’s (1949) review of the genus. Simmons and Voss (1998) provided an emended diagnosis for the genus. The most recent morphological review of *Micronycteris* (Simmons et al., 2002) recognized 9 species, including 4 dark-bellied species (*hirsuta*, *matses*, *megalotis*, *microtis*), and 5 pale-bellied species (*brosseti*, *homezi*, *minuta*, *sanborni*, *schmidtorum*). Only 3 of these (*hirsuta*, *megalotis*, *minuta*) have been recorded in Ecuador (Albuja, 1999; Tirira, 1999). Specimens of *Micronycteris* from Ecuador are poorly represented in museum collections, and some important areas within the country considered as centers of endemism have few voucher specimens.

During July and August 2001, researchers from Texas Tech University (TTU) and the Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador were involved in the Sowell Expedition to northwest Ecuador with the main purpose of documenting the mammalian diversity of several localities surrounding San Lorenzo. During this fieldtrip, we collected a small series of dark-bellied specimens of *Micronycteris*, giving us the opportunity to study interspecific variation within the genus in this poorly sampled geographic region. The purpose of this paper is to document variation present in dark-bellied species from San Lorenzo, to place this variation in the context of the genus, and to describe a new taxon from the *M. megalotis* complex.

MATERIALS & METHODS

Study Area. The study area constitutes the surroundings of San Lorenzo (01° 16’ N, 78° 49’ W), a small town located in Esmeraldas Province of Ecuador (Fig. 1). The area is part of the southernmost limit of the Chocó region, characterized by high endemism of plants and animal species (Dodson and Gentry, 1991; Myers et al., 2000). The plant community is dominated by palms and species of the family Moraceae (Gentry, 1986). Common species are *Brosimum utile*, *Castilla elastica* (Moraceae); *Wettinia quinaria*, *Phytelaphas aequatorialis* (Areaceae); *Guarea polymera* (Meliaceae); *Otoba gordonifolia* (Myristicaceae); *Inga sichalensis* (Mimosaceae); *Theobroma gileri* (Sterculiaceae); and
Xanthosoma daguense (Araceae). A detailed description of soils and vegetation is presented by Gentry (1986) and Cerón et al. (1999).

Morphological Comparisons. To identify specimens of *Micronycteris* from San Lorenzo, we compared the morphological features of this series with other dark-bellied specimens of the genus from several localities in South America. We examined external and cranial differences and measured available specimens with a digital caliper to the nearest 0.01 mm. Measurements (following Simmons, 1996) included for comparisons are: total length, tail length, hind foot length, ear length, forearm length, metacarpal III length, length of the first phalanx of the third digit, second phalanx of the third digit, first phalanx of the fourth digit, thumb length, tibia length, calcar length, greatest length of the skull, condylobasal length, zygomatic width, mastoid width, braincase width, braincase height, palatal length, post-palatal length, post-orbital constriction width, interorbital width, greatest width across the molars, greatest width across the canines, maxillary tooththrow length, mandibular tooththrow length, coronoid process length, and mandibular length.

Genetic Comparisons. We extracted genomic DNA from liver tissue of 15 bats by standard methods (Longmire et al., 1997) representing most of the recognized species within the

Figure 1. Geographic distribution of dark-bellied species of *Micronycteris* in Ecuador. Records are based on museum specimens and Albuja (1999). Circles represent records of *M.megalotis*; solid triangles represent records of *M. hirsuta*. The area in this study is represented by a white square. Inset: Map of South America with Ecuador shaded.
genus (*M. brosseti, M. hirsuta, M. homezi, M. matses, M. megalotis, M. microtis, M. minuta, M. schmidtorum*). We amplified and sequenced the mitochondrial cytochrome-\(b\) gene (Cyt \(b\); 1,140 base pairs) using primers and conditions reported in Hoffmann and Baker (2001). We amplified and sequenced intron 7 (Fgb-I7; approximately 530 base pairs) of the fibrinogen, B beta polypeptide (Fgb) using primers and conditions modified from those in Wickliffe et al. (2003); those modifications will be described elsewhere (Porter et al, unpubl. ms).

We purified double-stranded amplicons with the QIAquick® PCR Purification Kit (QIAGEN, Inc., Valencia, California) and sequenced both strands with Big-Dye™ chain terminators followed by electrophoresis on a 3100-Avant automated sequencer (Applied Biosystems, Inc., Foster City, California). We used AssemblyLIGN™ 1.0.9 software (Oxford Molecular Group PLC, 1998) to assemble overlapping fragments. We performed multiple sequence alignment for the mitochondrial and nuclear data separately in CLUSTAL X software (Thompson et al., 1997), with default parameters for costs of opening and extending gaps. We viewed resulting alignments in MacClade (version 4; Maddison and Maddison, 2002) to assure there were no gaps or stop codons in mitochondrial coding alignment and to inspect gapped regions in nuclear intron alignment.

We coded nucleotides as unordered, discrete characters (G, A, T, C), multiple states as polymorphisms, and gaps as missing. In PAUP* software (test version 4.0b10; Swofford, 2002), we examined levels of phylogenetic signal via \(g_1\)-statistics (relative to 100,000 randomly drawn trees) for each data set separately; we compared \(g_1\)-values with critical values of Hillis and Huelsenbeck (1992). We inferred phylogenetic relationships by using two optimality criteria: Minimum Evolution, with Tamura-Nei (1993) distances and with starting trees obtained via neighbor-joining; and Parsimony, with equal weights applied to all characters and substitution types. For both criteria and data sets, we designated two outgroups (*Trachops* and *Lampronycteris*) and assessed clade reliability via bootstrap analysis (Felsenstein, 1985) of 500 heuristic iterations, each with 10 random additions of input taxa, random starting trees, and tree-bisection-reconnection.

*Karyological Comparisons.* Karyotypes were prepared from nine individuals of *Micronycteris*. Karyotypic preparations were made within 24 hours of capture using the methods described in Baker et al. (2003b). Images were recorded and karyotypes were prepared using the GENUS System by Applied Imaging.

**RESULTS**

*Morphological Comparisons.* A combination of external and cranial characters, as well as size differences, allows distinguishing 3 morphotypes among dark-bellied forms of *Micronycteris* from northwestern Ecuador. These 3 morphotypes correspond to *M. hirsuta, M. megalotis*, and one specimen (QCAZ 7200) externally similar to *M. matses*. Differences among these types with other dark-bellied species are explained below.

External size differences distinguish *M. megalotis* as the smallest species of the genus inhabiting the San Lorenzo area. The specimen QCAZ 7200 represents an intermediate form in size, whereas specimens assignable to *M. hirsuta* constitute the largest species from the area.
Length and coloration of the fur are similar among specimens of *Micronycteris* from San Lorenzo. In all of them, a basal whitish band is present, but is less conspicuous in QCAZ 7200. Differences in the length of the hair covering the inner border of ears are also evident. Specimens assignable to *M. megalotis* from San Lorenzo possess hair on the inner border of the ears exceeding 5 mm in length, similar to values reported for other populations of *M. megalotis* and *M. matses* (according to Simmons et al., 2002). The specimen QCAZ 7200 and specimens referable to *M. hirsuta* possess shorter hair on the inner border of the ears. Wings and other membranes are naked in all *Micronycteris* specimens except those of *M. hirsuta*, which are hairy at the base of the thumb.

Skull structure differs substantially among *Micronycteris* forms from San Lorenzo. The specimen QCAZ 7200 is intermediate in size compared to *M. megalotis* and *M. hirsuta*, but similar to *M. matses*. The rostrum in QCAZ 7200 is longer than in *M. megalotis* and *M. matses*, proportional to the skull length, but is less elongated than in *M. hirsuta*. Maxillae in QCAZ 7200 are more inflated than the other dark-bellied species; in *M. matses* and *M. megalotis* the rostrum is slender and generally the cingulum of the upper molars is visible from a superior view (Fig. 2). The zygomatic arch in QCAZ 7200 is robust and well developed as in *M. hirsuta*, not weak as in *M. matses*; the fusion between the jugal and the squamosal bones is poorly developed in *M. matses*, distinguishing it from *M. megalotis, M. hirsuta*, and QCAZ 7200 in this feature. In QCAZ 7200, *M. matses*, and *M. megalotis* the sagittal crest is elevated in similar proportions from the skull, whereas in *M. hirsuta* this structure is more elevated than in the former species, especially in specimens from San Lorenzo. Furthermore, the lambdoidal crest and the mastoid process in *M. hirsuta* are developed more than in the rest of the species included in our comparisons. Backward projection of interparietals also differs among these species: in QCAZ 7200 and *M. matses* the projection of the interparietals gives the skull a rounded ending from a superior view; the skull of *M. megalotis* possesses a more globular ending whereas in *M. hirsuta* this projection results in a sharp ending of the skull. Paraoccipital processes, occipital condyles, and auditory bullae have similar

![Figure 2. Dorsal and ventral views of *Micronycteris giovanniae* [Holotype: QCAZ 7200 (= TTU 85445); left] and *M. matses* (ANMH 15231; right) showing size and cranial differences. Notice the differences in the width of rostrum, length of palatal extension, and width of basioccipital. Scale bar equals 5 mm.](image-url)
proportions in all these dark-bellied species. There are noticeable differences in several basicranium structures between QCAZ 7200 and other species, especially compared to *M. matses*. The basioccipital bone is wide in QCAZ 7200, forming a narrow and elongated basicochlear fissure; shape of basioccipital is similar to that found in some populations of *M. megalotis*, especially from San Lorenzo, but is always narrower in *M. hirsuta* in which it forms a wide basicochlear fissure (Fig. 3). Shape of basioccipital in *M. matses* is the narrowest among dark-bellied species, forming an extremely wide and long fissure that distinguishes it from QCAZ 7200.

Simmons (1996) indicated that basisphenoid pits are present in species of *Micronycteris*. According to Debaeremaeker and Fenton (2003), basisphenoid pits are absent and basioccipital pits are present in *M. megalotis* and *M. minuta*, but in *M. hirsuta* both types of pits are absent. From our examinations we conclude that the structures present in *Micronycteris* are basisphenoid pits. The shallow basisphenoid pits present in QCAZ 7200 contrast with the extremely deep pits typical in *M. megalotis*; in *M. matses* and *M. hirsuta*, the pits are shallower than in QCAZ 7200, almost indistinguishable in some specimens examined of *M. hirsuta*. A septum dividing the basisphenoid pits is present in all forms, but it is highly developed in *M. megalotis*. The anterior opening of the alisphenoid canal is small, ovoid, and with similar dimensions to the posterior opening in QCAZ 7200 and *M. megalotis*; but in *M. hirsuta* and *M. matses* the anterior opening is large, elongated and differing in size from the posterior and anterior openings in QCAZ 7200 and *M. megalotis* (Fig. 4). The extension of the palate over the mesopterygoid fossa in QCAZ 7200 is noticeably shorter than in *M. matses*. The palate is wider in QCAZ 7200 than in *M. matses*.

Dentition of QCAZ 7200 is robust in relation to the size of the skull compared to other dark-bellied species. Inner upper incisors are wider and more robust than those present in *M. matses* and *M. megalotis*, and wider and stronger than the outer incisors and canines. As in other species of the genus, P3 and P4 in QCAZ 7200 have similar dimensions but unlike some specimens of *hirsuta* and *megalotis* they are not separated by
Figure 4. Electron micrographs of the basicranium, showing the palate extension (pe) and differences in the shape and size of the anterior opening of the alisphenoid canal (ac) among *Micronycteris giovanniae* (QCAZ 7200), *M. hirsuta* (TTU 85429), and *M. megalotis* (TTU 85435) from San Lorenzo, Ecuador. Notice that *M. giovanniae* and *M. megalotis* have smaller openings compared to *M. hirsuta* (condition in *matses* is similar to *hirsuta*).

Table 1. Frequencies of the two types of postero-internal projection of P4 in the dark-bellied species of *Micronycteris* included in our comparisons. Type I: reduced; Type II: well developed.

<table>
<thead>
<tr>
<th>Populations</th>
<th>N</th>
<th>Type I</th>
<th>Type II</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. giovanniae</em>: Western Ecuador</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><em>M. matses</em>: Peru</td>
<td>8</td>
<td>0.25</td>
<td>0.75</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Brazil</td>
<td>20</td>
<td>0.05</td>
<td>0.95</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Colombia</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Ecuador</td>
<td>10</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Honduras</td>
<td>7</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Panama</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Peru</td>
<td>5</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Trinidad</td>
<td>7</td>
<td>0.14</td>
<td>0.86</td>
</tr>
<tr>
<td><em>M. megalotis</em>: Venezuela</td>
<td>13</td>
<td>0.08</td>
<td>0.92</td>
</tr>
<tr>
<td><em>M. hirsuta</em>: Western Ecuador</td>
<td>8</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>
a short diastema. The posterior projection of P4 (“lingual heel” according to Simmons et al., 2002) stands out from the lingual side of the upper toothrow in M. matses and M. megalotis, whereas it is highly reduced in QCAZ 7200 and hirsuta (Table 1). Lower dentition in QCAZ 7200 is as robust as that of hirsuta. Lower incisors of QCAZ 7200 are not hypsodont as in hirsuta (Fig. 5), but are wider and longer than those present in matses and megalotis; lower incisors of matses are about 2/3 the size of those in QCAZ 7200. The gap separating the canines posterior-medially in QCAZ 7200 is also present in M. matses and M. megalotis but reduced in M. hirsuta. Compared to M. hirsuta and M. megalotis, the angular process is less developed, in lateral view, in QCAZ 7200.

Descriptive statistics indicate features with no overlap in measurements among dark-bellied forms of Micronycteris from San Lorenzo (Table 2). Specimens of M. megalotis are distinguished by having shorter forearm length, metacarpal III length, greatest length of the skull, condylobasal length, zygomatic width, mastoid width, interorbital width, maxillary toothrow length, and mandibular length. Specimens assignable to M. hirsuta are distinguished mainly by greater forearm length, metacarpal III length, greatest length of the skull, palatal length, post-palatal length, mandibular toothrow length, and coronoid process length. The specimen QCAZ 7200 differs in all measurements from M. megalotis and M. hirsuta, but falls in the size range of M. matses (see Table 2 and Simmons et al., 2002).

Genetic Comparisons. We deposited in GenBank complete sequences of the cytochrome b gene (1,140 base pairs) and intron 7 of the fibrinogen B beta polypeptide (510—529
Due to the morphological differences between the specimen QCaZ 7200 and other dark-bellied forms from San Lorenzo, we focused on determining the genetic identity of QCaZ 7200. Phylogenetic analysis of both nuclear and mitochondrial DNA sequences places QCAZ 7200 in a clade (bootstrap value >75%) along with 3 other dark-bellied forms (M. matses, M. microtis, M. megalotis; Fig. 6). The exact position of QCaZ 7200 within this clade differs between nuclear and mitochondrial data sets. Whereas nuclear data support QCaZ 7200 as sister to matses, mitochondrial data support a basal position for QCAZ 7200, sister to a (M. matses (M. microtis, M. megalotis)) clade. The relationship of QCAZ 7200 to the other dark-bellied forms indicates that M. hirsuta clearly is more distant based on phylogenetic analysis and percent sequence distance (Table 3).

Uncorrected genetic distances between QCAZ 7200 and other dark-bellied species in the genus range from 5.3% to 9.8% in the complete cytochrome-b gene, and from 1.0% to 5.8% in intron 7 of the fibrinogen, B beta polypeptide. In each case, the genetic distances are similar to those for comparisons between other currently recognized species within the genus Micronycteris (Porter et al., unpubl. ms).

### Table 2

Mean (± 1 standard deviation) values for 18 characters measured in four species of *Micronycteris*. Abbreviations: Forearm length (FA), metacarpal III length (Mc3), greatest length of the skull (GLS), condylobasal length (CBL), zygomatic width (ZW), mastoid width (MW), braincase width (BCW), braincase height (BCH), palatal length (PL), post-palatal length (PPL), post-orbital constriction width (PC), interorbital width (IOW), greatest width across molars (GMW), greatest width across canines (GCW), maxillary toothrow length (MxL), mandibular toothrow length (MnL), coronoid process length (CPL), and mandibular length (MDL).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>FA</th>
<th>Mc3</th>
<th>GLS</th>
<th>CBL</th>
<th>ZW</th>
<th>MW</th>
<th>BCW</th>
<th>BCH</th>
<th>PL</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. hirsuta</em></td>
<td>42.19</td>
<td>37.00</td>
<td>23.57</td>
<td>20.96</td>
<td>11.55</td>
<td>10.51</td>
<td>8.69</td>
<td>9.42</td>
<td>10.79</td>
</tr>
<tr>
<td></td>
<td>(1.48)</td>
<td>(1.34)</td>
<td>(0.91)</td>
<td>(1.12)</td>
<td>(0.38)</td>
<td>(0.32)</td>
<td>(0.22)</td>
<td>(0.29)</td>
<td>(0.36)</td>
</tr>
<tr>
<td><em>M. megalotis</em></td>
<td>33.58</td>
<td>29.55</td>
<td>18.01</td>
<td>16.11</td>
<td>8.83</td>
<td>8.24</td>
<td>7.41</td>
<td>7.43</td>
<td>8.02</td>
</tr>
<tr>
<td></td>
<td>(1.60)</td>
<td>(1.34)</td>
<td>(0.56)</td>
<td>(0.56)</td>
<td>(0.38)</td>
<td>(0.32)</td>
<td>(0.24)</td>
<td>(0.24)</td>
<td>(0.36)</td>
</tr>
<tr>
<td><em>M. matses</em></td>
<td>–</td>
<td>–</td>
<td>20.28</td>
<td>18.01</td>
<td>9.98</td>
<td>9.25</td>
<td>8.08</td>
<td>8.10</td>
<td>9.46</td>
</tr>
<tr>
<td></td>
<td>(–)</td>
<td>(–)</td>
<td>(0.30)</td>
<td>(0.35)</td>
<td>(0.13)</td>
<td>(0.16)</td>
<td>(0.13)</td>
<td>(0.10)</td>
<td>(0.36)</td>
</tr>
<tr>
<td><em>M. giovanniae</em></td>
<td>37.03</td>
<td>32.79</td>
<td>20.86</td>
<td>19.02</td>
<td>10.25</td>
<td>9.35</td>
<td>8.18</td>
<td>8.30</td>
<td>9.45</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>PPL</th>
<th>PC</th>
<th>IOW</th>
<th>GMW</th>
<th>GCW</th>
<th>MxL</th>
<th>MnL</th>
<th>CPL</th>
<th>MDL</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. hirsuta</em></td>
<td>7.12</td>
<td>4.81</td>
<td>5.32</td>
<td>7.43</td>
<td>4.24</td>
<td>9.21</td>
<td>10.04</td>
<td>5.92</td>
<td>15.87</td>
</tr>
<tr>
<td></td>
<td>(0.42)</td>
<td>(0.12)</td>
<td>(0.19)</td>
<td>(0.28)</td>
<td>(0.19)</td>
<td>(0.42)</td>
<td>(0.39)</td>
<td>(0.26)</td>
<td>(0.66)</td>
</tr>
<tr>
<td><em>M. megalotis</em></td>
<td>5.59</td>
<td>3.93</td>
<td>4.47</td>
<td>5.90</td>
<td>3.18</td>
<td>6.87</td>
<td>7.43</td>
<td>3.91</td>
<td>11.83</td>
</tr>
<tr>
<td></td>
<td>(0.23)</td>
<td>(0.16)</td>
<td>(0.27)</td>
<td>(0.24)</td>
<td>(0.15)</td>
<td>(0.25)</td>
<td>(0.30)</td>
<td>(0.22)</td>
<td>(0.45)</td>
</tr>
<tr>
<td><em>M. matses</em></td>
<td>6.01</td>
<td>4.45</td>
<td>4.97</td>
<td>6.68</td>
<td>3.62</td>
<td>7.90</td>
<td>8.38</td>
<td>4.65</td>
<td>13.52</td>
</tr>
<tr>
<td></td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.19)</td>
<td>(0.20)</td>
<td>(0.10)</td>
<td>(0.13)</td>
<td>(0.20)</td>
<td>(0.14)</td>
<td>(0.14)</td>
</tr>
<tr>
<td><em>M. giovanniae</em></td>
<td>6.76</td>
<td>4.72</td>
<td>5.19</td>
<td>6.77</td>
<td>4.00</td>
<td>8.28</td>
<td>8.86</td>
<td>4.89</td>
<td>14.29</td>
</tr>
</tbody>
</table>
Karyological Comparisons: Individuals identified as *M. hirsuta* have a diploid number (2N) of 26 and a fundamental number (FN) of 30 (Fig. 7). This karyotype is similar but not identical to those described for this species by Baker et al. (1973). Two karyotypes have been described for *M. hirsuta* (Baker et al., 1973). For specimens from Trinidad, 2N is 30 and FN is 32, and for specimens from Honduras and Nicaragua, 2N is 28 and FN is 32. The remainder of the specimens from northwestern Ecuador have a karyotype with a 2N=40 and a FN=68 (Fig. 8). This karyotype is like that described by Baker (1967) for *M. megalotis*. The specimen QCAZ 7200 also has this *M. megalotis*-type karyotype (Fig. 9).

**DISCUSSION**

Morphological, karyotypical, and molecular comparisons permit the distinction of 3 taxa among specimens of *Micronycteris* from San Lorenzo, northwestern Ecuador. The specimens smallest in size represent the species *megalotis*, which is widely distributed throughout South America and present on both sides of the Andes in Ecuador (Albuja, 1999; Tirira, 1999). They are distinguishable from other dark-bellied species included in our comparisons mainly by their small size, the presence of fur on the inner border of the ears longer than 5 mm (character that distinguishes these specimens from *M. microtis* according to Simmons, 1996), and the shape of the basioccipital. Specimens of *M. hirsuta* are also distinguishable from other forms of *Micronycteris* from San Lorenzo mainly by their larger size and by the hypsodont dentition. In the case of both taxa, further analyses concerning intraspecific variation at both morphological and molecular levels are warranted. Karyotypic data distinguish *M. megalotis* (2N=40; FN=68) from *M. hirsuta* (2N=26; FN=30). Each of these karyotypes is unique among bats. The karyotype of QCAZ 7200 is indistinguishable from that described for *M. megalotis* (Baker, 1967), and unfortunately *M. matses* and *M. microtis* have not been karyotyped.

We found one dark-bellied specimen of *Micronycteris* (QCAZ 7200) to be unique, differing morphologically from all other dark-bellied members of the genus. Data from mitochondrial cytochrome-*b* gene and nuclear intron sequences indicate that this specimen is related closely to *M. matses*, *M. megalotis*, and *M. microtis*, and most similar to *M. matses*; however, several cranio-dental characters distinguish this specimen from any dark-bellied species currently recognized. Based on morphological data, this specimen is unique within *Micronycteris* and should be recognized as a distinct species; molecular data are compatible with this interpretation of the morphological evidence.

There are 3 synonyms available within the species *M. megalotis* (Alonso-Mejia and Medellin, 1991; Simmons, 1996): *M. elongata* (Gray, 1842), *M. pygmaeus* (Rehn, 1904), and *M. scrobiculatum* (Wagner, 1855). Based on original descriptions, the distribution of the type localities, taxonomic comments of Simmons (1996:4), and measurements of the holotypes of *M. elongata* and *M. scrobiculatum* provided by Carter and Dolan (1978), we conclude that none of these names are applicable to QCAZ 7200 from northwestern Ecuador. No synonym is available for *M. matses* (sensu Simmons et al., 2002). The section below introduces a new species name and provides a description of this taxon.
Table 3. Uncorrected (“p”) distances for all pairwise comparisons of DNA sequences of intron 7 of the beta-fibrinogen gene (below diagonal) and the complete mitochondrial cytochrome-b gene (above diagonal).

<table>
<thead>
<tr>
<th></th>
<th>giovanniae (TK104673)</th>
<th>broseti (KU155163)</th>
<th>hirsuta (TK104680)</th>
<th>hirsuta (TK104677)</th>
<th>homezi (TK86643)</th>
<th>matses (TK82756)</th>
<th>megalotis (TK104663)</th>
<th>megalotis (TK20558)</th>
<th>megalotis (TK16372)</th>
<th>microtis (TK16377)</th>
<th>minutia (TK16371)</th>
<th>schmidtorum (TK40447)</th>
<th>Lampronycteris (TK25239)</th>
<th>Trachops (TK18829)</th>
</tr>
</thead>
<tbody>
<tr>
<td>giovanniae (TK104673)</td>
<td>9.56 10.09 10.09 9.30 14.30 5.26 5.93 5.56 5.38 6.67 13.51 13.07 17.54 19.21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>broseti (KU155163)</td>
<td>4.01 11.32 11.32 11.40 15.00 9.39 9.56 8.95 10.18 13.33 13.77 16.75 19.21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hirsuta (TK104680)</td>
<td>5.61 2.53 0.35 2.02 15.53 10.00 9.91 10.26 10.53 11.14 13.86 14.12 17.54 18.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hirsuta (TK104677)</td>
<td>5.93 5.56 0.97 2.02 15.35 9.82 9.74 10.09 10.53 11.14 13.86 14.12 17.54 18.68</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>homezi (TK86643)</td>
<td>5.96 5.58 0.38 1.35 15.53 10.09 10.18 10.70 10.44 11.40 14.04 14.30 16.75 18.77</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>megalotis (TK104663)</td>
<td>0.95 4.20 5.79 6.11 6.14 4.38 4.47 4.04 4.39 5.18 13.77 12.89 16.49 18.86</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>megalotis (TK104663)</td>
<td>1.71 3.44 5.22 5.54 5.57 3.81 1.90 2.19 4.21 5.26 13.42 13.36 17.28 18.16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3 (continued).

<table>
<thead>
<tr>
<th>Species</th>
<th>1.71</th>
<th>3.25</th>
<th>5.03</th>
<th>5.35</th>
<th>5.38</th>
<th>3.62</th>
<th>1.90</th>
<th>0.38</th>
<th>3.60</th>
<th>5.00</th>
<th>14.04</th>
<th>13.42</th>
<th>17.54</th>
<th>19.04</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Micronycteris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>megalotis</em> (TK20558)</td>
<td>1.91</td>
<td>3.44</td>
<td>4.85</td>
<td>5.17</td>
<td>5.20</td>
<td>3.43</td>
<td>2.09</td>
<td>0.57</td>
<td>0.19</td>
<td>5.09</td>
<td>13.95</td>
<td>12.89</td>
<td>17.11</td>
<td>18.42</td>
</tr>
<tr>
<td><em>megalotis</em> (TK16372)</td>
<td>2.48</td>
<td>4.20</td>
<td>5.99</td>
<td>6.30</td>
<td>6.34</td>
<td>4.57</td>
<td>2.66</td>
<td>1.90</td>
<td>2.10</td>
<td>14.65</td>
<td>13.16</td>
<td>17.72</td>
<td>18.07</td>
<td></td>
</tr>
<tr>
<td><em>microtis</em> (TK16377)</td>
<td>4.40</td>
<td>4.61</td>
<td>4.66</td>
<td>4.98</td>
<td>5.01</td>
<td>0.19</td>
<td>4.58</td>
<td>4.01</td>
<td>3.82</td>
<td>3.63</td>
<td>4.58</td>
<td>5.79</td>
<td>18.68</td>
<td>19.39</td>
</tr>
<tr>
<td><em>minuta</em> (TK16371)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>schmidtorum</em> (TK40447)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lampronycteris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(TK25239)</td>
<td>8.57</td>
<td>9.81</td>
<td>10.11</td>
<td>10.57</td>
<td>10.44</td>
<td>9.33</td>
<td>8.96</td>
<td>8.94</td>
<td>8.74</td>
<td>9.73</td>
<td>9.56</td>
<td>--</td>
<td>20.96</td>
<td></td>
</tr>
<tr>
<td><em>Trachops</em> (TK18829)</td>
<td>10.18</td>
<td>11.17</td>
<td>10.72</td>
<td>11.95</td>
<td>11.06</td>
<td>10.55</td>
<td>10.36</td>
<td>10.54</td>
<td>10.35</td>
<td>10.36</td>
<td>11.31</td>
<td>10.77</td>
<td>--</td>
<td>9.15</td>
</tr>
</tbody>
</table>
Figure 7. Karyotype prepared from a male *Micronycteris hirsuta* (TK 104677) collected from ECUADOR: Esmeraldas: E. San Lorenzo (toward Lita), Finca San José.

Figure 8. Karyotype prepared from a male *Micronycteris megalotis* (TK 104663) collected from ECUADOR: Esmeraldas: San Lorenzo, Estación Científica la Chiquita.
Holotype. QCAZ 7200, adult male, skin, skull, and skeleton deposited in the Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador. Originally catalogued with the number TTU 85445 for the processing of the Sowell Expedition 2001. Collected on 6 August 2001 from ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (01° 3' 32.1" N, 78° 37' 20.7" W) by a TTU and QCAZ field party on the Sowell Expedition, 2001. The number TK 104673 identifies tissue samples housed in the Natural Science Research Laboratory (NSRL) at Texas Tech University and in the Museo de Zoología (QCAZ), as well as karyotype preparations housed in the Department of Biological Sciences, Texas Tech University.

The holotype was prepared as skin, skull, and postcranial skeleton by Jana L. Higginbotham (original number JLH-279). Standard measurements (in millimeters) of the holotype are: total length – 71; tail length – 16; hind foot – 11; ear – 21; weight – 8.6 grams. Wing and hand limb measurements of the dried specimen are: forearm length – 37; metacarpal III length – 46.7; first phalanx of third digit – 15.3; second phalanx of third digit – 16.1; first phalanx of fourth digit – 12.7; thumb length – 5.9; tibia length – 16.4; calcare length – 13.1. Cranial measurements (in mm) of the holotype are as follows: greatest length of the skull – 20.9; condylobasal length – 19.0; zygomatic width
Mastoid width – 10.3; braincase width – 9.4; braincase depth – 8.2; palatal length – 9.5; post-palatal length – 6.8; width of post-orbital constriction – 4.7; interorbital width – 5.2; greatest width across molars – 6.8; greatest width across canines – 4.0; maxillary tooththrow length – 8.3; mandibular tooththrow length – 8.9; coronoid process length – 5.0; mandibular length – 14.3. The holotype had testes 6 x 5 mm.

Etymology. This species is named to honor Nikki Giovanni in recognition of her poetry and writings.

Distribution. Known only by the type specimen from the type locality (Fig.1). ECUADOR: Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (01° 3’ 32.1” N, 78° 37’ 20.7” W).

Diagnosis. Morphologically, M. giovanniae warrants taxonomic comparisons only with other dark-bellied species within the genus. Genetic distances indicating that M. matses may be the sister taxon to M. giovanniae and therefore special attention is paid to comparisons of these 2 species. The distribution of M. giovanniae (restricted to the type locality) and M. matses (known only from the type locality; Simmons, 2005) are geographically distant from each other and separated by the Andes; nonetheless both species are externally similar, further justifying close comparison of these 2 taxa. M. megalotis and M. microtis differ from M. giovanniae by having thinner, longer fur on the inner border of ears (only in M. megalotis), deeper basisphenoid pits, a globular ending of the skull in the interparietal region, and a well developed posterior projection of the P4 on the lingual side. M. hirsuta differs from M. giovanniae by having a hairy base of the thumb, a stronger and well developed zygomatic arch, more developed sagittal and lambdoidal crests and mastoid processes, a sharp ending of the skull in the interparietal region, a narrower basioccipital bone, a larger and elongated anterior opening of the alisphenoid canal, hypsodont lower incisors, and a reduced posterior-medial gap separating the lower canines. M. matses differs from M. giovanniae by having a shorter rostrum, a weaker and poorly developed zygomatic arch, a narrower basioccipital bone, a larger and elongated anterior opening of the alisphenoid canal, a longer palate extension, a narrower palate, weaker canines, a well developed posterior projection of P4 on the lingual side, and shorter lower incisors. Also, M. giovanniae can be distinguished from other dark-bellied species by a combination of external and cranial variables (Table 2).

Genetically, M. giovanniae can be distinguished from other species in the genus by variation in the cytochrome-\(b\) gene and in the Fgb-I7 (Fig. 6). Application of the Genetic Species Concept (Dobzhansky, 1950) requires identification of the species related most closely to the taxon being described (= sister taxon; Bradley and Baker, 2001). M. giovanniae is sister to a complex of 3 dark-bellied species (M. matses, M. megalotis, and M. microtis) in the cytochrome-\(b\) tree, whereas it is sister to M. matses in the Fgb-I7 tree. Therefore, to apply the Genetic Species Concept, comparisons among M. giovanniae to M. megalotis, M. microtis, and M. matses are warranted. Uncorrected distances in the cytochrome-\(b\) gene distinguishing M. giovanniae from these species are > 9% for M. hirsuta, > 5% for M. megalotis, > 6% for M. microtis, and > 5% for M. matses. In all comparisons, genetic distance values are more typical of interspecific rather than intraspecific variation (Bradley and Baker, 2001). These 4 taxa are also distinguished by the sequence variation in the Fgb-I7 (Fig. 6; Table 3). Whereas there are few sequences
available for Fgb-I7 to facilitate meaningful comparisons (as with cytochrome-b data), the distances between *M. giovanniae* and other taxa in the *M. megalotis* complex are similar to those values distinguishing other *Micronycteris* species (recognized on a morphological basis; Table 3). We interpret these data as support for recognizing *M. giovanniae* as a specific level taxon rather than a sub-specific level taxon. According to percent sequence distance (but not necessarily phylogenetic analysis), *M. giovanniae* and *M. matses* are most similar in both mitochondrial and nuclear datasets.

Karyotypic data for the genus *Micronycteris* (sensu lato) were reviewed by Baker (1979). Most species of *Micronycteris* have a unique karyotype. However, karyotypic data are missing for *Glyphonycteris sylvestris*, *M. matses*, *M. microtis*, *M. sanborni*, and *Neonycteris pusilla*. The karyotype of *M. giovanniae* (2N=40, FN=68; Fig. 9) is easily distinguished from *M. hirsuta* (2N=26, FN=30, Fig. 6). The karyotype for *M. giovanniae* (Fig. 9) appears to be indistinguishable from *M. megalotis* (Fig. 8) and this unique derived karyotype [assuming *Macrotis waterhousii* has the primitive karyotype for the Phyllostomidae (Baker, 1979; Baker et al., 2003a)] places *M. giovanniae* in the *M. megalotis* complex. This conclusion is compatible with the relationships implied in the two trees generated from DNA sequence data (Fig. 6).

**Description.** *Micronycteris giovanniae* is a medium-sized dark-bellied species, Mummy Brown dorsally, Buffy Brown ventrally, and Blackish Brown on wings and membranes except on ears, which also are Mummy Brown (capitalized color names from Ridgway, 1912). Fur is uniformly colored throughout dorsum, including areas between the ears and the forehead. Dorsal fur is pale basally, but not forming a distinguishable white band. This pale region is reduced on the upper back and behind the ears, covering 1/5 of the fur length, whereas it is lighter on the shoulders and extends over 2/5 of the fur length. Fur coloration tends to be uniform in the lower dorsal region; no basal pale band is present. Dorsal fur is long, exceeding 7 mm. Fur on rostrum and areas between ears tends to be shorter, but also exceeding 5 mm. Hair behind the ears and on the inner border of ears is extremely short (<5 mm), extending no more than the half of ear length. A band with an evident notch connects the ears, but the skin preparation of the holotype does not allow determining if this is deep or shallow. Hair on rostrum is variable in length, with short fur (<5 mm) covering the forehead, areas between and below the eyes, and areas below the ears. Ventral fur is also short (<6 mm). Dorsal and ventral pelage does not extend over the uropatagium; wings and other membranes are also naked, as well as the forearm and the thumb. Wing formula is the same as that described for the genus (Simmons, 1996; Simmons et al., 2000).

Skull is medium-sized and robust (Fig. 10). Rostrum is elongated; premaxillae are short and wide; maxillae are large and highly inflated, especially over the region between the premolars and the first molar in the upper toothrow, giving a slight appearance of a globular rostrum. Incisive foramina are wide and considerably elongated. A small foramen anterior to the incisive foramina is also present. Infranarial foramen is wide and deep. Maxillae join the frontal in the middle of the orbital. A moderately elevated sagittal crest arises from this point and has a constant height along the skull. Lambdoidal crest is present, and is obvious from lateral and posterior views. Interparietals are not projected backward. Mastoid process is slender and elongated, and slightly protrudes from the skull in superior view. Mastoid width is less than zygomatic width. Zygomatic arch is robust, with the fusion between the jugal and the squamosal highly developed upward. Paraoccipital processes are poorly developed and do not exceed the occipital
condyles. Foramen magnum is wide and ovoid. Shallow basisphenoid pits are present, separated medially by a poorly developed septum. Basioccipital bone is fairly wide. Basicochlear fissure is narrow and elongate. Anterior and posterior openings of the alisphenoid canal are small and ovoid. Palate is wide and convex. Postpalatal extension is short and narrow over the mesopterygoid fossa. Dental formula (i 2/2, c 1/1, p 2/3, m 3/3) is typical of the genus (see Simmons et al., 2002). Inner upper incisors are large, robust, and protruding from the skull in superior view. Outer upper incisors are smaller and convergent, not completely filling the space between the inner incisor and the canines. Canines are large, with the cingula well developed. P3 and P4 have the same dimensions, not separated by a diastema. Posterior projection of P4 on the lingual side is reduced. M1 and M2 are of unequal size. M2 and M3 are not separated by a gap. Lower incisors are small, robust, bilobated, and not hypsodont. A wide gap separates the canines posterior-medially. Mandibular ramus is thin and straight. Coronoid process is projected forward. Coronoid fossa is deep and hollow. Angular process appears poorly developed in lateral view and does not extend beyond the

Figure 10. Dorsal, ventral, and lateral views of the skull and lower jaw of the holotype (QCAZ 7200) of Micronycteris giovanniae. Bar represents 10 mm. Drawing by Michael W. Nickell.
mandibular condyle. 

Ecological Notes. Finca San José is a private property consisting of secondary-growth forest that, at the time of collecting the holotype, was being deforested. As other areas surrounding San Lorenzo town, the vegetation is typical from the southern border of the Chocó region. Gentry (1986) and Baker et al. (2004) provide information and references on the plant community structure in the area. The holotype was collected in a mist net stretched under a narrow bridge above an active stream. Among the species collected at Finca San José are Artibeus planirostris, Carollia castanea, Lonchophylla mordax, Micronycteris hirsuta, Platyrrhinus dorsalis, Platyrrhinus cf. helleri, Rhinophylla alethina, and Sturnira lilium. Other than the testes size (6 x 5 mm), no information on reproduction is available for the holotype.

ACKNOWLEDGMENTS

We thank Mr. James Sowell for funding the Sowell Expedition 2001 to Ecuador that resulted in our discovery of this new species. We thank Laura Arcos Terán and Luis Coloma (Escuela de Ciencias Biológicas of the Pontificia Universidad Católica del Ecuador) and Xavier Viteri (Fundación Natura) for the institutional support during the expedition. The Ministerio del Ambiente in Ecuador kindly provided permits for collecting the specimens. Sergio Solari provided invaluable assistance with issues resulting from René Fonseca’s untimely death as well as providing editorial support. Other members of the field party to northwest Ecuador were Carl Phillips, Jana Higginbotham, and Lynda Richardson. Members of the field party to Puyo were Clyde Jones, Joel Brandt, Trashanda Johnson, Michelle Haynie, Rex McAliley, and Marcy Revelez. We extend our appreciation to the curators and curatorial staff who allowed us to examine specimens and tissues under their care: Mariko Kageyama, Richard Monk, Nancy Simmons, and S. Jean Spence (American Museum of Natural History, New York); Santiago Burneo (Museo de Zoología of the Pontificia Universidad Católica del Ecuador, Pontificia Universidad Católica del Ecuador, Quito); Linda Gordon and Don Wilson (National Museum of Natural History, Washington, D.C.); Duane Schlitter (Texas Cooperative Wildlife Collection, Texas A&M University, College Station); Cheryl Parmenter and Terry Yates (Museum of Southwestern Biology, University of New Mexico, Albuquerque); Robert Timm and Thor Holmes (Museum of Natural History, University of Kansas, Lawrence); and Heath Garner (Natural Science Research Laboratory, Museum of Texas Tech University, Lubbock). Vicky Swier assisted in preparing karyotypes. Mark Grimson (Department of Biological Sciences, Texas Tech University) assisted with photography and electron microscopy. Robert P. Anderson kindly provided facilities to René Fonseca during his visit to the AMNH. Michael Nickell made the drawing for Figure 10. Enrique Lessa (Universidad de la República, Uruguay) and an anonymous reviewer provided helpful suggestions to a previous draft.

APPENDIX 1: SPECIMENS EXAMINED

List of specimens examined with respective museum catalog numbers and localities. Voucher specimens are housed in a mammal collection at the American Museum of
Micronycteris giovanniae (1): ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3’ 32.1” N, 78° 37’ 20.7” W), QCAZ 7200 (holotype; previously catalogued as TTU 85445).


APPENDIX 2: TISSUES EXAMINED

List of tissues examined with respective tissue numbers and localities. Acronyms for tissue numbers are: KU, University of Kansas, Museum of Natural History; NK, Museum of Southwestern Biology, University of New Mexico; TK, Museum of Texas Tech University, Natural Science Research Laboratory. Acronyms for museums where voucher specimens are housed are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Peru; QCAZ, Museo de Zoología of the Pontificia Universidad Católica del Ecuador; MSB, Museum of Southwestern Biology, University of New Mexico; TTU, Museum of Texas Tech University, Natural Science Research Laboratory, and ROM, Royal Ontario Museum. With 1 exception, 4 numbers are given for each specimen. In order, they are tissue number, museum voucher number, cytochrome-b GenBank accession number, and beta fibrinogen GenBank accession number (the latter 2 numbers in parentheses). The exception is Micronycteris schmidtorum, for which the cytochrome-b sequence is from one specimen (TK 70447) and the beta fibrinogen sequence from another (TK 82837).


Micronycteris brosseti: GUYANA — Potaro-Siparuni: Inokrame Reserve, KU 155163, KU 155163 (AY380771, DQ077455).

Micronycteris giovanniae: ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3’ 32.1” N, 78° 37’ 20.7” W), TK 104673, QCAZ 7200 (AY380750, DQ077456).

Micronycteris hirsuta: ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3’ 32.1” N, 78° 37’ 20.7” W), TK 104677, TTU 85449 (DQ077410, DQ077448), TK 104680, TTU 85452 (DQ077412, DQ077449). PANAMA — Veraguas, Montijo; Corregimiento de Arenas, Portobelo, NK 101615, MSB 94372 (AY380769, DQ077445).

Micronycteris homezi: GUYANA — East Berbice: Dubulay Ranch (5° 40’ 91” N, 57° 51’ 52” W), TK 86643, USNM 582262 (AY380754, DQ077441).


Micronycteris microtis: BRAZIL — Sao Paulo: Caetetus Ecological Station (222300 S, 049400 W), TK 16377, ROM 111099 (AY380755, DQ077463).

Micronycteris minuta: ECUADOR — Orellana: 30 km S Pompeya Sur, Parque Nacional Yasuni, TK 16371, ROM 104067 (AY380752, DQ077438).


Trachops cirrhosus: FRENCH GUIANA — Paracou, TK 18829, AMNH 267129 (DQ233669, DQ233670).

LITERATURE CITED

Albuja, L.

Alonso-Mejía, A., and R. A. Medellín

Baker, R. J.


Baker, R. J., H. H. Genoways, W. J. Bleier, and J. W. Warner

Baker, R. J., M. Hamilton, and D. E. Parish
Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche  
2003a Diversification among New World leaf-nosed bats: An evolutionary  
hypothesis and classification inferred from digenomic congruence of  
DNA sequence. Occasional Papers, Museum of Texas Tech University  
230: i+1–32.

Baker, R. J., C. A. Porter, J. C. Patton, and R. A. Van Den Bussche  
2000 Systematics of bats of the family Phyllostomidae based on RAG2 DNA  
sequences. Occasional Papers, Museum of Texas Tech University 202: i  
+1–16.

Bradley, R. D., and R. J. Baker  
2001 A test of the Genetic Species Concept: Cytochrome-b sequences and  

Carter, D. C., and P. G. Dolan  
1978 Catalogue of type specimens of Neotropical bats in selected European  
museums. Special Publications, The Museum, Texas Tech University  
15:1–136.

Cerón, R., W. Palacios, R. Valencia, and R. Sierra  
1999 Las formaciones naturales de la Costa del Ecuador. Pp. 55–78 in  
Propuesta Preliminar de un Sistema de Clasificación para el Ecuador  
Continental (Sierra, R., ed.). Proyecto INEFAN/GEF-BIRF y EcoCiencia,  
Quito, Ecuador. vi + 196 pp.

Debaeremaeker, K. R., and M. B. Fenton  
2003 Basisphenoid and basioccipital pits in microchiropteran bats. Biological  

Dobzhansky, T.  
1950 Mendelian populations and their evolution. American Naturalist  
74:312–321.

Dodson, C. H., and A. H. Gentry  
1991 Biological extinction in western Ecuador. Annals of the Missouri  

Felsenstein, J.  
1985 Confidence limits on phylogenies: an approach using the bootstrap.  

Gentry, A. H.  
1986 Species richness and floristic composition of Chocó region plant  
Gray, J. E.

Hillis, D. M., and J. P. Huelsenbeck

Hoffmann, F. G., and R. J. Baker
2001 Systematics of bats of the genus Glossophaga (Chiroptera: Phyllostomidae) and phylogeography in G. soricina based on the cytochrome-

Koopman, K. F.

Longmire, J. L., M. Maltbie, and R. J. Baker

Maddison, W. P., and D. R. Maddison

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B da Fonseca, and J. Kent

Oxford Molecular Group PLC


Rehn, J. A. G.

Ridgway, R.
Sanborn, C. C.  

Simmons, N. B.  

Simmons, N. B., and R. S. Voss  

Simmons, N. B., R. S. Voss, and D. W. Fleck  

Swofford, D. L.  

Tamura, K., and M. Nei  

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins  

Tirira, D.  

Wagner, J. A.  
Wetterer, A. L, M. V. Rockman, and N. B. Simmons

Wickliffe, J. K., F. G. Hoffmann, D. S. Carroll, Y. V. Dunina-Barkovskaya, R. D. Bradley, and R. J. Baker