A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Bolivia

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Although significant work has been done to define species relationships within the Neotropical genus *Micronycteris*, the group has yet to be fully resolved. In Bolivia *Micronycteris* is represented by 4 species: *M. hirsuta*, *M. megalotis*, *M. minuta*, and *M. sanborni*. Through examination of morphological characters and analyses of cranial measurements and genetic data, we determine that *M. sanborni* is not found in Bolivia and describe a new species closely related to it. The new species is morphometrically distinct from its congeners, forming a cluster separate from *M. schmidtorum*, *M. minuta*, and *M. brosseti* along principal component (PC) 1 (explaining 57.3% of the variation and correlated with maxillary toothrow length) and also separate from *M. sanborni* along PC 2 (explaining 35.4% of the variation and correlated with condylobasal length). The new species forms a statistically supported clade in all phylogenetic analyses; however, a sister relationship to *M. sanborni* is not supported. Genetic distance values that separate *Micronycteris* sp. nov. from its closest relatives range from 5.3% (versus *M. sanborni*) to 10.4% (versus *M. minuta* from Guyana). We diagnose and describe the new species in detail and name it in honor of the late Terry Lamon Yates for his contributions to Bolivian mammalogy. *Micronycteris* sp. nov. is Bolivia's 1st endemic bat species and because of its importance, the conservation implications are discussed.

Key words: Cerrado, cytochrome-*b* gene, Inter-Andean Dry Forest, *Micronycteris sanborni*, principal component analysis, Terry Yates, Yungas

The genus *Micronycteris* Gray, 1866 (sensu stricto), currently comprises at least 10 species that are distributed across distinct habitat types in the Neotropical region (Fonseca et al. 2007; Williams and Genoways 2007; Larsen et al. 2011). Significant work has taken place in the past 16 years to help better define species limits within this group (e.g., Simmons 1996; Simmons et al. 2002; Tavares and Taddei 2003; Fonseca et al. 2007; Porter et al. 2007; Williams and Genoways 2007; Larsen et al. 2011). Despite the extensive research effort, the genus is not yet resolved; examination of molecular data shows evidence of paraphyletic relationships within several species and the genus probably contains a number of undescribed species (Porter et al. 2007; Larsen et al. 2011).

In Bolivia the genus *Micronycteris* is represented by 4 species: *M. hirsuta*, *M. megalotis*, *M. minuta*, and *M. sanborni* (Williams and Genoways 2007). Although *M. schmidtorum* is

noted as a Bolivian species (Aguirre and Terán 2007; Aguirre et al. 2010a; Terán 2010), no voucher specimen supporting this information is cited. Williams and Genoways (2007) indicate the range of *M. schmidtorum* to be from southern Mexico to eastern Brazil, noting that specimens from Peru were reidentified as *M. brosseti*. Given the current distribution of the species and the difficulty of its identification, we follow the proposed distribution of Williams and Genoways (2007) until more information on Bolivian specimens is presented. Emmons (1998) reported a specimen of *M. microtis* from Parque Nacional Noel Kempff Mercado (Department Santa Cruz), which is presented as a valid record in Aguirre et al. (2010a). Considering the known distribution of the species and the difficulty in discriminating this species from *M. megalotis*, we follow the assessment of Williams and Genoways (2007), which treats this specimen as a misidentified *M. megalotis*.

The presence of *M. sanborni* in Bolivia is based upon previous designations of 2 voucher specimens: voucher CBF 6154 collected in 1999 and deposited at the Colección Boliviana de Fauna in La Paz, Bolivia (Brooks et al. 2002; Salazar-Bravo et al. 2003; Simmons 2005) and voucher MHNC-M 141 collected in 2005 and deposited at the Museo de Historia Natural Alcide d'Orbigny in Cochabamba, Bolivia (museum records, in litt.). Aguirre and Terán (2007) presented this latter specimen as a 2nd record of *M. sanborni* for Bolivia but no information on the voucher was included.

Upon closer examination of the morphological characters and analyses of cranial measurements and genetic data of the 2 specimens previously identified as *M. sanborni*, we determine these represent an undescribed species. Based on available voucher specimens we conclude that *M. sanborni* is not found in Bolivia and we describe a previously unknown species of *Micronycteris*.

MATERIALS AND METHODS

Background and study regions.—In mid-April 1999 we undertook a mammalian expedition to eastern Bolivia (Brooks et al. 2002). On the evening of 17 April 1999 a single mist net was erected in drizzling weather in the middle of a small patch of savanna surrounded by patches of forest at Estancia Patuju (Fig. 1; 17°37′04.9″S, 59°32′9.5″W; 220 m). A single bat (voucher CBF 6154) was netted—a specimen of the genus *Micronycteris* that could not be assigned to any known species previously reported for the region (e.g., Anderson 1997). The regional landscape was Cerrado, a semideciduous savanna composed of a mosaic of open grassland and dry forest (Redford and da Fonseca 1986) found predominantly in central Brazil (Ratter et al. 1997). Cerrado is typified by low cover composed of grasses and small shrubs, and tree species that are at low densities and often have adaptations to water stress such as twisted trunks, deep roots, and hard, leathery leaves (Redford and da Fonseca 1986; Ibisch et al. 2002).

The specimen was caught in 1 of the 4 subecoregions of Bolivian Cerrado known as Cerrado Chiquitano, which is found in central and eastern Santa Cruz Department and is a
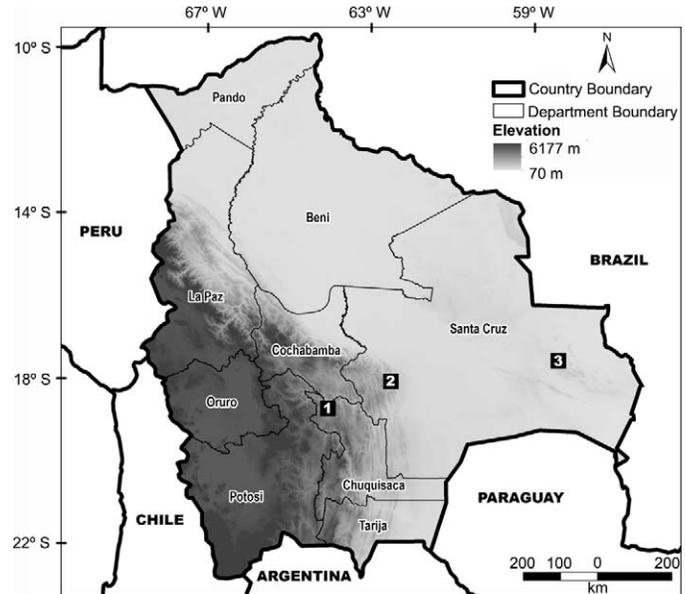

FIG. 1.—Map of collecting localities of specimens of *Micronycteris* sp. nov. in Bolivia. 1) Zurima, 33 km northeast of Sucre (MHNC-M 157—Holotype). 2) Refugio Los Volcanes (MHNC-M 141). 3) Estancia Patuju, 370 km east of Santa Cruz de la Sierra (CBF 6154).

continuation of the Brazilian Cerrado (Ibisch et al. 2003). Cerrado Chiquitano is 23,500 km^2 in size, ranges from 120 to 1,000 m above sea level, has an average annual temperature range of 21–27°C, and has a landscape dominated by plains and inselbergs with open and wooded savanna and fire-resistant forests that are short in height (Ibisch et al. 2003).

Once the specimen (CBF 6154) was determined to be something potentially unique, we put the call out to other chiropterologists working in Bolivia to be on the lookout for this *Micronycteris*, yet none were found. Then we caught what was then unbeknownst to be an additional specimen on 14 November 2005 (voucher MHNC-M 141) in a private reserve called Refugio Los Volcanes (Fig. 1; 18°06′42.5″S, 63°36′07.8″W; 1,060 m). This reserve is approximately 300 ha in size and adjacent to the southern border of Amboró National Park, directly on the transition from the humid inner tropics to the seasonally dry subtropics (Linares-Palomino et al. 2008). Although the site is located in the Yungas ecoregion, Los Volcanes is adjacent to the Tucuman–Bolivian Forest and Chaco Serrano ecoregions (Ibisch et al. 2003). The substrate in this area consists primarily of red sandstone that forms cliffs several hundred meters high that are intersected by narrow valleys (Linares-Palomino et al. 2008). Annual precipitation is approximately 120–150 cm with most of the rainfall from October–November through March–April, with high temporal variability (Linares-Palomino et al. 2008).

A 3rd specimen was collected on 18 February 2007 (voucher MHNC-M 157) from a house in the small town of Zurima (Fig. 1; 18°46′40.2″S, 65°07′40.3″W; 1,800 m). Zurima is located on the main road between the cities of Cochabamba and Sucre. The area is located in Inter-Andean Dry Forest, an ecoregion of 44,805 km^2 with an altitudinal range of 500–3,300 m above sea

level, an average annual temperature range of 12–16°C, and a landscape dominated by moderately dissected valleys and small plains with largely disturbed or destroyed deciduous dry forest ranging 10–20 m in height (Ibisch et al. 2003). All specimens collected for this study were captured in accordance with animal welfare guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Specimens examined.—The 3 specimens of the new species of *Micronycteris* were deposited in Bolivian natural history collections: Colección Boliviana de Fauna (CBF) in La Paz and Museo de Historia Natural Alcide d'Orbigny (MHNC) in Cochabamba. For comparison, 84 specimens of 10 species of *Micronycteris* were used for phylogenetic and morphometric analyses. Specimens examined (see Supporting Information S1, DOI: 10.1644/12-MAMM-A-259.S1) were deposited in the following natural history collections: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), Colección Boliviana de Fauna (CBF), Museo de Historia Natural Alcide d'Orbigny (MHNC), Museum of Southwestern Biology (MSB—catalog number, NK—tissue number), Museum of Texas Tech University (TTU—voucher number, TK—tissue number), Pontificia Universidad Católica del Ecuador (QCAZ), Royal Ontario Museum (ROM), and United States National Museum of Natural History (NMNH).

Morphological methods.—Morphological characters and measurements were used to describe the new taxon and make comparisons with other *Micronycteris* specimens. Morphological terminology was based on Lira et al. (1994), Czaplewski and Morgan (2003), and Giannini et al. (2006). Measurements of study skins were taken with digital calipers to the nearest 0.01 mm following Lira et al. (1994) and Simmons and Voss (1998). Measurements of only adult specimens were taken by 1 person to ensure consistency. External measurements included total body length (TL), tail length (Tail), length of hind foot (HF), ear length (Ear), forearm length (FA), 3rd metacarpal length (Mc3), 4th metacarpal length (Mc4), thumb length (Thu), tibia length (Tib), calcar length (Cal), and dorsal hair length (DHL) at the shoulder region. Cranial measurements included greatest skull length (GSL), condylobasal length (CBL), zygomatic breadth (ZB), postorbital constriction width (POC), braincase breadth (BB), mastoid breadth (MB), maxillary toothrow length (MTL), greatest breadth across upper molars (BAM), and braincase height (BH).

Cranial measurements also were taken from other species of pale-bellied *Micronycteris* (sensu Simmons et al. [2002]—*M. brosseti*, *M. minuta* [includes *M. homezi*—Ochoa and Sánchez 2005], *M. sanborni*, and *M. schmidtorum*) that were available (see Supporting Information S1, DOI: 10.1644/12-MAMM-A-259.S1). Measurements of *M. brosseti* presented by Simmons and Voss (1998) and of a marginal record of *M. sanborni* from western Brazil presented by Ferreira Santos et al. (2010) also were used to make comparisons. Measurements presented in Simmons and Voss (1998), Simmons et al. (2002), Fonseca et al. (2007), and Larsen et al. (2011) were

used to compare dark-bellied *Micronycteris* (sensu Simmons et al. 2002—*M. buriri*, *M. giovanniae*, *M. hirsuta*, *M. matses*, *M. megalotis*, and *M. microtis*) with the new taxon. Because of the small sample size of most taxa, comparisons were made using descriptive statistics and measurement ranges.

We performed a principal component analysis of 8 cranial characters (ZB was excluded) using PAST version 2.14 (Hammer et al. 2001). Only pale-bellied specimens ($n = 43$) of *Micronycteris* were compared, including *M. brosseti* ($n = 1$), *M. minuta* ($n = 27$), *M. sanborni* ($n = 3$), *M. schmidtorum* ($n = 9$), and *Micronycteris* sp. nov. ($n = 3$). Principal components (PCs) were calculated using the covariance matrix to preserve the information about relative scale among variables.

Molecular methods.—Genomic DNA was extracted and sequenced for 5 specimens: *Micronycteris* sp. nov. ($n = 3$) and paratypes of *M. sanborni* ($n = 2$). DNA extractions were conducted using standard phenol–chloroform methods (Sambrook et al. 1989) on biopsies taken from the plagiopatagium of 3 skin vouchers (CBF 6154 and *M. sanborni* [CMNH 98915 and CMNH 98916]) and muscle preserved in ethanol (MHNC-M 141 and MNHC-M 157). Amplification of cytochrome-*b* was performed using primers LGL765 and LGL766 (Bickham et al. 2004). Reaction volumes of 25 µl included approximately 200 ng of DNA, 0.12 µM of each primer, 1.5 mM of $MgCl_2$, 0.012 mM of deoxynucleoside triphosphates, 1X reaction buffer, 0.32 mg/ml of bovine serum albumin, and 0.625 U of Taq DNA polymerase (Promega Corporation, Madison, Wisconsin). Thermal cycling conditions were 94°C for 2 min followed by 30–34 cycles of denaturation at 94°C for 45 s, annealing at 47°C for 1 min, extension at 72°C for 1 min 15 s, followed by a final extension of 72°C for 10 min. When necessary, further optimization was performed with alternate DNA template quantities. Polymerase chain reation amplicons were purified using QIAquick PCR Purification Kits (Qiagen Inc., Chatsworth, California) and sequenced using ABI Big Dye chemistry version 3.1 and an ABI 3100–Avant Genetic Analyzer (PE Applied Biosystems, Foster City, California). For all 3 specimens of *Micronycteris* sp. nov., the entire cytochrome-*b* gene of 1,140 base pairs (bp) was sequenced by using amplification primers in addition to 4 internal primers: ART16 (Larsen et al. 2007), G1L and G7L (Hoffmann and Baker 2001), and MVZ04 (Smith and Patton 1993). Sequences were manually checked and aligned using Sequencher version 4.9 (Gene Codes Corporation, Ann Arbor, Michigan).

Amplification of cytochrome-*b* from paratypes of *M. sanborni* required the design of primers encompassing approximately 250-bp regions. These primers were Micro_First_F (5′ ACC-CTC-AAG-CCT-GAC-ATC-CT 3′), Micro_First_R (5′ TAC-AGG-CCT-CGG-CCT-ACA-T 3′), Micro_Mid_F (5′ CCA-CCG-CAT-TTA-TGG-GTT-AC 3′), and Micro_Mid_R (5′ CGT-AGG-GTT-GTT-GGA-TCC-TG 3′). Primers were designed to be exact matches for *Micronycteris*. We tested multiple manufacturers' polymerases for amplification success because DNA yield was very low for these samples. Phire polymerase (Fisher Scientific, Pittsburg,
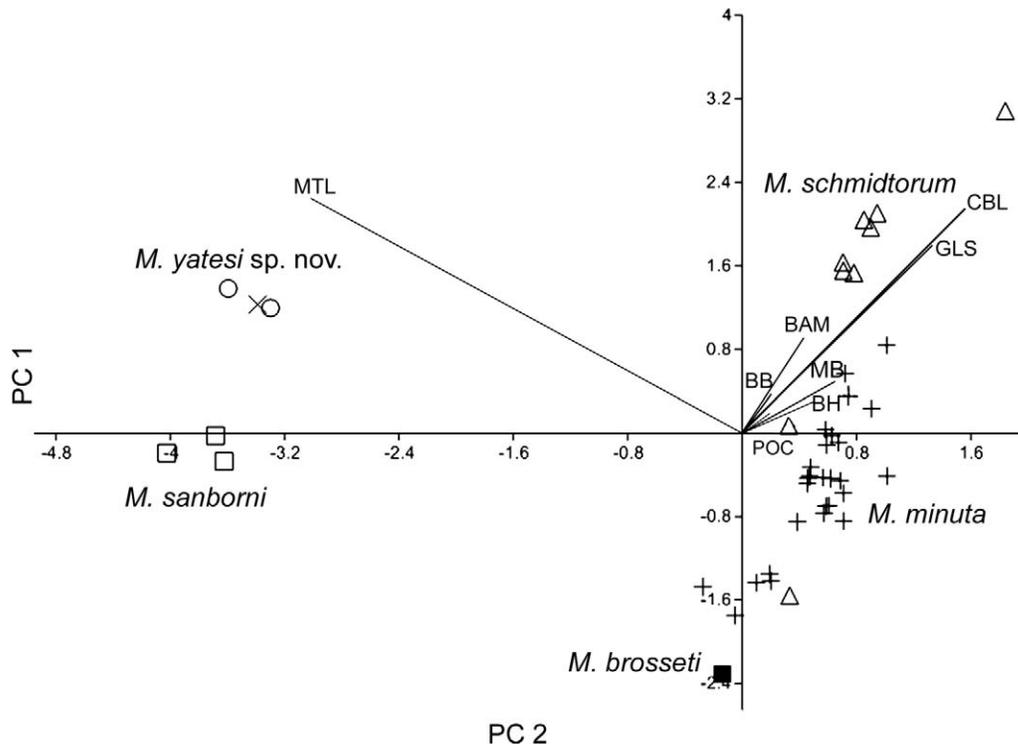
Fig. 2.—Principal component analysis showing the scatter plot of the 1st and 2nd principal component scores (symbols) and the projection of the variable loadings (lines) based on 8 cranial measurements from 43 specimens of 5 species: *Micronycteris brosseti* (■), *M. minuta* (+), *M. sanborni* (□), *M. schmidtorum* (△), and *Micronycteris* sp. nov (holotype [✕] and paratypes [○]). See the "Materials and Methods" for abbreviations.

Pennsylvania) was subsequently used based on these comparisons. Reaction conditions were 12.5 μM of each deoxynucleoside triphosphate, 1 μl of Phire polymerase, manufacturer buffer, and 25 pM of each primer in a total volume of 50 μl. Thermal conditions were 98°C for 1 min 45 s, followed by 40 cycles of 98°C for 20 s, 55°C for 20 s, 72°C for 40 s, followed by a final extension of 72°C for 10 min. Amplicons were sized on 1.5% agarose gels and purified and sequenced as described above using the amplification primers. Two partial cytochrome-*b* fragments were obtained for CMNH 98915 (241 and 212 bp) and CMNH 98916 (226 and 254 bp).

Additionally, 45 complete cytochrome-*b* sequences from 9 species of *Micronycteris* were compiled from GenBank (Porter et al. 2007; Larsen et al. 2011) and used for phylogenetic comparisons (list of specimens in Supporting Information S1, DOI: 10.1644/12-MAMM-A-259.S1). Maximum-likelihood and maximum-parsimony analyses were performed using MEGA version 5 (Tamura et al. 2011). The HKY+G+I model was selected using the Akaike information criterion in MEGA 5 (Tamura et al. 2011). Genetic distance values were estimated using the Kimura 2-parameter model (Kimura 1980). *Lampronycteris* and *Macrotus* were used as outgroups for all phylogenetic analyses, because previous studies indicate these genera are outgroups with respect to *Micronycteris* (Simmons 1996; Simmons and Voss 1998; Simmons et al. 2002; Baker et al. 2003). The partial sequences obtained from the 2 specimens of *M. sanborni* were analyzed independently to verify their

position in the phylogenetic tree. Once confirmed, we compiled the 4 fragments into 1 sequence of 495 bp (see Supporting Information S2, DOI: 10.1644/12-MAMM-A-259.S2) to reduce the number of missing data and to increase the power of the analyses. A Bayesian analysis was performed on the complete data set using MrBayes version 3.2 software (Ronquist et al. 2012), running 5×10^6 generations with 1 cold and 3 incrementally heated Markov chains, random starting trees for each chain, and trees sampled every 100 generations.

RESULTS

Principal component analysis.—Principal components 1 and 2 accounted for 92.7% of the total variation (PC 1 = 57.3% and PC 2 = 35.4%) and were correlated with maxillary toothrow length and condylobasal length (Fig. 2; Table 1). The new species formed a cluster separate from *M. schmidtorum*, *M. minuta*, and *M. brosseti* along PC 1 and also separate from *M. sanborni* along PC 2 (Fig. 2). These results indicate that the new species of *Micronycteris* is morphometrically distinct from its congeners (Fig. 2).

Phylogenetic analyses.—The 3 Bolivian specimens and their closest relatives (*M. minuta*, *M. schmidtorum*, and *M. sanborni*) showed fixed nucleotide differences that resulted in 23 amino acid changes in the cytochrome-*b* gene (Table 2). Three of the 23 amino acid changes were unique to

TABLE 1.—Results of the principal component analysis of 8 cranial characters from specimens of *Micronycteris schmidtorum*, *M. minuta*, *M. brosseti*, *M. sanborni*, and *Micronycteris* sp. nov. Loadings of the first 2 principal components (PCs) are presented and accounted for 92.7% of the total variation. Variables are defined in the "Materials and Methods".

Variable	PC 1	PC 2
MTL	−0.80	0.59
CBL	0.41	0.57
GSL	0.35	0.48
MB	0.17	0.13
BH	0.13	0.08
BAM	0.11	0.24
BB	0.05	0.1
POC	0.05	0.05

Micronycteris sp. nov. and are located at positions 67, 181, and 316 out of the 380 amino acids in the cytochrome-*b* gene. At position 67, threonine in *M. minuta*, *M. sanborni*, and *M. schmidtorum* was replaced by alanine in *Micronycteris* sp. nov. At position 181, phenylalanine in *M. minuta*, *M. sanborni*, and *M. schmidtorum* was replaced by leucine in *Micronycteris* sp. nov. At position 316, a polymorphism of methionine or threonine in *M. minuta* and methionine in *M. schmidtorum* was replaced by alanine in *Micronycteris* sp. nov. (Table 2).

Alignment of 50 cytochrome-*b* sequences was unequivocal and without internal stop codons. Of the 1,140 characters, 678 were conserved and 373 were parsimony informative across the entire data set. Maximum-likelihood analysis resulted in 1 tree with a ln-likelihood of −7,645.41 and maximum-parsimony analyses resulted in 25 most-parsimonious trees (length = 1,334; consistency index = 0.46, retention index = 0.78, composite index = 0.37). The 3 Bolivian *Micronycteris* formed a statistically supported clade in all phylogenetic analyses (Fig. 3). The sister relationship to *M. sanborni* is not supported (Fig. 3) and the maximum-likelihood tree grouped *M. sanborni* with *M. minuta* and *M. schmidtorum*. Genetic distance values between clades ranged from 17.89% (*M. hirsuta* versus *M. minuta* clade 1) to 2.75% (*M. buriri* versus *M. megalotis* clade 3; Table 3). The intraspecific genetic distance value for the Bolivian *Micronycteris* was 1.3% and the lowest genetic distance value separating the new taxon from any other species within the genus was 5.3% (*M. sanborni*, based on 495 bp; Table 3).

Systematic Description

Family Phyllostomidae Gray, 1825
Subfamily Micronycterinae sensu Baker et al. 2003
Genus *Micronycteris* Gray, 1866
Micronycteris yatesi Siles and Brooks, new species

Micronycteris sanborni: Brooks et al. 2002:514; Salazar-Bravo et al. 2003:3; Aguirre and Terán 2007:209; Aguirre et al. 2010a:3.

TABLE 2.—Amino acid (AA) changes in cytochrome-*b* among *Micronycteris minuta* (n = 4), *M. schmidtorum* (n = 3), *M. sanborni* (n = 1), and *Micronycteris* sp. nov. (n = 3). Amino acids are presented in standard 3-letter abbreviations.

AA position	*M. minuta*	*M. sanborni*	*M. schmidtorum*	*Micronycteris* sp. nov.
16/380	Ser, Asn	—	Ser, Asn	Asn
42/380	Ala, Thr	Ala	Ala	Ala
56/380	Thr, Met	Thr	Thr	Thr
67/380	Thr	Thr	Thr	Ala
101/380	Gly	Gly	Gly, Ser	Gly
158/380	Thr	Thr	Thr	Thr, Ala
181/380	Phe	Phe	Phe	Leu
188/380	Ile, Val	Ile	Ile	Ile
238/380	Ala, Thr	—	Ala	Ala
241/380	Thr, Met	—	Thr	Thr
257/380	Thr	—	Thr	Thr, Ala
316/380	Met, Thr	—	Met	Ala
320/380	Leu	—	Leu, Phe	Leu
333/380	Leu, Phe	—	Leu, Phe	Leu
334/380	Thr	—	Met	Thr
345/380	Tyr	—	His	His
348/380	Ile, Val	—	Val	Ile
364/380	Ile, Val	—	Val	Ile
365/380	Leu	—	Phe	Leu
369/380	Ile	—	Thr, Ile	Ile, Ala
372/380	Met, Val	—	Met	Met, Ile
376/380	Leu	—	Leu	Leu, Phe
377/380	Leu	—	Leu	Leu, Val

Micronycteris sanborni [in partim]: Simmons 2005:408; Williams and Genoways 2007:281.

Holotype.—Voucher MHNC-M 157; adult male; standard skin and skull deposited at the Museo de Historia Natural Alcide d'Orbigny (Cochabamba, Bolivia). Collected on 14 February 2007 by L. Siles and A. Muñoz. Prepared by L. Siles, field number LSM 146. The skin and skull are well preserved, with the exception of broken zygomatic arches and separated mandibles. External measurements (mm) were: TL, 48.50; Tail, 7.00; HF, 11.71; Ear, 18.27; FA, 36.70; Mc3, 29.30; Mc4, 30.68; Thu, 8.11; Tib, 13.24; and Cal, 9.48. Cranial measurements (mm) were: GSL, 17.85; CBL, 15.92; ZB, 8.18; POC, 3.91; MB, 8.4; MTL, 6.25; BAM, 5.32; BB, 7.47; and BH, 6.52. This individual was initially identified as *M.* aff. *sanborni* (MHNC-M records, in litt.).

Type locality.—Bolivia: Chuquisaca Department, Provincia Oropeza, Zurima, 33 km northeast of Sucre (18°46′40.2″S, 65°07′40.3″W). Collected at 1,800 m above sea level.

Paratypes.—Two additional specimens were collected from Bolivia and based on morphological and genetic data are designated as paratypes. The 1st paratype is voucher CBF 6154; adult female; standard skin and skull deposited at the Colección Boliviana de Fauna (La Paz, Bolivia). Collected on 17 April 1999 by H. Aranibar, R. J. Vargas M., and J. M. Rojas from Estancia Patuju, 370 km east of Santa Cruz de la Sierra (17°37′04.9″S, 59°32′9.5″W; 220 m), Provincia Chiquitos, Santa Cruz Department. Prepared by J. M. Rojas (field number JMR 319). The skin and mandible are well preserved; the skull has broken palatine bones, mastoid bones, zygomatic arches,
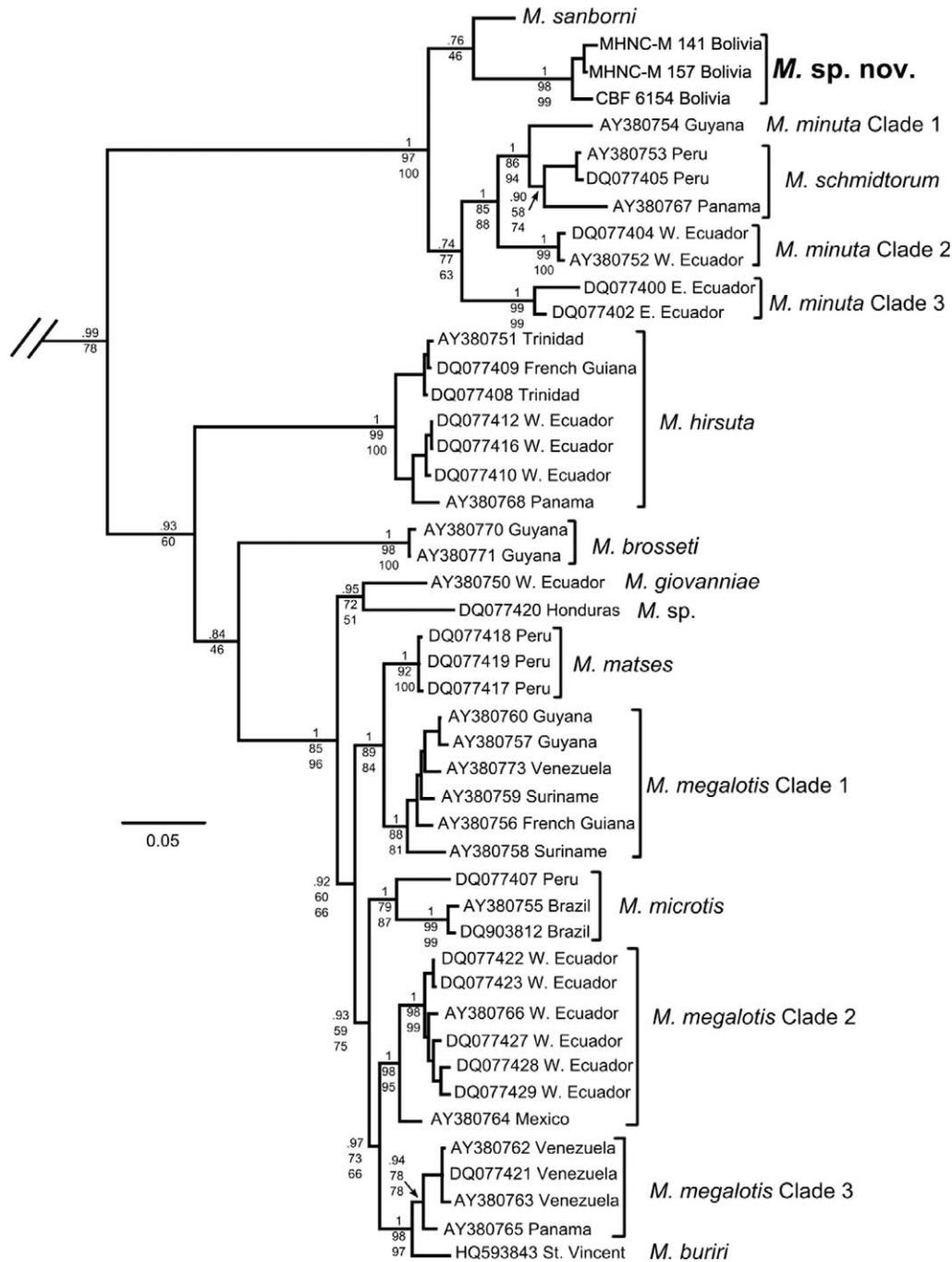
Fig. 3.—Bayesian phylogram based on DNA sequence data of the cytochrome-*b* gene. Scores are Bayesian posterior probabilities (top score) and bootstrap support values (percentage of 500 iterations) from maximum-likelihood (middle score) and minimum-evolution (bottom score) analyses. *Lampronycteris brachyotis*, *Macrotus californicus*, and *M. waterhousii* were used as outgroups.

and auditory bullae. This specimen was originally identified as *M. sanborni* (Brooks et al. 2002).

The 2nd paratype is voucher MHNC-M 141; adult male; standard skin and skull deposited at the Museo de Historia Natural Alcide d'Orbigny (Cochabamba, Bolivia). Collected on 18 November 2005 by L. Siles from Refugio Los Volcanes (18°06′42.5″S, 63°36′07.8″W; 1,060 m), Provincia Florida, Santa Cruz Department. Prepared by L. Siles (field number LSM 131). The skin, skull, and mandibles are well preserved

with the exception of 1 broken zygomatic arch. This specimen was initially identified as *M. sanborni* (MHNC-M records, included in Aguirre and Terán [2007]). Measurements of paratypes are presented in Tables 4 and 5.

Distribution.—The specimens are known from 3 localities in Bolivia spanning approximately 700 km (Fig. 1). The 3 collecting localities represent distinct ecoregions: Inter-Andean Dry Forest, Cerrado, and Yungas (sensu Ibisch et al. 2003) ranging from 220 to 1,800 m above sea level.

TABLE 3.—Average Kimura 2-parameter pairwise distances among and within (boldface type) species and clades of *Micronycteris* based on 1,140 base pairs (bp) of the cytochrome-*b* gene (except *M. sanborni*, based on 495 bp). The analysis involved 47 nucleotide sequences; codon positions included were 1st + 2nd + 3rd + noncoding.

No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*M. buriri* (*n* = 1)	—																
2	*M. brosseti* (*n* = 2)	9.6	**0.3**															
3	*M. giovanniae* (*n* = 1)	6.5	10.4	—														
4	*M. hirsuta* (*n* = 7)	11.9	12.5	10.8	**1.9**													
5	*M. matses* (*n* = 3)	5.3	10.0	5.6	10.8	**0.2**												
6	*M. megalotis* clade 1 (*n* = 6)	6.2	10.1	5.9	10.3	3.1	**1.7**											
7	*M. megalotis* clade 2 (*n* = 7)	4.7	10.3	5.9	10.9	4.5	4.9	**1.3**										
8	*M. megalotis* clade 3 (*n* = 4)	2.7	9.5	5.8	10.9	4.6	5.2	4.4	**0.9**									
9	*M. microtis* (*n* = 2)	5.6	10.8	7.2	12.5	5.5	5.6	5.4	5.7	**0.7**								
10	*M. minuta* clade 1 (*n* = 1)	16.5	16.9	16.3	17.9	15.5	15.5	16.3	16.6	16.8	—							
11	*M. minuta* clade 2 (*n* = 2)	15.7	14.8	15.1	15.6	15.3	14.7	15.1	15.9	16.4	6.4	**0.5**						
12	*M. minuta* clade 3 (*n* = 3)	15.4	15.1	15.1	16.0	15.0	14.6	15.1	15.4	16.1	8.8	7.5	**0.5**					
13	*M. sanborni* (*n* = 1)	13.5	13.1	11.8	15.4	12.2	12.4	14.3	12.6	14.6	6.2	5.1	6.6	—				
14	*M.* cf. *schmidtorum* (*n* = 3)	15.1	15.5	15.1	16.4	14.8	14.3	15.1	14.7	14.7	5.2	6.4	7.6	6.7	**3.0**			
15	*Micronycteris* sp. Honduras (*n* = 1)	6.7	11.4	5.5	11.1	6.4	6.1	6.3	6.3	7.8	16.6	15.4	15.7	13.0	15.0	—		
16	*Micronycteris* sp. Peru (*n* = 1)	5.6	10.5	5.9	11.7	5.0	5.2	5.3	5.4	4.7	16.7	15.6	15.3	12.8	14.7	7.6	—	
17	*Micronycteris* sp. nov. (*n* = 3)	14.5	14.0	13.5	16.1	13.8	13.8	14.7	14.4	14.2	10.4	9.7	9.2	5.4	9.5	13.4	14.0	**1.3**

Etymology.—This species is named in honor of Terry Lamon Yates (1950–2007) for his pivotal contributions to the knowledge of Bolivian mammals, training Bolivian biologists, and starting collaborations that strengthened mammalian research and shaped current science and field biology in Bolivia. We suggest that the common name of this species be the Yates's big-eared bat.

Diagnosis.—*Micronycteris yatesi* is distinguished from its congeners by a combination of external and craniodental features. The ventral hair on the throat and sternal region in *M. yatesi* is white, whereas the abdominal area presents pale buff coloration (Fig. 4). The skull of *M. yatesi* presents palatine bones that are short and parallel with a pointed arch shape anteriorly (Fig. 5). The sutura palatomaxillaris is located between M2 and M3 (Fig. 5). Medial upper incisors are long, unilobate, and projected slightly upward.

Micronycteris yatesi also can be distinguished from its congeners based on DNA sequence data, which present nucleotide differences that result in unique amino acids in the cytochrome-*b* protein at positions 67, 181, and 316 (alanine, leucine, and alanine, respectively; Table 2). Phylogenetically, the cytochrome-*b* sequence positions *M. yatesi* in a clade that is divergent and statistically supported from other members of the genus studied thus far (Fig. 3).

Description.—*Micronycteris yatesi* is a medium-sized bat (forearm 34.54–36.7 mm). The dorsal fur is long (8–10 mm in the shoulder region) and bicolored with a white base that composes approximately one-half of each hair (white portion = 4.3–5.6 mm). The terminal portions of the dorsal fur are olive brown (Ridgway 1912:plate XL) in color in the holotype (MHNC-M 157), Prout's brown (Ridgway 1912:plate XV) in MHNC-M 141, and tawny (Ridgway 1912:plate XV) in CBF 6154. MHNC-M 157 and MHNC-M 141 have the ventral hair on the throat and sternal region completely white, whereas the abdominal area presents pale buff coloration. CBF 6154 has dorsal and ventral fur with a white base that composes one-

third of each hair, and the ventral fur presents pale yellowish coloration. Fur on external surface of leading edge of the pinna (sensu Simmons 1996) is dense and of variable length; MHNC-M 157 and CBF 6154 have short hair (≤3.5 mm), and MHNC-M 141 has long hair (5.5 mm). The ears are large (15.50–18.27 mm) with rounded tips and a high, notched band connects their bases. Interauricular membrane is deeply notched with triangular flaps (observations only on dry skins). Hind feet are hairy. The calcar is shorter than the foot in MHNC-M 157 and MHNC-M 141, and similar in size to the foot in CBF 6154 (Table 4). Uropatagium and wing membranes are naked.

Rostrum is elongated; premaxillae are short and wide; maxillae are inflated over the region of the 2nd premolar and 1st molar; nasal bones are slightly inflated (Fig. 6). CBF 6154 has a less inflated rostrum than the other 2 specimens. Incisive foramina are triangular. Infraorbital canal is narrow and deep. Sagittal crest and lambdoidal crest are absent. Zygomatic arch is slender (complete arch in MHNC-M 141). Paraoccipital processes are not well developed and do not surpass the occipital condyles. Foramen magnum is oval. Basisphenoid pits are deep, separated by a well-developed septum. Basioccipital bone is narrow. There are 2 pairs of foraminae ovale; the anterior is larger than the posterior. Palatine bones are short with a pointed arch shape anteriorly (Fig. 5). The sutura palatomaxillaris is located between M2 and M3. Postpalatal extension is narrow over the mesopterygoid fossa and has a U-shaped posterior margin.

Medial upper incisors (I1) are large, unilobate, and projected slightly upward (more so in CBF 6154 than the other 2 specimens). Lateral upper incisors (I2) are unilobate, convergent, and small, less than one-half the size of the inner upper incisors. A gap is present between I2 and the canines. Upper canines are slender with cingula well developed, especially the antero- and posterolingual cingular styles. CBF 6154 has slightly smaller canines than the other 2 specimens. P4 is slightly larger than P3 in anteroposterior length. In occlusal

TABLE 4.—Descriptive statistics of 11 external measurements (mm, acronyms defined in the "Materials and Methods") for A) females and B) males of *Micronycteris yatesi, M. sanborni, M. minuta, M. schmidtorum,* and *M. brosseti*. Values include mean ± standard deviation, sample size (in parentheses), and range (in parentheses).

	A) Females					B) Males					
	M. yatesi	M. sanborni[a]	M. minuta[a]	M. schmidtorum[b]	M. brosseti[c]	M. yatesi	M. sanborni[a]	M. sanborni[d]	M. minuta[a]	M. schmidtorum[b]	M. brosseti[c]
TL	55.80	58.86 ± 1.15 (2) (58.05–59.67)	47.62 ± 2.04 (6) (45.08–50.31)	64.14 ± 2.19 (7) (61.00–67.00)	57.33 ± 2.52 (3) (55–60)	54.29 ± 8.19 (2) (48.50–60.08)	55.02	51.70	46.00 ± 4.07 (13) (41.27–57.30)	60.80 ± 3.26 (10) (56.00–66.00)	57.20 ± 3.70 (5) (52.00–61.00)
Tail	10.80	10.09 ± 0.73 (2) (9.57–10.60)	8.38 ± 1.96 (6) (6.25–10.91)	13.57 ± 2.64 (7) (9.00–17.00)	12.67 ± 0.58 (3) (12.00–13.00)	8.09 ± 1.53 (2) (7.00–9.17)	13.60	12.70	9.21 ± 2.47 (13) (6.23–13.08)	13.50 ± 1.51 (10) (12.00–17.00)	12.20 ± 1.64 (5) (10.00–14.00)
HF	10.32	10.12 ± 0.22 (2) (9.96–10.27)	10.61 ± 0.46 (7) (9.83–11.29)	10.57 ± 0.79 (7) (10.00–12.00)	10.33 ± 0.58 (3) (10.00–11.00)	11.56 ± 0.22 (2) (11.40–11.71)	10.11	9.10	10.86 ± 0.71 (18) (9.57–12.68)	9.70 ± 1.42 (10) (8.00–12.00)	10.60 ± 0.55 (5) (10.00–11.00)
Ear	15.50	17.48 ± 0.06 (2) (17.44–17.52)	14.96 ± 3.72 (5) (8.63–18.28)	17.57 ± 2.70 (7) (15.00–21.00)	19.00 ± 0.00 (3)	16.96 ± 1.86 (2) (15.64–18.27)	18.77	20.30	18.23 ± 1.89 (10) (14.08–20.59)	19.10 ± 2.64 (10) (14.00–23.00)	19.60 ± 0.55 (5) (19.00–20.00)
FA	34.54	32.80 ± 0.03 (2) (32.78–32.82)	35.79 ± 0.71 (7) (34.59–36.60)	35.54 ± 1.97 (7) (32.53–37.46)	32.83 ± 1.26 (3) (31.50–34.00)	36.60 ± 0.14 (2) (36.50–36.70)	33.78	33.90	34.83 ± 1.15 (18) (32.57–36.73)	34.64 ± 1.56 (10) (32.67–37.23)	33.00 ± 1.06 (5) (31.50–34.00)
Mc3	26.25	26.30 ± 1.13 (2) (25.50–27.10)	28.13 ± 1.48 (7) (26.92–31.29)	31.14 ± 2.09 (7) (28.65–33.87)	—	29.04 ± 0.37 (2) (28.78–29.30)	26.19	28.90	26.31 ± 1.80 (18) (21.27–28.30)	29.45 ± 1.73 (10) (26.92–32.03)	—
Mc4	27.35	27.42 ± 1.34 (2) (26.47–28.36)	28.72 ± 0.74 (7) (27.75–29.98)	—	—	30.34 ± 0.48 (2) (30.00–30.68)	26.85	29.50	27.71 ± 1.13 (18) (25.37–29.58)	28.46	—
Thu	8.39	7.61 ± 0.01 (2) (7.60–7.61)	8.56 ± 0.53 (7) (8.03–9.44)	—	7.90	8.16 ± 0.07 (2) (8.11–8.21)	7.12	7.60	8.34 ± 0.74 (18) (7.08–9.66)	9.89	7.88 ± 0.23 (5) (7.50–8.10)
Tib	14.23	13.27 ± 0.61 (2) (12.84–13.70)	15.42 ± 0.52 (7) (14.58–15.95)	—	13.25 ± 0.64 (2)	13.35 ± 0.16 (2) (13.24–13.46)	13.77	15.80	15.67 ± 0.91 (18) (13.91–17.16)	17.05	13.66 ± 0.46 (5) (13.2–14.2)
Cal	10.52	9.01 ± 0.55 (2) (8.62–9.40)	8.02 ± 0.14 (3) (7.91–8.18)	—	—	9.74 ± 1.23 (2) (9.48–10.00)	9.55	9.50	7.97 ± 1.23 (14) (4.34–9.61)	—	—
DHL	8.22	8.86 ± 073 (2) (8.34–9.37)	7.80 ± 1.23 (7) (6.34–9.72)	—	—	8.95 ± 1.38 (2) (7.97–9.92)	8.30	—	7.90 ± 1.32 (17) (6.17–10.06)	11.51	—

[a] Specimens examined.

[b] Measurements presented by Larsen et al. (2011), except Mc4, Thu, Tib, and DHL measured from specimen TTU 13165.

[c] Based on measurements of the type series presented by Simmons and Voss (1998).

[d] Specimen reported from western Brazil by Ferreira Santos et al. (2010).

TABLE 5.—Descriptive statistics of 9 cranial measurements (mm, acronyms defined in the "Materials and Methods") for A) females and B) males of *Micronycteris yatesi*, *M. sanborni*, *M. minuta*, *M. schmidtorum*, and *M. brosseti*. Values include mean ± standard deviation, sample size (in parentheses), and range (in parentheses). NA = not available.

A) Females

	M. yatesi	M. sanborni[a]	M. minuta[a]	M. schmidtorum[a]	M. brosseti[b]
GSL	17.66	16.94 ± 0.04 (2) (16.91–16.97)	18.55 ± 0.39 (8) (18.15–19.22)	19.76 ± 0.19 (6) 19.54–20.01	17.05 ± 0.53 (3) (16.60–17.63)
CBL	15.76	14.95 ± 0.20 (2) (14.81–15.09)	16.62 ± 0.34 (8) (16.27–16.62)	18.12 ± 0.88 (6) (17.48–19.84)	15.47 ± 0.21 (3) (15.31–15.71)
ZB	NA	8.19	8.63 ± 0.23 (6) (8.35–8.97)	9.61 ± 0.25 (6) (9.22–9.88)	8.39 ± 0.10 (3) (8.28–8.47)
POC	4.03	3.89 ± 0.25 (2) (3.71–4.06)	4.06 ± 0.11 (8) (3.95–4.28)	4.17 ± 0.08 (6) (4.07–4.25)	3.89 ± 0.09 (3) (3.80–3.98)
BB	7.52	7.38 ± 0.10 (2) (7.31–7.45)	7.59 ± 0.28 (8) (7.19–8.00)	7.79 ± 0.11 (6) (7.67–7.92)	7.26 ± 0.02 (3) (7.24–7.28)
MB	8.33	7.88 ± 0.17 (2) (7.76–8.00)	8.70 ± 0.20 (8) (8.42–8.93)	8.86 ± 0.17 (5) (8.6–9.09)	8.06 ± 0.17 (3) (7.91–8.24)
MTL	6.20	5.92 ± 0.11 (2) (5.84–6.00)	6.66 ± 0.25 (8) (6.30–7.06)	7.77 ± 0.15 (6) (7.61–8.01)	6.38 ± 0.21 (3) (6.24–6.62)
BAM	6.31	5.13 ± 0.09 (2) (5.06–5.19)	5.72 ± 0.22 (8) 5.42–6.12	6.47 ± 0.08 (6) (6.39–6.62)	5.50 ± 0.05 (3) (5.45–5.55)
BH	6.54	6.91 ± 0.05 (2) (6.87–6.94)	7.10 ± 0.37 (8) 6.75–7.9	7.41 ± 0.13 (6) (7.27–7.59)	6.84

B) Males

	M. yatesi	M. sanborni[c]	M. sanborni[a]	M. minuta[a]	M. schmidtorum[a]	M. brosseti[b]
GSL	17.90 ± 0.07 (2) (17.85–17.95)	17.90	17.07	18.39 ± 0.47 (20) (17.64–19.21)	18.82 ± 0.97 (4) (17.7–19.83)	17.26 ± 0.23 (4) (16.97–17.5)
CBL	15.94 ± 0.02 (2) (15.92–15.95)	15.90	14.80	16.43 ± 0.47 (20) (15.43–17.38)	17.10 ± 0.96 (4) (15.9–18.03)	15.67 ± 0.26 (4) (15.30–15.89)
ZB	8.18	—	7.89	8.40 ± 0.28 (18) (7.76–8.81)	8.88 ± 0.82 (4) (7.80–9.70)	8.49 ± 0.18 (4) (8.22–8.61)
POC	3.91 ± 0.01 (2) (3.90–3.91)	4.00	4.10	4.15 ± 0.20 (20) (3.68–4.50)	4.23 ± 0.26 (4) (4.00–4.60)	3.96 ± 0.05 (4) (3.90–4.00)
BB	7.46 ± 0.01 (2) (7.45–7.47)	7.30	7.37	7.51 ± 0.21 (20) (7.12–7.88)	7.84 ± 0.23 (4) (7.60–8.15)	7.36 ± 0.11 (7.23–7.51)
MB	8.13 ± 0.45 (2) (7.81–8.45)	8.10	7.95	8.60 ± 0.37 (19) (7.70–9.18)	8.71 ± 0.32 (4) (8.30–8.98)	8.04 ± 0.16 (4) (7.91–8.18)
MTL	6.23 ± 0.04 (2) (6.20–6.25)	6.10	5.79	6.61 ± 0.22 (20) (6.31–7.05)	7.21 ± 0.78 (4) (6.15–7.83)	6.51 ± 0.08 (4) (6.42–6.59)
BAM	5.36 ± 0.05 (2) (5.32–5.39)	5.70	5.35	5.63 ± 0.20 (20) (5.16–6.03)	5.99 ± 0.51 (4) (5.30–6.51)	5.68 ± 0.06 (4) (5.61–5.74)
BH	6.65 ± 0.18 (2) (6.52–6.78)	—	6.53	7.14 ± 0.31 (19) (6.63–7.9)	7.44 ± 0.13 (4) (7.25–7.55)	—

[a] Specimens examined.
[b] Based on measurements of the type series presented by Simmons and Voss (1998), except BH, which was measured from specimen AMNH 266033.
[c] Specimen reported from western Brazil by Ferreira Santos et al. (2010).
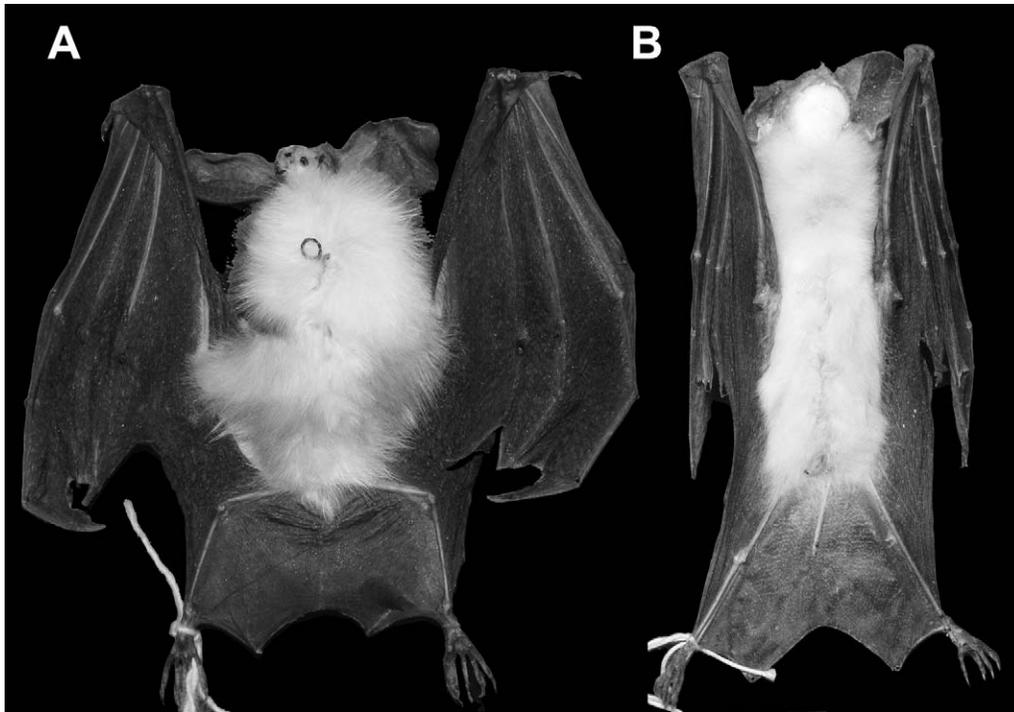
Fɪɢ. 4.—Ventral view of the specimens displaying pelage color. A) *Micronycteris yatesi* (MHNC-M 157) and B) *M. sanborni* (CMNH 98913).

view P3 is rectangular. The antero- and posterolingual cingula of P4 are well developed. M1 and M2 have a similar size with a square outline in occlusal view. Parastyle of M2 and M3 have a distinct accessory cusp that projects anteriorly. M2 parastyle is the most developed of all molar styles. The metacone of M2 and M3 is taller than the paracone, and the protocone is taller than the hypocone.

Lower incisors are small and bilobed with lobes parallel to each other. Lower canines are robust with cingula well developed. Crown height of lower premolars varies; p3 is much smaller than p2 and p4. Coronoid process is low; angular process is well developed and extends out to the same level of the mandibular condyle.

Dɪscussɪon

Taxonomic remarks.—Phylogenetic analyses indicate that *M. yatesi* is within the subgenus *Schizonycteris* (sensu Porter et al. 2007). Available names for new species of the genus *Micronycteris* include *M. typica* and *M. mexicana*; however, Larsen et al. (2011) established that those names would be best applied to *M. megalotis* clades 1 or 3, and *M. megalotis* clade 2, respectively (Fig. 3). Another available name is *M. hypoleuca* Allen, 1900, a white-bellied *Micronycteris* that was synonymized with *M. minuta* by Andersen (1906) due to the lack of diagnostic characters other than a completely white belly. Because the description of *M. hypoleuca* is based on a single specimen from the Santa Marta region of Colombia, this name would be available for *M. minuta* clades 2 or 3 (Fig. 3).

Morphological comparisons.—*Micronycteris yatesi* is distinguished from its congeners by a combination of

external, cranial, and dental characters, as well as size variation. Dorsal pelage is bicolored with white bases and tawny to brown tips, a character that is shared with all the members of the genus (Simmons and Voss 1998; Simmons et al. 2002; Fonseca et al. 2007; Larsen et al. 2011). The ventral fur in *M. yatesi* is paler than the dorsal fur, a character that is shared with *M. sanborni*, *M. minuta*, *M. schmidtorum*, and *M. brosseti*. The color of the ventral fur in *M. yatesi* is completely white on the throat and sternal region, whereas the abdominal area presents pale buff coloration (Fig. 4). *M. sanborni* is the only pale-bellied species with a bright white ventral region, including throat, sternal, and abdominal areas (Fig. 4). All other pale-bellied *Micronycteris* have pale gray or pale buff underparts (i.e., *M. brosseti*, *M. minuta*, and *M. schmidtorum*— Simmons and Voss 1998).

Although the relative proportion of the calcar and hind foot varies among species of *Micronycteris* and is used as a diagnostic character (Simmons 1996; Williams and Genoways 2007), its usefulness comes into question because it relies heavily on the subjective perception of the calcar being longer or shorter than the foot (Ferreira Santos et al. 2010), and also on preparation methods (Simmons 1996), which can deform the structure. In *M. yatesi* the calcar is shorter than the foot in 2 specimens, and 0.2 mm longer in a 3rd specimen. Although Simmons (1996) established that *M. sanborni* has calcar and foot of similar size, of the 3 specimens we examined the calcar was shorter than the foot (Table 4). We report these measurements here, but based on our observations we cannot determine which category should be assigned to *M. yatesi* and *M. sanborni*.
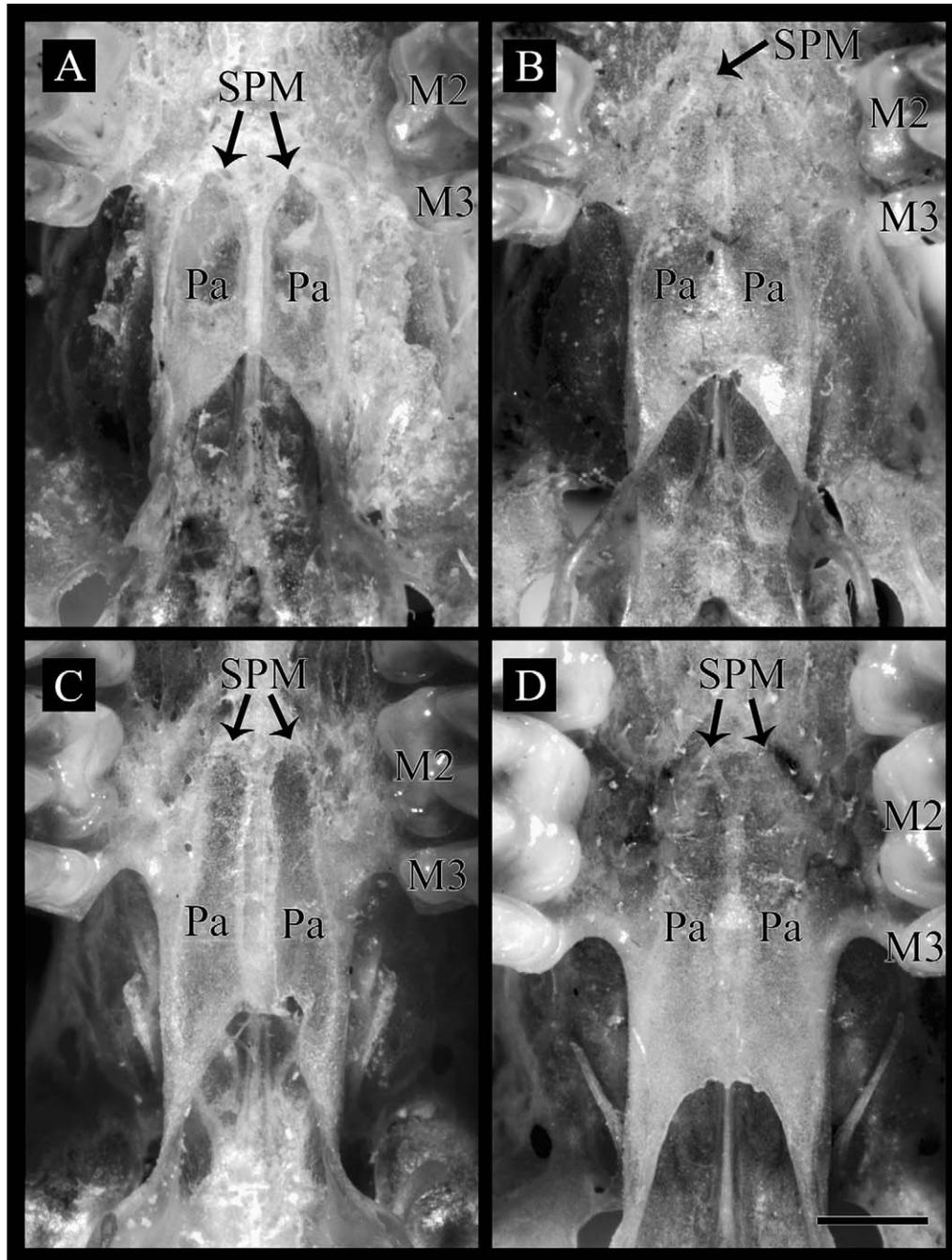
FIG. 5.—Ventral views of the palatine bones (20×, scale bar = 1 mm). A) *Micronycteris yatesi* (MHNC-M 157), B) *M. sanborni* (CMNH 98915), C) *M. minuta* (TTU 9785), and D) *M. schmidtorum* (TTU 13165). SP = sutura palatomaxillaris, M = upper molar, Pa = palatine bone.

When comparing external and cranial measurements with the dark-bellied members of the genus (Tables 4–6), *M. yatesi* was smaller than *M. buriri*, *M. giovanniae*, *M. hirsuta*, and *M. matses* in most measurements, with overlapping values of hind foot and ear lengths for all 4 of these species. Other overlapping values include forearm length and postorbital constriction with *M. buriri*. *M. yatesi* has a larger thumb length compared to *M. giovanniae*. *M. yatesi* was of similar size to *M. megalotis* and *M. microtis*, with most external and cranial measurements overlapping. Exceptions include greater maxil-

lary toothrow length and braincase height in *M. megalotis* and *M. microtis*, and a larger thumb length in *M. megalotis*.

Most external measurements of *M. yatesi* overlapped with the pale-bellied *M. schmidtorum*, *M. brosseti*, and *M. minuta* (Tables 4 and 6). Exceptions included a larger thumb in *M. schmidtorum*, a smaller calcar in *M. minuta*, and a smaller forearm length in *M. brosseti*. External measurements between *M. yatesi* and *M. sanborni* overlap in body length, tail, metacarpals 3 and 4, tibia, and calcar. *M. sanborni* is smaller

FIG. 6.—Dorsal, ventral, and lateral views of the skull and lower jaw of the holotype of *Micronycteris yatesi* (MHNC-M 157). Scale bar = 5 mm.

than *M. yatesi* in hind foot, forearm, and thumb length, and is only larger in ear length.

Comparing cranial measurements among pale-bellied *Micronycteris* (Tables 5 and 6), *M. yatesi* completely overlaps all measurements with *M. minuta*. Compared to *M. brosseti* most

measurements overlap except greatest length of skull (smaller in *M. brosseti*), zygomatic breadth, and breadth across upper molars (both larger in *M. yatesi*). *M. schmidtorum* presented greater values of condylobasal length, postorbital constriction, braincase breadth, and braincase height; all other measurements overlapped. *M. sanborni* was smaller than *M. yatesi* in greatest length of skull, condylobasal length, braincase breadth, and maxillary toothrow length; with overlapping values of postorbital constriction, mastoid breadth, breadth across upper molars, and braincase height. Based on our observations it seems that maxillary toothrow and condylobasal lengths will be very important in discriminating *M. yatesi* from other similar species in the genus, an assessment that also is supported by the results of the principal component analysis (Fig. 2; Table 1).

Based on the phylogenetic analysis (Fig. 3), we present a more detailed comparison of the morphology between *M. yatesi* and specimens of the closely related *M. sanborni*, *M. schmidtorum*, and *M. minuta*. The rostrum is elongated in *M. yatesi*, *M. schmidtorum*, and *M. minuta*, whereas *M. sanborni* has a relatively short rostrum. Palatine bones in *M. yatesi* are short and parallel with a pointed arch shape anteriorly (Fig. 5). In contrast *M. sanborni*, *M. schmidtorum*, and *M. minuta* have longer, convergent, and fusiform-shaped palatine bones (Fig. 5). The sutura palatomaxillaris is located between M2 and M3 in *M. yatesi*, whereas in *M. sanborni*, *M. schmidtorum*, and *M. minuta* this sutura is located between M1 and M2 (Fig. 5). The shape and size of the palatine bones described for *M. yatesi* are unique to this taxon and not found in any other species of the genus.

Like other members of the genus, *M. yatesi* has a dental formula of i 2/2, c 1/1, p 2/3, m 3/3, total 34. Medial upper incisors are similar in shape and size in *M. minuta*, *M. sanborni*, and *M. yatesi*; all specimens examined from these taxa presented unilobate I1, with 2 exceptions (TTU 48093 and TTU 33282 from Venezuela). Lateral upper incisors are similar in size in *M. minuta*, *M. sanborni*, and *M. yatesi*; however, the shape and presence of lobes is variable in *M. minuta*. A gap between I2 and the canines is present only in *M. yatesi* and *M. sanborni* and varies in width. The upper canines, premolars, and molars are similar in the specimens examined of *M. minuta*, *M. sanborni*, and *M. yatesi*. Lower incisors are round in *M. sanborni* and *M. yatesi*, whereas *M. minuta* has more rectangular incisors. The rest of the lower dentition and mandibular characters are similar in *M. minuta*, *M. sanborni*, and *M. yatesi*.

A specimen of *M. sanborni* was reported from the western region of the Brazilian Cerrado in the state of Mato Grosso do Sul, a state adjacent to southeastern Bolivia (Ferreira Santos et al. 2010). Although some of the measurements of this specimen are within the range of *M. sanborni*, maxillary toothrow length and condylobasal length seem to be closer to the range of *M. yatesi* (Table 5). Ferreira Santos et al. (2010) also mention that the specimen has a gap between the lateral upper incisors and the canines, a character that defines both *M. sanborni* and *M. yatesi*. We recommend that all specimens

TABLE 6.—Comparisons of external and cranial measurements (acronyms defined in the "Materials and Methods") between *Micronycteris yatesi* and congeners. Numbers indicate the source for each species or specific measurement: (1) Simmons and Voss (1998), (2) Simmons et al. (2002), (3) Fonseca et al. (2007), and (4) Larsen et al. (2011). NA = not available.

	M. buriri (4)	*M. giovanniae* (3)	*M. hirsuta*	*M. matses* (2)	*M. megalotis*	*M. microtis*	*M. brosseti* (1)	*M. minuta*	*M. sanborni*	*M. schmidtorum*
TL	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Overlap	Overlap (4)
Tail	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Overlap	Overlap (4)
HF	Overlap	Overlap	Overlap (4)	Overlap	Overlap (4)	Overlap (4)	Overlap	Overlap	Smaller	Overlap (4)
Ear	Overlap	Overlap	Overlap (4)	Overlap	Overlap (4)	Overlap (4)	Overlap	Overlap	Larger	Overlap (4)
FA	Overlap	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Smaller	Overlap	Smaller	Overlap (4)
Mc3	Larger	NA	Larger (4)	NA	Overlap (4)	Overlap (4)	NA	Overlap	Overlap	Overlap (4)
Mc4	NA	NA	NA	NA	NA	NA	NA	Overlap	Overlap	Overlap
Thu	NA	Smaller	Larger (1)	Larger	Larger (1)	Overlap (1)	Overlap	Overlap	Smaller	Larger (1)
Tib	NA	Larger	Larger (1)	Larger	Overlap (1)	Overlap (1)	Overlap	Overlap	Overlap	Overlap (1)
Cal	NA	Larger	NA	NA	NA	NA	NA	Smaller	Overlap	NA
GSL	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Smaller	Overlap	Smaller	Overlap
CBL	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Smaller	Larger
ZB	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Larger	Overlap	NA	Overlap
POC	Overlap	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Overlap	Larger
BB	Larger	NA	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Smaller	Larger
MB	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Overlap	Overlap	Overlap	Overlap
MTL	Larger	Larger	Larger (4)	Larger	Larger (4)	Larger (4)	Overlap	Overlap	Smaller	Overlap
BAM	Larger	Larger	Larger (4)	Larger	Overlap (4)	Overlap (4)	Larger	Overlap	Overlap	Overlap
BH	Larger	Larger	Larger (4)	NA	Larger (4)	Larger (4)	NA	Overlap	Overlap	Larger

from this region be examined with respect to the diagnostic characters presented here, because they may represent additional specimens of *M. yatesi*.

Molecular data.—Specimens of *M. sanborni*, clades 1–3 of *M. minuta*, and *M. schmidtorum* are most closely related to *M. yatesi* (Fig. 3); therefore, we restrict discussion of molecular comparisons to these groups. The cytochrome-*b* gene analyses statistically support *M. yatesi* being genetically divergent from its closely related congeners. The genetic distance value (Table 3) separating *M. yatesi* from *M. sanborni* is 5.3%, a value that is typical for mammalian species recognized by classical morphology and is interpreted as indicative of sufficient isolation for 2 clades to speciate by an allopatric model of speciation involving the Bateson-Dobzhansky-Muller process (Bradley and Baker 2001; Baker and Bradley 2006). The genetic distance separating *M. yatesi* from *M. schmidtorum* is 9.5%. Values separating *M. yatesi* from members of *M. minuta* clades range from 9.2% (eastern Ecuador *M. minuta*) to 10.4% (Guyana *M. minuta*). Although values between 2% and 11% genetic divergence may indicate a high probability of conspecific populations (Bradley and Baker 2001), comparable values of genetic distance are found between recognized species of *Micronycteris* (including sister species) and of other genera of phyllostomid bats (e.g., *Carollia*, *Glossophaga*, and *Mesophylla* [Baker and Bradley 2006]; *Artibeus* [Larsen et al. 2007]; and *Dermanura* [Solari et al. 2009]). Furthermore, in this study we used these molecular data coupled with morphometric data and qualitative morphological characters. This combination of data sets is desirable to avoid unnecessary taxonomic splitting and makes our assessment conclusive.

Final remarks and conservation.—The molecular data analyzed provide statistical support for recognizing *M. yatesi* as distinct from its congeners. Moreover, discrete external and cranial morphological characters discriminate this species from other congeners. Additionally we found evidence that some cranial measurements can be used to discriminate *M. yatesi*, but a larger sample size is needed to provide statistical support. The number of bat species recognized for Bolivia does not increase because *M. yatesi* replaces the record of *M. sanborni*. As far as we can ascertain, *M. sanborni* is restricted to Brazil (Simmons 1996) and *M. yatesi* is restricted to Bolivia.

Special attention should be given to records of pale-bellied *Micronycteris* from the ecoregions where *M. yatesi* was recorded; for example, Peñaranda and Pérez-Zubieta (2010) mention 2 records of *M. minuta* in the valleys of Cochabamba. *M. yatesi* constitutes the only species of bat thus far to be described from Bolivian specimens only. As for the specimen reported from Mato Grosso do Sul, Brazil, based on the information provided by Ferreira Santos et al. (2010) we cannot determine whether it is *M. sanborni* or an additional specimen of *M. yatesi*. We recommend that the specimen be reanalyzed under the evidence presented herein. Until more specimens are found in neighboring countries and for conservation planning purposes, we consider this species Bolivia's 1st endemic bat of the more than 130 species occurring in that country (Aguirre et al. 2010a).

In terms of conservation status, 7 species of threatened bats currently are listed in the Bolivian *Red List of Vertebrates* (Tarifa and Aguirre 2009) and *Bat Action Plan* (Aguirre et al. 2010b). An additional 5 are considered Near Threatened and 23 species are Data Deficient (Tarifa and Aguirre 2009). Only 1 species of *Micronycteris* (*M. schmidtorum*) is currently listed (but see the introduction regarding validity of this record) and its status is considered Data Deficient (Tarifa and Aguirre 2009; Aguirre et al. 2010b). We must consider *M. yatesi* Data Deficient until more long-term data are obtained. With only 3 known specimens captured over the last 15 years it is

impossible to assess population stability, which is inherent to applying *IUCN Red List* criteria (International Union for Conservation of Nature and Natural Resources 2011). Nonetheless, of the thousands of net-hours and > 2,500 individuals netted in over a decade of fieldwork we were only able to obtain 3 individuals of *M. yatesi*, suggesting it is an extremely rare species in terms of relative abundance compared to more common taxa.

The Yungas, Cerrado, and Chiquitano Dry Forest ecoregions harbor most of the threatened species of Bolivian bats (Tarifa and Aguirre 2009; Aguirre et al. 2010b), and the paratypes were collected in Yungas (male MHNC-M 141) and Cerrado near Chiquitano (female CBF 6154). The serendipitous events leading to the initial discovery of *M. yatesi* are a paradox, because the site was not even targeted for sampling; inclement weather postponed our field team from visiting designated sites in Chiquitano forest and Pantanal habitats. Nonetheless, 9 (41%) of the 22 mammalian species accounted for at these sites are considered threatened enough to warrant placement on the Bolivian *Red List* of mammals (Brooks et al. 2002). Thus, we wish to highlight the conservation potential of this region.

RESUMEN

A pesar de que se ha realizado un trabajo significativo para definir las relaciones interespecíficas en el género *Micronycteris*, estas todavía no han sido plenamente resueltas. En Bolivia, el género *Micronycteris* está representado por 4 especies: *M. hirsuta*, *M. megalotis*, *M. minuta* y *M. sanborni*. Mediante el examen de caracteres morfológicos y análisis de medidas craneanas y datos genéticos, determinamos que *M. sanborni* no se encuentra en Bolivia y describimos una nueva especie cercanamente relacionada a esta. La nueva especie es morfométricamente distinta de sus congéneres, formando un grupo separado de *M. schmidtorum*, *M. minuta* y *M. brosseti* en el componente principal 1 (el cual explica 57.3% de la variación y está correlacionado con el largo dentario del maxilar) y separado de *M. sanborni* en el componente principal 2 (el cual explica 35.4% de la variación y está correlacionado con la longitud condilobasal). La nueva especie forma un clado con soporte estadístico en todos los análisis filogenéticos, sin embargo su relación de especie hermana con *M. sanborni* carece de soporte. Los valores de distancias genéticas que separan *Micronycteris* sp. nov. de sus parientes más cercanos varía de 5.3% (versus *M. sanborni*) a 10.4% (versus *M. minuta* de Guyana). Diagnosticamos y describimos la nueva especie en detalle y la nombramos en honor del fallecido Terry Lamon Yates por sus contribuciones a la mastozoología boliviana. *Micronycteris* sp. nov. es la primera especie de murciélago endémica de Bolivia y debido a su importancia discutimos las implicaciones para su conservación.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—List of specimens examined, geographic origin, voucher number, tissue number, and GenBank accession numbers for cytochrome-*b* sequences.

Found at DOI: 10.1644/12-MAMM-A-259.S1

SUPPORTING INFORMATION S2.—Sequence of *Micronycteris sanborni* used in the phylogenetic analyses based on 4 fragments obtained from vouchers CMNH 98915 and CMNH 98916 (see "Materials and Methods").

Found at DOI: 10.1644/12-MAMM-A-259.S2

LITERATURE CITED

AGUIRRE, L. F., C. J. MAMANI, K. BARBOZA-MARQUEZ, AND H. MANTILLA-MELUK. 2010a. Lista actualizada de los murciélagos de Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 27:1–7.

AGUIRRE, L. F., ET AL. 2010b. Plan de acción de los murciélagos amenazados de Bolivia. Ministerio de Medio Ambiente y Agua-Vicerninisterio de Medio Ambiente, Biouniversidad, Cambios Climáticos y de Gestión y Desarrollo Forestal-Dirección General de Bioversidad. Centro de Estudios en Biología Teórica Aplicada-Programa para la Conservación de los Murciélagos de Bolivia. International Union for Conservation of Nature-Species Survival Commission-Bat Specialist Group, Centro de Bioversidad y Genética-Universidad Mayor de San Simon, Cochabamba, Bolivia.

AGUIRRE, L. F., AND M. TERÁN. 2007. Subfamilia Phyllostominae. Pp. 187–226 in Historia natural, distribución y conservación de los murciélagos de Bolivia (L. F. Aguirre, ed.). Fundación Simón I. Patiño, Santa Cruz, Bolivia.

ALLEN, J. A. 1900. List of bats collected by Mr. H. H. Smith in the Santa Marta region of Colombia, with descriptions of new species. Bulletin of the American Museum of Natural History 13:87–94.

ANDERSEN, K. 1906. On the bats of the genera *Micronycteris* and *Glyphonycteris*. Annals and Magazine of Natural History, Series 7, 18:50–65.

ANDERSON, S. 1997. Mammals of Bolivia: taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1–652.

BAKER, R. J., AND R. D. BRADLEY. 2006. Speciation in mammals and the genetic species concept. Journal of Mammalogy 87:643–662.

BAKER, R. J., S. R. HOOFER, C. A. PORTER, AND R. A. VAN DEN BUSSCHE. 2003. Diversification among the New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1–33.

BICKHAM, J. W., J. C. PATTON, D. A. SCHLITTER, I. L. RAUTENBACH, AND R. L. HONEYCUTT. 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). Molecular Phylogenetics and Evolution 33:333–338.

BRADLEY, R. D., AND R. J. BAKER. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

BROOKS, D. M., T. TARIFA, J. M. ROJAS, R. J. VARGAS-M., AND H. ARANIBAR. 2002. A preliminary assessment of mammalian fauna of the eastern Bolivian panhandle. Mammalia 65:509–520.

CZAPLEWSKI, N. J., AND G. S. MORGAN. 2003. Fossil bats of the Americas. Sam Noble Museum of Natural History, Norman, Oklahoma.

EMMONS, L. 1998. Mammal fauna of the Parque Nacional Noel Kempff Mercado. Pp. 129–135 in A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia (T. J. Killeen and T. S. Schulenberg, eds.). RAP Working Paper 10. Conservation International, Washington, D.C.

FERREIRA SANTOS, C., M. RODRIGUES NOGUEIRA, N. LEME DA CUNHA, AND L. F. ALVES DA CUNHA CARVALHO. 2010. Southernmost record of the Sanborn's big-eared bat, *Micronycteris sanborni* (Chiroptera, Phyllostomidae). Mammalia 74:457–460.

FONSECA, R. M., ET AL. 2007. Morphological and molecular variation within little big-eared bats of the genus *Micronycteris* (Phyllostomidae: Micronycterinae) from San Lorenzo, Ecuador. Pp. 721–746 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1–981.

GIANNINI, N. P., J. R. WIBLE, AND N. B. SIMMONS. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bulletin of the American Museum of Natural History 295:1–134.

GRAY, J. E. 1825. An attempt at a division of the family Vespertilionidae into groups. Zoological Journal 2:242–243.

GRAY, J. E. 1866. Revision of the genera of Phyllostomidae, or leaf-nosed bats. Proceedings of the Zoological Society of London 1866:111–118.

HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST. Palaeontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9.

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-*b* gene. Journal of Mammalogy 82:1092–1101.

IBISCH, P. L., S. G. BECK, B. GERKMANN, AND A. CARRETERO. 2003. Ecoregiones y ecosistemas. Pp. 47–88 in Biodiversidad: la riqueza de Bolivia (P. L. Ibisch and G. Mérida, eds.). Editorial Fundación Amigos de la Naturaleza (FAN–Bolivia), Santa Cruz, Bolivia.

IBISCH, P. L., S. REICHLE, K. COLUMBA, R. VIDES, AND H. JUSTINIANO (eds.). 2002. Plan de conservación y desarrollo sostenible para el bosque seco Chiquitano, Cerrado, y Pantanal Boliviano. Versión Resumida. Fundación para la Conservación del Bosque Chiquitano. Editorial Fundación Amigos de la Naturaleza (FAN–Bolivia), Santa Cruz, Bolivia.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2011. Guidelines for using the IUCN red list categories and criteria. Version 9.0. Prepared by the Standards and Petitions Subcommittee. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111–120.

LARSEN, P. A. ET AL. 2007. Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on cytochrome-*b* DNA sequences. Journal of Mammalogy 88:712–727.

LARSEN, P. A., L. SILES, S. C. PEDERSEN, AND G. G. KWIECINSKI. 2011. A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Saint Vincent, Lesser Antilles. Mammalian Biology 76:687–700.

LINARES-PALOMINO, R., ET AL. 2008. Non-woody life-form contribution to vascular plant species richness in a tropical American forest. Plant Ecology 201:87–99.

LIRA, I. E., C. MUDESPACHER, AND B. GARCÍA GUIDO. 1994. Theria diccionario de mamíferos. A. G. T. Editors, S. A., México, Distrito Federal, México.

OCHOA, J. G., AND J. H. SÁNCHEZ. 2005. Taxonomic status of *Micronycteris homezi* (Chiroptera: Phyllostomidae). Mammalia 69:323–335.

PEÑARANDA, D. A., AND J. C. PÉREZ-ZUBIETA. 2010. Ensamblaje de murciélagos en los valles secos interandinos de Cochabamba (Bolivia). Revista Boliviana de Ecología y Conservación Ambiental 27:35–42.

PORTER, C. A., S. R. HOOFER, C. A. CLINE, F. G. HOFFMAN, AND R. J. BAKER. 2007. Molecular phylogenetics of the phyllostomid bat genus *Micronycteris* with descriptions of two new subgenera. Journal of Mammalogy 88:1205–1215.

RATTER, J. A., J. F. RIBEIRO, AND S. BRIDGEWATER. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Annals of Botany 80:223–230.

REDFORD, K. H., AND G. A. B. DA FONSECA. 1986. The role of gallery forests in the zoogeography of the Cerrado's non-volant mammalian fauna. Biotropica 18:126–135.

RIDGWAY, R. 1912. Color standards and color nomenclature. R. Ridgway, Washington, D.C.

RONQUIST, F., ET AL. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542.

SALAZAR-BRAVO, J., T. TARIFA, L. F. AGUIRRE, E. YENSEN, AND T. L. YATES. 2003. Revised checklist of Bolivian mammals. Occasional Papers, Museum of Texas Tech University 220:1–27.

SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. Molecular cloning: a laboratory manual. 2nd ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SIMMONS, N. B. 1996. A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from northeastern Brazil, with comments on phylogenetic relationships. American Museum Novitates 3158:1–34.

SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

SIMMONS, N. B., AND R. S. VOSS. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna, part 1. Bats. Bulletin of the American Museum of Natural History 237:1–219.

SIMMONS, N. B., R. S. VOSS, AND D. W. FLECK. 2002. A new Amazonian species of *Micronycteris* (Chiroptera: Phyllostomidae) with notes on the roosting behavior of sympatric congeners. American Museum Novitates 3358:1–14.

SMITH, M. F., AND J. L. PATTON. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnaean Society 50:149–177.

SOLARI, S., ET AL. 2009. Operational criteria for genetically defined species: analysis of the diversification of the small fruit-eating bats, *Dermanura* (Phyllostomidae: Stenodermatinae). Acta Chiropterologica 11:279–288.

TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI, AND S. KUMAR. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28:2731–2739.

TARIFA, T., AND L. F. AGUIRRE. 2009. Mamíferos. Pp. 429–571 in Libro rojo de la fauna silvestre de vertebrados de Bolivia. Ministerio de Medio Ambiente y Agua, La Paz, Bolivia.

TAVARES, V. C., AND V. A. TADDEI. 2003. Range extension of *Micronycteris schmidtorum* Sanborn, 1935 (Chiroptera: Phyllostomidae) to the Brazilian Atlantic forest, with comments on taxonomy. Mammalia 67:463–467.

TERÁN, M. 2010. Nuevos registros de murciélagos (Chiroptera: Phyllostomidae: Phyllostominae) para el Departamento de La Paz, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 27:85–91.

WILLIAMS, S. L., AND H. H. GENOWAYS. 2007. Subfamily Phyllostominae. Pp. 255–299 in Mammals of South America (A. L. Gardner, ed.). University of Chicago Press, Chicago, Illinois. Vol. 1.