



Original Investigation

A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Saint Vincent, Lesser AntillesPeter A. Larsen^{a,*}, Lizette Siles^a, Scott C. Pedersen^b, Gary G. Kwiecinski^c^a Department of Biological Sciences and the Museum, Texas Tech University, Lubbock, TX 79409-3131, USA^b Department of Biology and Microbiology, South Dakota State University, Brookings, SD 57007, USA^c Department of Biology, University of Scranton, Scranton, PA 18510, USA

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ABSTRACT

We describe and formally name a species of big-eared bat (genus: *Micronycteris*), collected from the Lesser Antillean island of Saint Vincent. The new species is distinguished from its closest relative, *Micronycteris megalotis*, by its large size, distinct craniodental features, and by mitochondrial DNA variation. The distribution of the new species is restricted to the island of St. Vincent, southern Lesser Antilles. Relaxed molecular clock analyses indicate the most recent common ancestor between the St. Vincent species of *Micronycteris* and mainland populations of *M. megalotis* is less than 1 million years. Rising sea levels during the late Pleistocene likely contributed to the geographic isolation and subsequent allopatric speciation of this new species. Our data reinforce previous hypotheses regarding unrecognized species diversity within the *M. megalotis* complex.

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Introduction

Big-eared bats of the genus *Micronycteris* Gray 1866 are a common component of the Neotropical bat fauna and occur throughout South America, Central America, and Mexico. The most recent assessment of the genus (Porter et al., 2007) indicates that at least nine species, partitioned into four subgenera, are included within *Micronycteris*. Of these, *Micronycteris megalotis* (Gray 1842) is traditionally viewed as the most widely distributed species occurring from southeastern Brazil northward throughout northern South America, in the southern Caribbean as far north as Saint Vincent, and in Middle America northward to southern Mexico (Alonso-Mejía and Medellín, 1991; Vaughan and Hill, 1996; Porter et al., 2007; Williams and Genoways, 2008). However, this expansive distribution is largely dependent upon taxonomic interpretations of putative subspecific variation within *M. megalotis*, with some authors considering *M. megalotis microtis* as a distinct species, *M. microtis* Miller 1898 (Handley, 1976; Simmons, 1996; Simmons and Voss, 1998). The uncertainty regarding the taxonomic arrangements within the *M. megalotis* complex is reinforced with arbitrary identifications based on external morphology (see Williams and Genoways, 2008) and by paraphyletic relationships in genetic datasets (Porter et al., 2007). Moreover, the phylogenetic analy-

ses presented in Porter et al. (2007) indicate unrecognized species diversity within *M. megalotis* (*sensu stricto*).

In 2005 and 2006, nineteen specimens of *M. megalotis* were collected during field expeditions to the island of St. Vincent, southern Lesser Antilles (Fig. 1). Although *M. megalotis* had been previously reported from the island (Vaughan and Hill, 1996), our morphological and genetic data indicate that the St. Vincent population of *Micronycteris* represents a distinct species separate from *M. megalotis*. The purpose of this paper is to formally describe the new species of *Micronycteris* from St. Vincent. Furthermore, using a relaxed molecular clock, we provide a hypothesis for the timescale of the diversification of the genus and discuss our results with respect to the origin of the St. Vincent population of the new species. In light of our data, we re-evaluate the conclusions of Porter et al. (2007) regarding additional species-level variation within mainland species historically identified as *M. megalotis*.

Materials and methods

Specimens examined

Nineteen voucher specimens of *Micronycteris* (16 male; 3 female) were collected from St. Vincent in 2005 and 2006. All materials (including tissues and blood samples) collected during these expeditions are housed in the Natural Science Research Laboratory of the Museum of Texas Tech University. For comparison, voucher specimens of an additional 234 specimens were examined from six species of *Micronycteris* (*M. hirsuta*: *n* = 32; *M. matses*:

* Corresponding author. Tel.: +1 806 742 3722x283; fax: +1 806 742 2963.

E-mail address: peter.larsen@ars.usda.gov (P.A. Larsen).

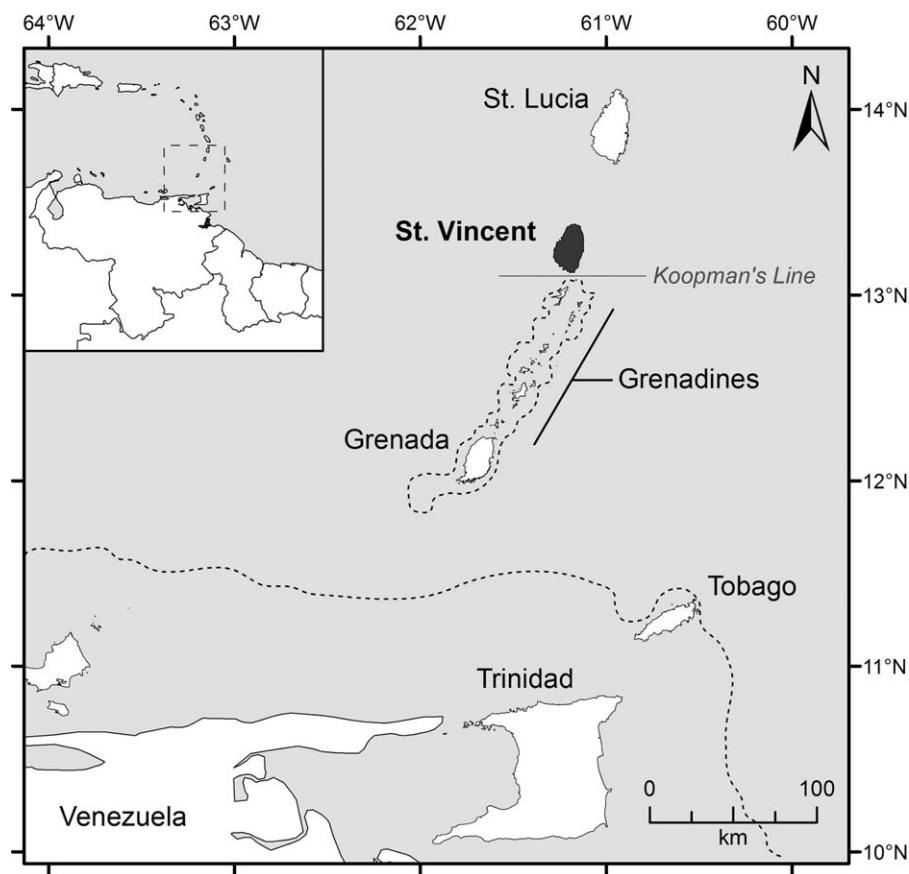


Fig. 1. Map of the southern Lesser Antilles. Specimens of *Micronycteris* were collected from St. Vincent (shaded region) during field expeditions in 2005 and 2006. Inlay shows geographic position of the region of interest relative to northern South America and the Greater Antilles. Dotted line identifies approximate land area of the Grenadines Bank and northern South American continental shelf during last glacial maximum (Rohling et al., 1998; MacPhee et al., 2000). A solid gray line depicts the southern Lesser Antillean portion of Koopman's Line (as defined in Genoways et al., 2010).

n=6; *M. megalotis*: *n*=100; *M. microtis*: *n*=34; *M. minuta*: *n*=45; *M. schmidtorum*: *n*=17). Specimens examined are deposited in the following natural history collections: American Museum of Natural History, New York (AMNH); Natural Science Research Laboratory of the Museum of Texas Tech University, Lubbock (NSRL; TTU = voucher number, TK = tissue number); Carnegie Museum of Natural History, Pittsburgh (CMNH); University of Kansas Museum of Natural History, Lawrence (KU); the National Museum of Natural History, Washington, D.C. (NMNH); and the Royal Ontario Museum, Toronto, Ontario, Canada (ROM). Museum voucher numbers for all specimens examined are listed in Appendix A.

Morphological methods

Sixteen cranial and mandibular measurements were used to assess the phenetic variation among species of *Micronycteris*. Measurements were taken to the nearest 0.01 mm with digital calipers. Only adult specimens were included in our analyses. 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), dorsal hair length (including length of basal and terminal colors), and presence/absence of the hair on the leading edge of the pinnae (Simmons et al., 2002). Cranial and mandibular measurements included: greatest skull length (GSL); braincase height (BH); braincase width (BW); coronoid process length (CPL); condylobasal length (CL); mastoid breadth (MB); zygomatic breadth (ZB); postorbital constriction width (POW); interorbital width (IW); breadth across upper canines (C1C1); greatest breadth across upper molars (GBM);

palatal length (PL); post-palatal length (PPL) maxillary toothrow length (MXTR); mandible length (ML); and mandibular toothrow length (MTL).

We performed a Principal Component Analysis of the 16 cranial and mandibular characters using the statistical package PAST version 1.86b (Hammer et al., 2001). The specimens used for this analysis included the dark-bellied *Micronycteris* (*sensu* Simmons et al., 2002) from which all sixteen cranial and mandibular measurements were available (see Appendix A). Species included in the analysis were *M. megalotis* (*n*=85), *M. microtis* (*n*=27), *M. matses* (*n*=5), *M. hirsuta* (*n*=26), and *M. sp. nov.* (*n*=12). Principal components were calculated using the covariance matrix to preserve the information about relative scale among variables.

Molecular methods

Whole genomic DNA was extracted from 15 specimens of *M. megalotis* collected from St. Vincent (*n*=14) and Tobago (*n*=1) using the Qiagen DNeasy Extraction Kit (Qiagen Inc., Valencia, California). The entire cytochrome-*b* gene (1140 base pairs) was amplified and sequenced for all 15 individuals following the methods of Larsen et al. (2007). An ABI 3100-Avant Genetic Analyzer (PE Applied Biosystems, Foster City, California) was used to generate sequence data. Sequences were manually checked and aligned using Sequencher v.4.9 (Gene Codes Corporation, Ann Arbor, MI) and Clustal W v.2.0 (Larkin et al., 2007), respectively. MacClade v.4.05 (Maddison and Maddison, 2000) was used to further check for discontinuities and stop codons.

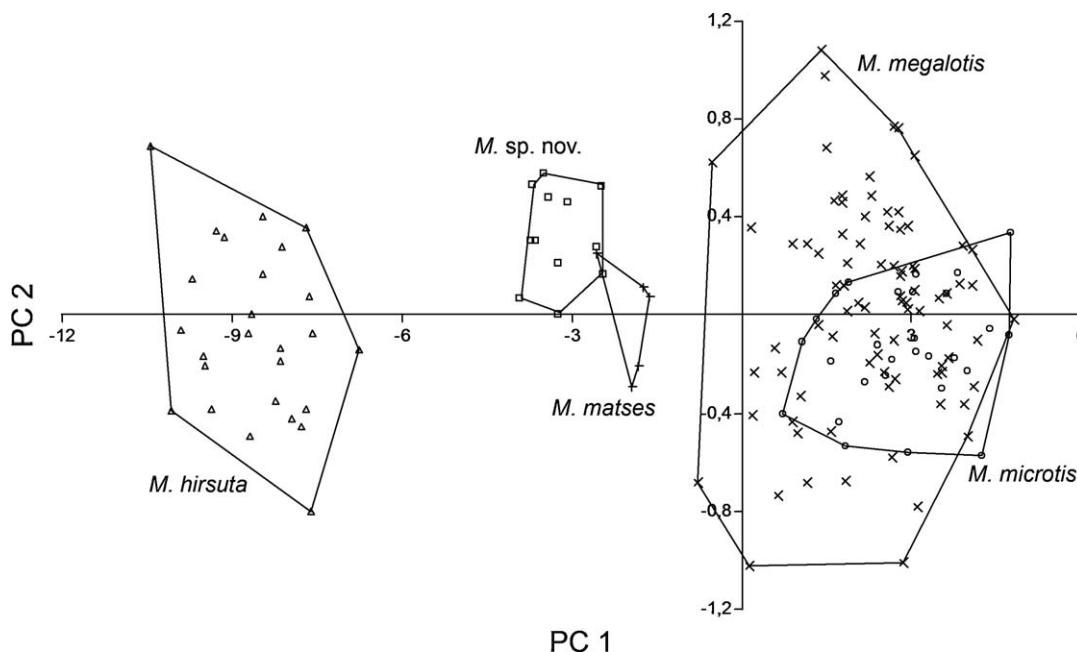


Fig. 2. Scatter plot of the first and second principal component scores of a Principal Components Analysis based on 16 cranial and mandibular measurements from 4 species of *Micronycteris* (*M. hirsuta*, *M. matses*, *M. microtis*, and *M. megalotis*) and *M. sp. nov.* from St. Vincent.

An additional 42 complete cytochrome-*b* gene sequences from 10 species of *Micronycteris* were gathered from GenBank and were included for phylogenetic comparisons (Appendix A). A Bayesian analysis was performed on the complete dataset using MrBayes v.3.1 software (Ronquist and Huelsenbeck, 2003), running 10×10^6 generations with 1 cold and 3 incrementally heated Markov chains, random starting trees for each chain, and trees sampled every 100 generations. Maximum likelihood and maximum parsimony analyses were performed using PhyML v.3.0 (Guindon and Gascuel, 2003) and MEGA v.4.1 (Tamura et al., 2007), respectively. The GTR + Γ + I model was selected by jModeltest (Posada, 2008) and was used for maximum likelihood and minimum evolution analyses. Statistical support for resulting phylogenies was measured by bootstrap support values (of 500 iterations) and Bayesian posterior probabilities. Genetic distance values were estimated using the Kimura 2-parameter model (Kimura, 1980). *Lampronycteris* and *Macrotus* were used as outgroups for all phylogenetic analyses as previous studies have indicated that these genera are outgroups with respect to *Micronycteris* (Simmons, 1996; Simmons and Voss, 1998; Simmons et al., 2002; Baker et al., 2003).

Timescale of diversification

Cytochrome-*b* gene sequences (1140 bp) reported herein and from Porter et al. (2007) were used to estimate the timescale of diversification of *Micronycteris* (~10 species; see Appendix A). Relaxed molecular clock analyses were performed using BEAST v.1.5 (Drummond and Rambaut, 2007). Given the poor fossil record for the genus, previously estimated diversification dates for the family Phyllostomidae were used as secondary calibration points with normal distribution priors (Baker et al., in press; Ho, 2007). Secondary priors used were: time to the most recent common ancestor (TMRCA) between *Lampronycteris* and *Micronycteris* approximately 23.2 million years ago (MYA) (25.5–21.0 MYA) and TMRCA between *M. megalotis* and *M. hirsuta* approximately 11.9 MYA (12.3–11.6 MYA). The GTR + Γ + I model of nucleotide substitution best fit the data (see above) and was used in all BEAST analyses. Node dates were examined using a Yule species prior and random selection of single representatives of each species with pre-

liminary analyses consisting of 5 runs at 20×10^6 generations. Final analyses consisted of combining log and tree files generated from 2 runs at 50×10^6 generations.

Results

Principal Components Analysis

Principal components (PC) 1 and 2 accounted for 97.3% of the total variance (PC 1 = 96.6% and PC 2 = 0.7%), and were correlated with greatest skull length and condylobasal length (Table 1). The new species formed a cluster separate from the remainder of the *M. megalotis* complex as well as *M. hirsuta* and *M. microtis* along PC 1 (Fig. 2). The results of the principal components analysis indicate that the new species of *Micronycteris* is morphometrically more similar to *M. matses* than to *M. megalotis* (Fig. 2).

Table 1

Results of the principal component analysis of 16 cranial and mandibular characters from specimens of *Micronycteris hirsuta*, *M. matses*, *M. megalotis*, *M. microtis*, and *M. sp. nov.*. Loadings of the first two principal components are presented and accounted for 97.3% of the total variance. Variables and sample sizes are defined in Materials and methods.

| Variable | PC1 | PC2 |
|----------|-------|-------|
| GSL | -0.51 | 0.10 |
| BH | -0.18 | -0.26 |
| BW | -0.16 | -0.26 |
| CPL | -0.18 | -0.20 |
| CL | -0.43 | 0.26 |
| MB | -0.20 | -0.33 |
| ZB | -0.26 | -0.45 |
| POW | -0.09 | -0.09 |
| IW | -0.10 | -0.08 |
| C1C1 | -0.08 | -0.14 |
| GBM | -0.14 | -0.14 |
| PL | -0.26 | 0.53 |
| PPL | -0.13 | -0.25 |
| MXTR | -0.21 | 0.07 |
| ML | -0.36 | 0.14 |
| MTL | -0.23 | 0.08 |



Fig. 3. Bayesian phylogram based on DNA sequence data of the entire 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 *Macrotus waterhousii* were used as outgroups but are not shown.

Phylogenetic analyses

Sequence alignment of the 59 cytochrome-*b* sequences was unequivocal and without internal stop codons. Of 1140 characters, 695 were invariant, and 361 were parsimony informative. Including outgroups, 65 of the informative characters were at 1st codon positions, 16 at 2nd position, and 280 at 3rd positions. Of the 14 specimens examined from St. Vincent, there were 5 unique hap-

lotypes. Identical sequences were excluded from some analyses to prevent repetitive sampling. Maximum likelihood analysis resulted in 1 tree with a ln-likelihood of -7285.09 and minimum evolution resulted in a single least-evolved tree with a score of 1.06. All phylogenetic analyses resulted in congruent clade topologies and revealed a sister relationship between the St. Vincent *Micronycteris* and *M. megalotis* from Tobago (Fig. 3). The clade comprised of the St. Vincent *Micronycteris* was statistically supported in all analyses

Table 2

Average Kimura 2-parameter distances within (bold) and among species of *Micronycteris* based on 1140 base pairs of the cytochrome-*b* gene. Clades within *M. megalotis* and *M. minuta* are shown in Fig. 3. *M. sp. Honduras* and *M. sp. Peru* are presented in Porter et al. (2007).

| No. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | |
|-----|--|------------|------|------------|------------|------------|------------|------------|------|------|------|------------|------------|------------|-----|-----|------------|
| 1 | <i>M. brossetti</i> (<i>n</i> =2) | 0.3 | | | | | | | | | | | | | | | |
| 2 | <i>M. giovanniae</i> (<i>n</i> =1) | 10.4 | — | | | | | | | | | | | | | | |
| 3 | <i>M. hirsuta</i> (<i>n</i> =7) | 12.5 | 10.8 | 1.9 | | | | | | | | | | | | | |
| 4 | <i>M. matses</i> (<i>n</i> =3) | 10.0 | 5.6 | 10.8 | 0.2 | | | | | | | | | | | | |
| 5 | <i>M. megalotis</i> Clade 1 (<i>n</i> =6) | 10.1 | 5.9 | 10.3 | 3.1 | 1.7 | | | | | | | | | | | |
| 6 | <i>M. megalotis</i> Clade 2 (<i>n</i> =7) | 10.3 | 5.9 | 10.9 | 4.5 | 4.9 | 1.3 | | | | | | | | | | |
| 7 | <i>M. megalotis</i> Clade 3 (<i>n</i> =4) | 9.5 | 5.8 | 10.9 | 4.6 | 5.2 | 4.4 | 0.9 | | | | | | | | | |
| 8 | <i>M. megalotis</i> Clade 4 (<i>n</i> =1) | 9.6 | 6.2 | 12.0 | 5.2 | 6.0 | 4.5 | 2.7 | — | | | | | | | | |
| 9 | <i>M. microtis</i> Brazil (<i>n</i> =1) | 11.0 | 7.1 | 12.4 | 5.6 | 5.8 | 5.6 | 5.7 | 5.9 | — | | | | | | | |
| 10 | <i>M. minuta</i> Clade 1 (<i>n</i> =1) | 16.9 | 16.3 | 17.9 | 15.5 | 15.5 | 16.3 | 16.6 | 16.1 | 16.6 | — | | | | | | |
| 11 | <i>M. minuta</i> Clade 2 (<i>n</i> =2) | 14.8 | 15.1 | 15.6 | 15.3 | 14.7 | 15.1 | 15.9 | 15.9 | 16.6 | 6.4 | 0.5 | | | | | |
| 12 | <i>M. minuta</i> Clade 3 (<i>n</i> =2) | 15.1 | 15.1 | 16.0 | 15.0 | 14.6 | 15.1 | 15.4 | 15.2 | 16.3 | 8.8 | 7.5 | 1.7 | | | | |
| 13 | <i>M. schmidtorum</i> (<i>n</i> =3) | 15.5 | 15.1 | 16.4 | 14.8 | 14.3 | 15.1 | 14.7 | 15.0 | 15.0 | 5.2 | 6.4 | 7.6 | 3.0 | | | |
| 14 | <i>M. sp. Honduras</i> (<i>n</i> =1) | 11.4 | 5.5 | 11.1 | 6.4 | 6.1 | 6.3 | 6.3 | 7.0 | 7.7 | 16.6 | 15.4 | 15.7 | 15.0 | — | | |
| 15 | <i>M. sp. Peru</i> (<i>n</i> =1) | 10.5 | 5.9 | 11.7 | 5.0 | 5.2 | 5.3 | 5.4 | 5.5 | 4.6 | 16.7 | 15.6 | 15.3 | 14.7 | 7.6 | — | |
| 16 | <i>M. sp. nov.</i> (<i>n</i> =14) | 9.4 | 6.4 | 11.7 | 5.2 | 6.0 | 4.5 | 2.7 | 1.9 | 5.8 | 16.2 | 15.4 | 15.1 | 14.7 | 6.6 | 5.6 | 0.5 |

(Fig. 3). Genetic distance values between clades ranged from 17.9% (*M. hirsuta* versus *M. minuta* Clade 3) to 1.9% (*M. sp. nov.* versus *M. megalotis* [Tobago]) (Table 2).

Timescale of diversification

Our results indicate the majority of diversification events among extant species of *Micronycteris* occurred during the Pliocene and Pleistocene epochs (5.0–0.6 MYA; Fig. 4). The lineage comprised of *M. minuta* (Clades 1–3; Fig. 3) and *M. schmidtorum* (subgenus *Schizonycteris*; sensu Porter 2007) is sister to the remainder of the genus and likely originated during the mid-Miocene (Fig. 4). The TMRCA between Clade 1 of *M. megalotis* and *M. matses* was approximately 1.2 MYA (1.9–0.6 highest posterior density) and the TMRCA for Clades 2–4 of the *M. megalotis* complex was within the last 2 million years (3.1–1.4 highest posterior density). Our results indi-

cate that the TMRCA between the St. Vincent *Micronycteris* and *M. megalotis* from Tobago (Clade 4; Fig. 3) was within the last 1 million years (Fig. 4).

Systematic description

Family Phyllostomidae Gray, 1825

Subfamily Micronycterinae sensu Baker et al., 2003

Genus *Micronycteris* Gray, 1866

***Micronycteris buriri*, new species**

Holotype

Adult female; skin, skull, postcranial skeleton and associated tissues deposited at the Natural Science Research Laboratory of the Museum of Texas Tech University; TTU 105773 (Fig. 5). Collected on 1 August 2005. Original number, Peter A. Larsen (PAL) 365. TK 144656 identifies tissue samples (preserved in lysis buffer) deposited in the NSRL, TTU. External measurements (mm) recorded in the field by PAL are: total length, 70; tail length, 14; length of hind foot, 13; length of ear from notch, 20; tragus, 5. Body mass was 8.6 g. Forearm of the dried specimen, taken by GGK, is 39.18 mm. Selected cranial and mandibular measurements are presented in Table 3.

Type locality

Saint Vincent and the Grenadines, Saint Vincent; St. Andrew Parish: Vermont Nature Trail, Parrot Lookout; 2.3 km N, 1.75 km E Vermont (13°13'20.2" N, 61°12'43.4" W). Collected at 496 m in elevation.

Paratypes

Eighteen additional specimens (16 male; 2 female) were collected from St. Vincent and are hereby designated as paratypes. One adult male preserved in alcohol (TTU 105774 [skull not extracted]) was collected at the type locality on 1 August 2005. Additional paratypes consist of: four adult male specimens (TTU 105640 [skin and skull], TTU 105641 [alcohol; skull not extracted], TTU 105642 [alcohol], TTU 105643 [alcohol; skull not extracted]) collected from the Colonarie River 1 km S, 2.4 km W South Rivers, Charlotte Parish (13°14'10.4" N, 61°09'52.7" W; 248 m) on 28 July 2005; four adult males (TTU 105352–105355 [alcohol]) collected from La Soufrière Trail, 0.7 km N, 5.1 km W Orange Hill, Charlotte Parish (13°19'22.8" N, 61°10'1.2" W; 646 m) on 1 June 2006; two adult males (TTU 105507 and 105508 [alcohol]) collected 0.75 km S, 2.3 km E Rose Hall, St. David Parish on 3 June 2006 (13°15'51.2" N, 61°13'25.7" W; 377 m); two adult males (TTU 105971 and 105972 [alcohol; skull not extracted]) collected from Convent 0.4 km N, 3 km E Grove, St.

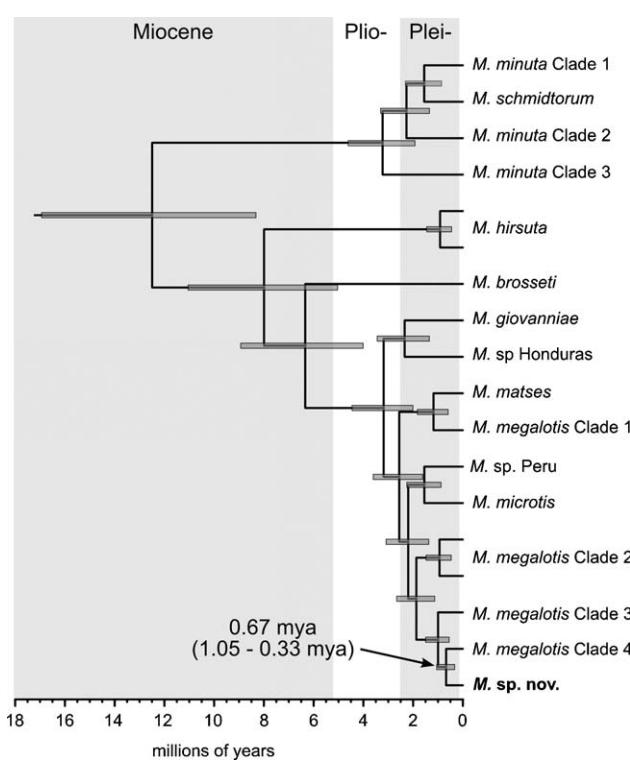


Fig. 4. Chronogram of *Micronycteris*. Horizontal gray bars represent 95% highest posterior density intervals for divergence estimates. Vertical gray bars indicate relative boundaries of the Miocene, Pliocene (Plio-) and Pleistocene (Plei-) epochs.



Fig. 5. Dorsal, ventral, and lateral views of the skull and lower jaw of the holotype of *Micronycteris buriri* (TTU 105773).

Patrick Parish ($13^{\circ}14'53.5''$ N, $61^{\circ}12'32.1''$ W; 440 m) on 3 August 2005; one adult male (TTU 105548 [alcohol]) captured on 4 June 2006 on Mount St. Andrew, 1.75 km N, 0.3 km E, Green Hill, St. George Parish ($13^{\circ}11'17.9''$ N, $61^{\circ}12'56.8''$ W; 633 m); one adult male (TTU 105473; [alcohol]) collected on 28 May 2006, 1.25 km N, 1.6 km E, Vermont, St. Andrew Parish ($13^{\circ}12'55.6''$ N, $61^{\circ}12'52''$ W; 310 m); one adult male (TTU 105535; [alcohol]) collected on 27 May 2006 from Morgan Woods, 0.4 km N, 2.4 km E Richmond, St. David Parish ($13^{\circ}18'28.9''$ N, $61^{\circ}12'27.9''$ W; 253 m); two juvenile females (TTU 105981; [alcohol, skull not extracted]) and (TTU 105982; [alcohol]) were collected from Mount Wynne Caves, Mount Wynne Bay, St. Patrick Parish ($13^{\circ}13'3.6''$ N, $61^{\circ}16'30.4''$ W; 0 m) on 6 August 2005. Measurements of adult paratypes are presented in Table 3.

Table 3

Selected measurements of the type material of *Micronycteris buriri*. Voucher numbers for paratypes are presented in the Systematic Description. Mean, standard deviation, range (in parentheses) and sample size (italics) are presented for adult paratypes.

| | Holotype (TTU 105773) | Paratypes |
|--------------------------------------|-----------------------------|-----------------------------------|
| Sex | Female | Males |
| Total body length | 70.00 | 68.92 ± 1.78 (66.00–72.00) 12 |
| Tail length | 14.00 | 14.75 ± 1.71 (12.00–18.00) 12 |
| Length of hind foot | 13.00 | 11.25 ± 1.36 (10.00–13.00) 12 |
| Ear length | 20.00 | 21.92 ± 1.93 (19.00–25.00) 12 |
| Forearm length | 39.18 | 38.35 ± 0.73 (36.36–39.47) 16 |
| 3rd metacarpal length | 33.99 | 33.65 ± 0.55 (32.47–34.23) 12 |
| Greatest skull length | 21.67 | 21.21 ± 0.34 (20.73–21.75) 12 |
| Braincase height | 8.76 | 8.64 ± 0.22 (8.22–9.03) 12 |
| Braincase width | 8.30 | 8.17 ± 0.12 (7.95–8.33) 12 |
| Coronoid process length | 4.58 | 4.53 ± 0.12 (4.35–4.75) 12 |
| Condyllobasal length | 19.25 | 18.78 ± 0.27 (18.33–19.23) 11 |
| Mastoid breadth | 9.38 | 9.28 ± 0.14 (9.05–9.46) 12 |
| Zygomatic breadth | 10.13 | 9.90 ± 0.16 (9.64–10.18) 12 |
| Postorbital constriction width | 4.59 | 4.41 ± 0.08 (4.32–4.60) 12 |
| Interorbital width | 5.10 | 4.86 ± 0.18 (4.56–5.20) 12 |
| Breadth across upper canines | 3.79 | 3.75 ± 0.09 (3.56–3.88) 12 |
| Greatest breadth across upper molars | 7.27 | 6.75 ± 0.16 (6.56–7.15) 12 |
| Palatal length | 10.12 | 10.25 ± 0.24 (9.85–10.58) 12 |
| Post-palatal length | 6.92 | 6.58 ± 0.27 (6.15–7.04) 11 |
| Maxillary toothrow length | 8.22 | 8.19 ± 0.14 (7.92–8.37) 12 |
| Mandible length | 13.81 | 13.67 ± 0.22 (13.29–13.97) 11 |
| Mandibular toothrow length | 9.07 | 8.87 ± 0.17 (8.62–9.14) 12 |

Distribution

Known only from Saint Vincent, southern Lesser Antilles (Fig. 1). Collecting localities ranged from sea level to 646 m in elevation (see above). Vaughan and Hill (1996) report an additional five specimens collected from Vermont and Wallilabou Valley.

Diagnosis

Micronycteris buriri is distinguished from its closest relative, *M. megalotis*, by its size and distinct craniodental features. The morphological phenotype of *M. buriri* is smaller than *M. hirsuta*, similar in size to *M. giovanniae* and *M. matuses*, and larger than the remaining species of the genus. *Micronycteris buriri* is a dark-bellied species similar, with respect to this character, to *M. giovanniae*, *M. hirsuta*, *M. matuses*, *M. megalotis*, and *M. microtis*. Diagnostic characters include upper incisors that are non-bilobed, hypodont lower incisors, very prominent cingula in upper and lower incisors, and very shallow basisphenoid pits, separated by a poorly developed septum only in the posterior region. Within the genus *Micronycteris*, the combination of these traits is unique to *M. buriri*.

Description

Micronycteris buriri is a medium-sized bat (forearm 36.4–39.5 mm). The dorsal fur is bicolor and long (10–13 mm in the shoulder region), with a white base of variable length, comprising half to one-tenth of each hair. Juveniles have unicolored dorsal fur. The ventral fur in juveniles is shorter in length (7 mm) and all adults show a narrow white band at the base, whereas juveniles have unicolored venter hairs. The terminal portions of the dorsal and ventral fur are snuff brown to bister (Ridgway, 1912: Plate XXIX) in color. Fur on the outside medial third of the pinna is dense and of variable length (3–6 mm), in juveniles the

fur is short and sparse. The ears are large with rounded tips, and a low-notched band connects their bases (examination of the fluid paratypes). The notch is very shallow. Hind feet and thumbs are hairy. Uropatagium and wing membranes are naked.

Rostrum is elongated and the premaxillae are short and wide. Maxillae are highly inflated over the region between the second premolar and first molar. The nasal bones are inflated, which gives the rostrum a globular appearance. The incisive foramina are ovoid and the infraorbital foramina are wide and deep. In most individuals of the type series, a narrow sagittal crest arises at the point where the maxillae and the frontal bones join and has a constant height along the skull. Nuchal crest is absent. Zygomatic arch is robust. Paraoccipital processes are not well developed and do not surpass the occipital condyles. Foramen magnum is round. Basisphenoid pits are shallow, separated by a poorly developed septum in the posterior region. Basioccipital bone is narrow. The openings in the alisphenoid canal are oval; the anterior is bigger than the posterior. Postpalatal extension is narrow over the mesopterygoid fossa and has a V-shaped posterior margin.

Medial upper incisors (I1) are large and not bilobed. Lateral upper incisors (I2) are not bilobed and are convergent and small, approximately 1/3 the length of the medial upper incisors. The canines are robust with cingula well developed; however the antero-lingual cingular style on the lower canines is essentially absent (Appendix C, Plate 2). Upper premolars are subequal in anteroposterior length, with P4 being slightly larger than P3. One individual (TTU 105548) presents a distinct gap between the upper premolars; three other individuals present a subtle narrow gap, whereas the remaining specimens do not present a gap. P3 in occlusal view has a rectangular shape, and the anterior end in P4 has a squared shape. The metastyle of P4 is well developed. M1 and M2 have a similar size; the occlusal outline of M1 is slightly more rectangular than M2; the parastyle of M2 is the most developed of all the molar styles. M2 and M3 are not separated by a gap.

Lower incisors are hypodont (height almost twice the width), with a triangular shape, and are not bilobed. Crown height of lower premolars varies with tooth wear; though it is noticeable that p3 is slightly smaller than p2 and p4. Coronoid process is high, and the upper margin of the ascending process has a steep slope (25–35°). Angular process is hook-shaped and well developed, extending outward to the same level of the mandibular condyle.

Molecular data

Phylogenetic analyses indicate that *M. buriri* is within the subgenus *Micronycteris* (sensu Porter et al., 2007) and is most closely related to specimens referable to *M. megalotis* (Fig. 3). Therefore, we restrict our molecular comparison to *M. megalotis*. The cytochrome-*b* gene genetic distance values which separate *M. buriri* from mainland members of the *M. megalotis* complex range from 1.9% (*M. buriri* versus Tobago *M. megalotis*) to 6.0% (*M. buriri* versus Suriname *M. megalotis*). These genetic distance values are similar to the interspecific variation found within other genera of phyllostomid bats (e.g. *Platyrrhinus*; Velazco and Patterson, 2008). Intraspecific genetic variation was approximately 0.5%. *Micronycteris buriri* forms a statistically supported clade sister to *M. megalotis* from Tobago (Fig. 3).

Etymology

The specific epithet *buriri* is a noun in apposition originating from the Garifuna word, Búriri, for bat. Búriri is derived from the words “Buriga-” and “Luburiga” meaning dark and darkness. We suggest that the common name of this species be the St. Vincent Big-eared Bat.

Comparisons

Micronycteris buriri is distinguished from its congeners by a combination of external, cranial, and dental characters, as well as phenotypic size variation. The dark-bellied *M. buriri* is larger than all pale-bellied *Micronycteris* in most external and cranial measurements (*M. brosseti*, *M. minuta*, *M. sanborni*, and *M. schmidtorum*; Table 2, Appendix B). Additionally, *M. buriri* is significantly larger than the dark-bellied species *M. microtis* in all cranial and external measurements (paired *t*-test, $P \leq 0.01$), with the exception of tail length. When compared to *M. megalotis*, although the external measurements may overlap, paired *t*-tests showed that *M. buriri* is significantly larger than *M. megalotis* in all cranial and external measurements ($P \leq 0.01$). Detailed comparisons between *M. buriri* and specific populations of *M. megalotis* are provided later in this section. *Micronycteris hirsuta* (subgenus *Xenoctenes*; sensu Porter et al., 2007) is the only species in the genus that shares with *M. buriri* the unique trait of hypodont lower incisors (Simmons et al., 2002). However, *M. hirsuta* is significantly larger than *M. buriri* in all measurements ($P \leq 0.01$), except tail length (Appendix B and Table 3). *Micronycteris hirsuta* also has very prominent nuchal and sagittal crests, in contrast with the absence of the nuchal crest, and the poorly developed sagittal crest in *M. buriri*. Moreover, the medial upper incisors in *M. hirsuta* are long and narrow, whereas in *M. buriri* they are short and robust. The remaining two species of dark-bellied *Micronycteris* (*M. matuses* and *M. giovanniae*) are of similar size to *M. buriri* (Appendix B and Table 3; Fonseca et al., 2007), however they do not have hypodont lower incisors. Additionally, those species are only known from their type localities (Simmons, 2005; Fonseca et al., 2007), and are phylogenetically distinct from the new species we describe (Fig. 3).

Based on our phylogenetic analysis, we present a more detailed comparison of the morphology between *M. buriri* and closely related specimens within the *M. megalotis* complex (see Clades 1–4 in Fig. 3). Our analyses indicate that the most closely related member of the *M. megalotis* complex with *M. buriri* was collected from Tobago (TTU 43944; *M. megalotis* Clade 4 in Fig. 3). This individual (see Fig. 6 and Appendix C), along with 11 other specimens collected from Trinidad and Tobago (Appendix A), were compared (morphologically) to *M. buriri*. The upper incisors of *M. megalotis* from Trinidad and Tobago are bilobed, whereas *M. buriri* presents non-bilobed upper incisors. The lower incisors are not lobed and are hypodont in *M. buriri*, whereas they are trilobed and non-hypodont in the Trinidad and Tobago specimens. The basisphenoid pits in specimens from Trinidad are deep, with a complete septum that separates them, whereas in *M. buriri* the basisphenoid pits are shallow, and the intervening septum is only noticeable in the posterior region. The canines in *M. buriri* are robust with prominent cingula, whereas the Trinidad and Tobago specimens present more slender canines with thinner cingula. When comparing the lower canines, the antero-lingual cingular style is greatly reduced in *M. buriri* and very developed in the specimen of *M. megalotis* from Tobago (Appendix C, Plate 2).

A single specimen of *M. megalotis* is reported from Grenada (an adult female collected in 1937 [NMNH 267684]). Despite additional surveys in 1967 and throughout the 1980s no additional specimens have been collected from Grenada (Genoways et al., 1998). This observation caused Genoways et al. (1998) to question whether or not the Grenada specimen represented an accidental record or an established population on the island. Although no genetic data are available from the specimen, our external and skull measurements of this specimen indicate that it is within the range of mainland *M. megalotis* from Trinidad and Tobago: FA, 34.15; Mc3, 29.66; GSL, 17.97; BH, 7.77; BW, 7.29; CPL, 3.84; CL, 16.00; MB, 8.25; ZB, 8.68; POW, 3.76; IW, 4.31; C1C1, 3.27; PL, 9.53; PPL, 4.56; MXTR, 6.87; ML, 11.77; MTL, 7.45 (acronyms defined in Materials

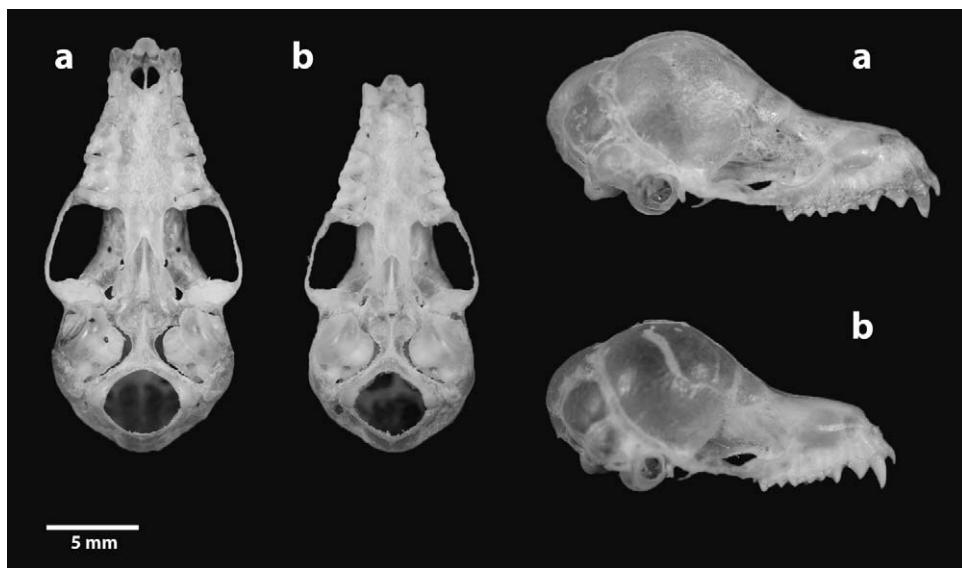


Fig. 6. Ventral and lateral views of the skulls of the holotype of *Micronycteris buriri* (a: TTU 105773) and *M. megalotis* from Tobago (b: TTU 43944).

and methods). With respect to phenotype, these data suggest that the Grenada specimen of *M. megalotis* is more similar to Trinidad and Tobago specimens than to *M. buriri* thus it is assigned to *M. megalotis*.

One individual from Clade 3 of the *M. megalotis* complex (Fig. 3) was available for comparison (TTU 33276 from Venezuela; Appendix C). The skull of this specimen showed similar characters to the Trinidad and Tobago specimens regarding the lower incisors, basisphenoid pits, canines, and cingula; all of which contrast with *M. buriri*. Also, P3 in occlusal view has an ovoid shape and is less prominent in the Venezuela specimen, whereas *M. buriri* has a more rectangular and prominent P3. Moreover, P4 has a pointed anterior end in the Venezuela specimen, whereas in *M. buriri*, the anterior end is more squared in shape. In the Venezuela specimen there is a gap between M1 and M2, and the metastyle and parastyle of M2 are highly developed, whereas in *M. buriri* there is no gap between molars, and only the parastyle of M2 is well developed.

Another specimen closely related to *M. buriri* (~4.5% in cytochrome-*b* variation) was collected from western Ecuador (TTU 103291; *M. megalotis* Clade 2 in Fig. 3; Appendix C), and we compared this and 3 other specimens from the same region in Ecuador (Guayas) with *M. buriri*. The four skulls examined showed very similar characters to the Venezuela specimen (TTU 33276; see above) regarding the basisphenoid pits and shape of premolars and molars. The canines and cingula have similar characteristics as the specimen from Tobago (TTU 43944; see above). Additionally, the Guayas–Ecuador specimens showed bilobed upper incisors, which contrast with the non-bilobed upper incisors in *M. buriri*. The lower incisors are similar in length in both *M. buriri* and *M. megalotis* from Guayas, but they are not lobed and have a more triangular shape in the former, and they are trilobed and have a more oval shape in the latter.

Skulls of *M. buriri* were also compared with seven skulls collected from Mexico, one of which was included in our phylogenetic analyses (TTU 36524; *M. megalotis* Clade 2 in Fig. 3). The examined skulls show similar characters to the Venezuela and Ecuador specimens regarding the basisphenoid pits, canines, cingula, and molars. However, the premolars seen in occlusal view have a rectangular shape, similar to the *M. buriri* specimens.

Vaughan and Hill (1996) report 5 additional specimens (1 female and 4 males; deposited in the Natural History Museum, London, UK) of *Micronycteris* collected from St. Vincent in 1994 and 1995. The external and cranial measurements reported in Vaughan and Hill

(1996) for these specimens are similar to those reported herein for *M. buriri*.

Discussion

Origin of *Micronycteris buriri*

The morphological features which separate *M. buriri* from its closest relatives in the *M. megalotis* complex are distinct and indicate that *M. buriri* is on a unique evolutionary trajectory separate from *M. megalotis*. This observation is better appreciated when discussed within the framework of evolutionary time. Our results indicate that the TMRCA between *M. buriri* and its most closely related South American taxon is less than 1.05 million years before present (~670,000 ybp; Fig. 4). We hypothesize that the ancestral form of *M. buriri* successfully established a population on St. Vincent after colonizing the southern Lesser Antilles from northern South America during the mid- to late Pleistocene. Support for this hypothesis is found by the close genetic relationship between specimens from St. Vincent, Tobago, and northern Venezuela (Table 1; Figs. 3 and 4). Moreover, fluctuating sea levels during the Pleistocene (Rohling et al., 1998) likely facilitated colonization of St. Vincent from northern South America, as a substantial portion of the Grenada Bank (~4000–4500 km²; MacPhee et al., 2000) and South American continental shelf would have been exposed during glacial maxima (see Fig. 1). Rising sea levels during the late Pleistocene (Rohling et al., 1998) and associated loss of habitat throughout the Grenadines likely contributed to reduced gene flow from mainland South America, Trinidad, Tobago, and Grenada, thus effectively isolating the St. Vincent population of *M. buriri*. The evolutionary history of *M. buriri* is most parsimoniously explained by allopatric speciation.

Previous hypotheses regarding the islands to the south of St. Vincent, the Grenadines (Fig. 1), serving as a barrier to chiropteran gene flow (Genoways et al., 1998, 2010; Phillips et al., 1989) reinforce our hypothesis regarding the origin of *M. buriri*. Indeed, *M. buriri* is distributed immediately north of the southern Lesser Antillean portion of Koopman's Line (Fig. 1; see Genoways et al., 2010), which defines the boundary of the West Indian chiropteran fauna (Genoways et al., 1998). This observation is important as *M. buriri* represents a recently evolved southern Lesser Antillean endemic.

Implications for diversity within *Micronycteris megalotis*

Recognition of *M. buriri* creates further paraphyly of the *M. megalotis* complex (Fig. 3; see Porter et al., 2007). The genetic data presented herein and in Porter et al. (2007) indicate the presence of four putative species-level clades within *M. megalotis* (Clades 1–4 in Fig. 3). The phylogeographic structure among these clades is noteworthy as it suggests some level of genetic isolation corresponding to the Guiana Shield (Clade 1) and the regions north of the Orinoco River in Venezuela, northward to Trinidad and Tobago, westward to Central America and southward to western Ecuador (Clades 2–4) (Fig. 3).

Andersen (1906) applied the name *typica* to the smaller form of *M. megalotis* distributed throughout southern Brazil and Peru, northward throughout Guiana and eastern Venezuela, to Trinidad and Tobago. To some extent the phylogeographic structuring within *M. megalotis* agrees with Andersen's assessment, in as much as there are distinct phylogroups across this region. Thus the name *typica* is available for Clades 1, 3, or 4 presented herein, however, additional data are required for formal application of *typica*. Although Simmons (1996) recognized the taxon *mexicana* Miller 1898 (type locality: Plantinar, Jalisco, México) as subspecific variation within *M. microtis*, it would seem that *mexicana* is applicable to Clade 2 presented herein (Fig. 3). Alternatively, genetic analyses of Central American specimens of *M. microtis* (type locality: Greytown, San Juan del Norte, Nicaragua) may reveal a monophyletic relationship with Clade 2. If such monophyly were documented then *M. microtis* would be applicable, as the name would be a senior synonym. We refrain from a formal taxonomic revision of the *M. megalotis* complex pending additional morphometric and/or genetic data from type specimens and from specimens collected at or near type localities, including from the type locality of *M. megalotis* (Perequé, São Paulo, Brazil).

Additional remarks

Micronycteris has not been collected north of St. Vincent (Genoways et al., 2001, 2007a,b; Larsen et al., 2006; Pedersen et al., 2006, 2007) and recent surveys failed to document *Micronycteris* on the Grenadine islands to south of St. Vincent (Genoways et al., 2010). *Micronycteris buriri* was primarily collected in forested areas and was also captured within banana plantations (see also Vaughan and Hill, 1996). Vaughan and Hill (1996) reported two roosts of *M. buriri* in sea caves on Mount Wynn beach (St. Patrick Parish) and we confirmed the presence of one of these roosts in 2005. Species captured alongside *M. buriri* include: *Artibeus schwartzi*, *Ardops nichollsi*, *Brachyphylla cavernarum*, *Monophyllus plethodon*, *Glossophaga longirostris*, *Molossus molossus*, *Pteronotus rubiginosus*, and *Sturnira lilium*.

See online Appendix D (available in the Supplementary information section) which provides an account of a species epithet previously considered for the new species of *Micronycteris* from St. Vincent.

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Appendix A.

List of specimens examined, including geographic origin, museum voucher number, tissue number, and GenBank accession numbers for cytochrome-*b* sequences. Voucher specimens are housed in the following institutions: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CMNH); 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); United States National Museum of Natural History (NMNH); University of Kansas Museum of Natural History (KU). GenBank accession numbers (AY–; DQ–; HQ–) identify specimens used in phylogenetic analyses. Asterisk (*) indicates specimen used in principal components analysis. Double asterisk (**) indicates specimen used in final BEAST analysis.

Lampronycteris brachyotis.—TRINIDAD AND TOBAGO: Trinidad: Mayaro: (CMNH 97174, TK 25239, AY380748**).

Macrotus californicus.—UNITED STATES OF AMERICA: Arizona (TK 28962, AY380744**).

Macrotus waterhousii.—MEXICO: Morelos (TTU 71435, TK 27889, AY380745**).

Micronycteris brosseti.—GUYANA: Potaro-Siparuni: (KU 155162, AY380770); (KU 155163, AY380771**).

M. giovanniae.—ECUADOR: Esmeraldas: (QCAZ 7200, TK 104673, AY380750**).

M. hirsuta.—COLOMBIA: Magdalena: (CMNH 2659*). COSTA RICA: Heredia: (CMNH 92466*). ECUADOR: Esmeraldas: (TTU 103130, TK 135937, DQ077416). Esmeraldas: (CMNH 112510*); (CMNH 112518*); (CMNH 112519*); (TTU 85449, TK 104677, DQ077410); (TTU 85452, TK 104680, DQ077412**). Pichincha: (NMNH 528479*); (NMNH 528480*). FRENCH GUIANA: (TK 82835, DQ077409**). GUYANA: Barima-Waini: (ROM 101033*). Upper Takutu: (ROM 32470). NICARAGUA: Atlantico Sur: (TTU 13156). Rivas: (TTU 30441). Zelaya: (TTU 30437); (TTU 30438). PANAMA: Canal Zone: Orchid Island: (NMNH 304871*); (NMNH 304872*). Veraguas: (MSB 94371, NK 101614, AY380768). PERU: Loreto: (AMNH 273153*). SURINAME: Brokopondo: (ROM 113969*). TRINIDAD AND TOBAGO: Trinidad: Blanchisseuse: (TTU 5449*). Mayaro: (TTU 10116*); (TTU 43943, TK 25229, DQ077408); (TTU 5299*). St. Andrew: (AMNH 175609*). St. George: (AMNH 179958); (CMNH 97177*, TK 25041, AY380751); (CMNH 97178*); (TTU 5410*). St. Patrick: (AMNH 179955); (AMNH 179957*); (AMNH 180032*); (AMNH 180033*). VENEZUELA: Amazonas: (NMNH 388687*); (NMNH 407239*). Aragua: (NMNH 517305*). Yaracuy: (NMNH 371407*).

M. matses.—PERU: Loreto: (AMNH 272814*, DQ077417**); (AMNH 273044*); (AMNH 273133); (AMNH 273196*); (MUSM 15229*); (MUSM 15231* [Holotype]); (AMNH 273043 [Paratype], DQ077418); (AMNH 273095 [Paratype], DQ077419).

M. megalotis.—**BRAZIL**: Amazonas: (AMNH 78648*); (AMNH 78649*). Sao Paulo: (ROM 111099, TK 16377, AY380755**). **COLOMBIA**: Cundinamarca: (AMNH 207775*); (AMNH 207776*); (AMNH 207777*); (AMNH 207780*); (AMNH 207781*). **COSTA RICA**: Puntarenas: (NMNH 565807*). **ECUADOR**: El Oro: (TTU 102602, TK 135244, DQ077427). Esmeraldas: (TTU 85289); (TTU 85389, TK 104617, DQ077422**); (TTU 85346*); (TTU 85436); (TTU 85424, TK 104652, AY380766); (TTU 102918, TK 135636, DQ077423); (TTU 103198*). Guayas: (TTU 103291*, TK 134837, DQ077428); (TTU 103437, TK 134960, DQ077429); (TTU 103387*); (TTU 103439*); (TTU 103491*). **FRENCH GUIANA**: Paracou: (AMNH 266020); (AMNH 267090*); (AMNH 267092*); (AMNH 267862*); (AMNH 267863*); (AMNH 267097, TK 18782, AY380756). **GRENADA**: (NMNH 267684). **GUYANA**: East Berbice: (NMNH 582262*). Essequibo River; Leguan Island: (AMNH 182731*). Potaro-Siparuni: (ROM 108745, TK 16375, AY380757); (ROM 108807, TK 16376, AY380760). Upper Demerara: (NMNH 588487*); (NMNH 588488*); (ROM 59912*); (ROM 59916*); (ROM 59922*). Upper Takutu: (NMNH 337274); (NMNH 338939*); (ROM 31709); (ROM 31710*); (ROM 31711); (ROM 31712); (ROM 31718). **MEXICO**: Chiapas: (TTU 36534, TK 20558, AY380764**); (TTU 36533*, TK 907693); (TTU 36534*, TK 20558); (TTU 46647*, TK 907732); (TTU 46648*, TK 907733); (TTU 46649*, TK 907734); (TTU 46652*, TK 907736). San Luis Potosi: (TTU 35355*, TK 16517). **NICARAGUA**: Carazo: (KU 110698*); (KU 110699*); (KU 114771*). Matagalpa: (KUM 70473*); (KUM 70474*). **PANAMA**: Canal Zone: Balboa: (AMNH 99344). Barro Colorado Island: (NMNH 296253*); (NMNH 296256*); (NMNH 296257*). Ft. Clayton: (NMNH 296250*); (NMNH 296251*); (NMNH 296252*). Ft. Kobbe: (NMNH 296402). Ft. Randolph: (NMNH 311904*); (NMNH 311905*). Orchid Island: (NMNH 304866); (NMNH 304867*). Cerro Azul: (NMNH 306544*); (NMNH 306545*). Darien: (AMNH 38146); (AMNH 38147); (AMNH 38149*). Gamboa: (ROM 104195, TK 16372, AY380765). **PERU**: Loreto: (AMNH 273169*). **SURINAME**: Brokopondo: (CMNH 63577). Marowijne: (CMNH 76768, TK 17606, AY380759). Sipaliwini: (CMNH 68390, TK 17071, AY380758). **TRINIDAD AND TOBAGO**: **Tobago**: Les Coteaux: (AMNH 175877*). St. John: (AMNH 184721*); (NMNH 537900*); (NMNH 537901*); (NMNH 537902*); (NMNH 537904*). St. Mary: (NMNH 540658*). St. Patrick: (TTU 43944*, TK 25147, HQ593853**). St. Paul: (NMNH 540659*); (NMNH 540660*); (NMNH 540661*). **Trinidad**: Cocorete: (KM 151140*). Guayaguayare: (TTU 10118*). Mayaro: (TTU 47491*). Nariva: (TTU 5275). St. Andrew: (AMNH 31239); (AMNH 31240*); (TTU 23760*, TK 8377). St. George: (AMNH 29707*); (AMNH 29708*); (AMNH 29709); (AMNH 29713*); (CMNH 97182*); (CMNH 97183*); (TTU 5438*); (TTU 5446*); (TTU 9788*); (TTU 5495*); (TTU 23754*, TK 8441); (TTU 23755*, TK 8425); (TTU 23757*, TK 8031); (TTU 23759*, TK 8436). **VENEZUELA**: Amazonas: (NMNH 388711*); (NMNH 388715); (NMNH 415209*); (NMNH 415212*); (NMNH 415214*); (NMNH 415215*). Los Venados: (NMNH 370069*); (NMNH 370070*). Barinas: (CMNH 78291, TK 19407, DQ077421**). Bolivar: (AMNH 130628*); (AMNH 16119*); (AMNH 30680*); (CMNH 78295, TK 19040, AY380773**); (CMNH 78294*); (CMNH 78296*); (CMNH 78761, TK 19047, AY380762). Carabobo: (AMNH 31508*).

Districto Federal: (AMNH 16685*); (NMNH 102913*); (NMNH 105417); (NMNH 105418); (NMNH 143762*); (NMNH 143764); (NMNH 143765*). El Callao: (NMNH 199598); (NMNH 199599*). Falcon: (NMNH 418878*); (NMNH 418880*); (NMNH 418881). Guarico: (TTU 33276*, TK 15175, AY380763). Margarita Island: (NMNH 63215*). Monagas: (AMNH 69961*); (AMNH 69962*); (AMNH 69964*). Santa Rosa: (KU 118008*). Sucre: (AMNH 69966*). Trujillo: (NMNH 371409); (NMNH 371410*). Yasracui: (AMNH 32135).

M. minuta.—**BRAZIL**: Amazonas: (AMNH 92689); (AMNH 92693); (AMNH 92695); (AMNH 92697). Apiamo: (ROM 77767). Minas Gerais: (ROM 91172). **COLOMBIA**: Putumayo: (ROM 56575). Rio Zulia: (ROM 84984). **COSTA RICA**: Alajuela: (KU 142698). **ECUADOR**: Esmeraldas: (CMNH 112524); (CMNH 112525); (CMNH 112526); (TTU 103201, TK 135801, DQ077402). Guayas: (TTU 103253, TK 134785, DQ077400**). Napo: (ROM 106320). Orellana: (ROM 104067, TK 16371, AY380752). Pastaza: (TTU 84825, TK 104053, DQ077404**). **GUYANA**: East Berbice: (ROM 100364). Potaro-Siparuni: (KUM 155164). Upper Demerara: (NMNH 582263); (NMNH 582262, TK 86643, AY380754**). Upper Takutu: (ROM 97958). **PANAMA**: Bocas Del Toro: (NMNH 575452). Chiriqui: (NMNH 331112). Darien: (NMNH 314557); (NMNH 362392). Los Santos: (NMNH 323058). **PERU**: Loreto: (AMNH 273172, TK 82836, DQ077405). **SURINAME**: Brokopondo: (CMNH 63579); (CMNH 63580); (CMNH 63581). Commewijne: (CMNH 63582). Saramacca: (CMNH 63583); (CMNH 63584). **TRINIDAD AND TOBAGO**: Trinidad: Guayaguayare: (KU 117401); (TTU 47942); (TTU 5225); (TTU 5226); (TTU 5294); (TTU 5295). Maracas Valley: (ROM 77769). Mayaro: (AMNH 183295). Santa Maria: (TTU 5456). St. George: (TTU 9785). **VENEZUELA**: Guarico: (NMNH 444232). Miranda: (NMNH 385291); (NMNH 385292). Sucre: (NMNH 388721). Zulia: (NMNH 444225); (NMNH 444229); (NMNH 444231).

M. schmidtorum.—**BELIZE**: Toledo: (CMNH 90108). **BRAZIL**: Pernambuco: (CMNH 98908); (CMNH 98909); (CMNH 98910); (NMNH 555703). **COSTA RICA**: Heredia: (NMNH 562753). **PANAMA**: (NK 27684, AY380767). Las Palmitas: (NMNH 323061); (NMNH 323062). **PERU**: (TK 40447, AY380753**). **VENEZUELA**: Amazonas: (NMNH 407257); (NMNH 407258). Lara: (AMNH 130715); (AMNH 130716); (AMNH 130717); (AMNH 130718); (AMNH 130719); (AMNH 130720); (AMNH 130725).

M. sp.—**HONDURAS**: Colon: (TTU 104168, TK 136752, DQ077420**). **PERU**: Loreto: (AMNH 273169, DQ077407**).

M. buriri.—**SAINT VINCENT AND THE GRENADINES**: St. Vincent: (TTU 105352*, TK 128425, HQ593840); (TTU 105353*, TK 128426, HQ593848); (TTU 105354*, TK 128427, HQ593849); (TTU 105355*, TK 128428); (TTU 105473*, TK 128362, HQ593847); (TTU 105507, TK 128474); (TTU 105508*, TK 128475); (TTU 105535*, TK 128329, HQ593845); (TTU 105548*, TK 128487); (TTU 105640*, TK 144582, HQ593851); (TTU 105641, TK 144583, HQ593841); (TTU 105642*, TK 144584, HQ593852); (TTU 105643, TK 144608); (TTU 105773* [Holotype], TK 144656, HQ593843**); (TTU 105774, TK 144657, HQ593850); (TTU 105971, TK 144729, HQ593846); (TTU 105972, TK 144730, HQ593842); (TTU 105981, TK 144776, HQ593839); (TTU 105982*, TK 144777, HQ593844).

Appendix B.

Descriptive statistics of 16 cranial and 6 external measurements (mm, acronyms defined in Materials and methods) for females and males (sample size in parentheses) of *Micronycteris hirsuta*, *M. matusse*, *M. megalotis*, *M. microtis*, *M. minuta*, and *M. schmidtorum*. Values include mean, standard deviation, and range (in parentheses) where applicable.

| External measurements of females | | | | | | |
|----------------------------------|------------------------------------|-----------------------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| | <i>M. hirsuta</i> | <i>M. matusse</i> | <i>M. megalotis</i> | <i>M. microtis</i> | <i>M. minuta</i> | <i>M. schmidtorum</i> |
| TL | 76.40 ± 6.00 (10) (65.00–85.00) | 38.12 ± 0.85 (3) (37.19–38.87) | 59.03 ± 5.54 (30) (43.00–68.00) | 60.23 ± 3.42 (13) (53.00–65.00) | 60.78 ± 5.09 (23) (51.00–69.00) | 64.14 ± 2.19 (7) (61.00–67.00) |
| Tail | 15.00 ± 2.14 (8) (12.00–18.00) | n/a | 13.42 ± 1.74 (30) (10.00–18.00) | 13.69 ± 1.84 (13) (10.00–17.00) | 11.57 ± 1.62 (23) (9.00–15.00) | 13.57 ± 2.64 (7) (9.00–17.00) |
| HF | 12.78 ± 0.97 (9) (12.00–15.00) | n/a | 9.38 ± 1.16 (21) (7.00–12.00) | 9.92 ± 0.86 (13) (8.00–11.00) | 11.26 ± 1.25 (23) (8.00–14.00) | 10.57 ± 0.79 (7) (10.00–12.00) |
| Ear | 25.00 ± 2.18 (9) (21.00–28.00) | n/a | 22.11 ± 2.70 (18) (14.00–25.00) | 20.54 ± 2.67 (13) (13.00–23.00) | 21.21 ± 1.51 (19) (17.00–23.00) | 17.57 ± 2.70 (7) (15.00–21.00) |
| FA | 43.28 ± 1.02 (13) (41.74–44.89) | n/a | 34.17 ± 1.38 (36) (30.15–36.95) | 33.51 ± 1.36 (16) (30.31–35.53) | 35.69 ± 1.75 (25) (31.83–40.53) | 35.54 ± 1.97 (7) (32.53–37.46) |
| Mc3 | 37.30 ± 1.16 (13) (35.56–39.56) | 33.97 ± 0.70 (3) (33.23–34.62) | 29.89 ± 1.10 (38) (27.19–33.19) | 29.22 ± 1.14 (16) (26.72–30.87) | 29.61 ± 2.93 (25) (27.37–39.46) | 31.14 ± 2.09 (7) (28.65–33.87) |
| External measurements of males | | | | | | |
| | <i>M. hirsuta</i> | <i>M. matusse</i> | <i>M. megalotis</i> | <i>M. microtis</i> | <i>M. minuta</i> | <i>M. schmidtorum</i> |
| TL | 71.50 ± 4.74 (10) (64.00–78.00) | 38.13 ± 0.22 (3) (37.98–38.38) | 56.37 ± 3.83 (35) (50.00–66.00) | 57.57 ± 5.46 (14) (43.00–65.00) | 60.11 ± 4.52 (18) (49.00–67.00) | 60.80 ± 3.26 (10) (56.00–66.00) |
| Tail | 13.33 ± 1.94 (9) (11.00–16.00) | n/a | 12.57 ± 2.28 (36) (9.00–18.00) | 12.07 ± 1.98 (14) (8.00–15.00) | 10.83 ± 1.58 (18) (7.00–13.00) | 13.50 ± 1.51 (10) (12.00–17.00) |
| HF | 11.70 ± 1.06 (10) (10.00–13.00) | n/a | 9.36 ± 1.54 (28) (6.00–12.00) | 9.50 ± 0.76 (14) (8.00–11.00) | 11.35 ± 1.37 (17) (9.00–13.00) | 9.70 ± 1.42 (10) (8.00–12.00) |
| Ear | 24.60 ± 1.35 (10) (22.00–26.00) | n/a | 21.00 ± 2.50 (25) (14.00–26.00) | 20.71 ± 1.68 (14) (17.00–23.00) | 21.12 ± 1.45 (17) (18.00–23.00) | 19.10 ± 2.64 (10) (14.00–23.00) |
| FA | 43.09 ± 1.26 (16) (40.90–45.55) | n/a | 33.63 ± 1.49 (58) (29.67–36.82) | 32.39 ± 1.05 (17) (30.33–34.43) | 35.03 ± 1.94 (20) (31.89–40.38) | 34.64 ± 1.56 (10) (32.67–37.23) |
| Mc3 | 36.71 ± 1.27 (16) (34.83–39.15) | 34.10 ± 0.17 (3) (33.97–34.29) | 29.19 ± 1.17 (58) (26.87–32.15) | 28.60 ± 1.09 (17) (26.87–29.99) | 29.04 ± 2.79 (19) (26.69–39.79) | 29.45 ± 1.73 (10) (26.92–32.03) |
| Cranial measurements of females | | | | | | |
| | <i>M. hirsuta</i> | <i>M. matusse</i> | <i>M. megalotis</i> | <i>M. microtis</i> | <i>M. minuta</i> | <i>M. schmidtorum</i> |
| GSL | 23.95 ± 0.48 (13) (23.15–24.71) | 20.65 ± 0.20 (3) (20.46–20.86) | 18.53 ± 0.53 (38) (17.67–19.79) | 18.29 ± 0.63 (14) (17.01–18.97) | 18.81 ± 0.89 (24) (17.82–21.36) | 19.96 ± 0.28 (7) (19.57–20.34) |
| BH | 9.72 ± 0.32 (13) (9.29–10.36) | 8.22 ± 0.37 (3) (7.85–8.58) | 7.75 ± 0.35 (38) (7.04–8.61) | 7.77 ± 0.20 (14) (7.36–8.09) | 7.60 ± 0.31 (24) (7.00–8.12) | 8.16 ± 0.39 (7) (7.72–8.70) |
| BW | 9.20 ± 0.17 (13) (8.91–9.55) | 8.30 ± 0.05 (3) (8.26–8.36) | 7.43 ± 0.22 (39) (7.02–8.20) | 7.36 ± 0.28 (15) (7.01–7.88) | 7.55 ± 0.31 (24) (7.06–8.48) | 8.14 ± 0.21 (7) (7.92–8.46) |
| CPL | 5.82 ± 0.27 (13) (5.27–6.09) | 4.68 ± 0.15 (3) (4.51–4.79) | 3.86 ± 0.20 (37) (3.54–4.75) | 3.82 ± 0.23 (16) (3.47–4.22) | 3.57 ± 0.34 (25) (3.17–4.59) | 4.47 ± 0.30 (7) (4.01–4.81) |
| CL | 20.86 ± 0.46 (13) (20.10–21.73) | 18.14 ± 0.17 (3) (17.94–18.26) | 16.40 ± 0.58 (38) (15.36–17.82) | 16.37 ± 0.46 (14) (15.56–17.17) | 16.69 ± 0.89 (24) (15.89–19.28) | 17.62 ± 0.38 (7) (17.21–18.12) |
| MB | 10.33 ± 0.37 (13) (9.80–11.24) | 9.26 ± 0.12 (3) (9.14–9.38) | 8.20 ± 0.33 (37) (7.51–9.21) | 8.19 ± 0.42 (14) (7.48–8.81) | 8.52 ± 0.28 (23) (7.73–8.92) | 8.94 ± 0.12 (7) (8.80–9.13) |
| ZB | 11.53 ± 0.30 (13) (11.03–12.08) | 10.04 ± 0.13 (3) (9.91–10.16) | 8.69 ± 0.33 (37) (7.82–9.63) | 8.64 ± 0.35 (15) (8.17–9.44) | 8.67 ± 0.42 (23) (8.11–9.87) | 9.50 ± 0.31 (7) (9.01–9.87) |
| POW | 4.88 ± 0.14 (13) (4.70–5.09) | 4.59 ± 0.06 (3) (4.53–4.63) | 3.96 ± 0.14 (39) (3.68–4.37) | 3.92 ± 0.17 (16) (3.63–4.35) | 4.15 ± 0.17 (25) (3.93–4.49) | 4.20 ± 0.11 (7) (4.05–4.35) |
| IW | 5.48 ± 0.33 (13) (5.04–6.14) | 5.06 ± 0.13 (3) (4.93–5.18) | 4.35 ± 0.14 (39) (4.11–4.65) | 4.27 ± 0.15 (16) (3.96–4.57) | 4.37 ± 0.24 (25) (4.03–5.16) | 4.67 ± 0.22 (7) (4.46–5.10) |
| C1C1 | 4.11 ± 0.20 (13) (3.77–4.43) | 3.61 ± 0.14 (3) (3.45–3.71) | 3.20 ± 0.19 (38) (2.58–3.58) | 3.25 ± 0.12 (15) (3.09–3.56) | 3.18 ± 0.14 (25) (2.93–3.60) | 3.42 ± 0.10 (7) (3.27–3.57) |
| GBM | 7.37 ± 0.19 (13) (7.10–7.77) | 6.58 ± 0.17 (3) (6.42–6.75) | 5.93 ± 0.21 (38) (5.31–6.56) | 5.92 ± 0.21 (16) (5.48–6.22) | 5.83 ± 0.26 (25) (5.43–6.49) | 6.32 ± 0.27 (7) (5.94–6.72) |
| PL | 11.28 ± 0.32 (13) (10.87–11.98) | 9.91 ± 0.42 (3) (9.58–10.38) | 8.60 ± 0.43 (39) (7.70–9.53) | 8.36 ± 0.39 (16) (7.34–8.91) | 8.38 ± 0.72 (25) (7.45–10.78) | 9.13 ± 0.35 (7) (8.59–9.64) |
| PPL | 7.10 ± 0.26 (13) (6.76–7.60) | 6.24 ± 0.26 (3) (6.00–6.52) | 5.65 ± 0.36 (38) (4.56–6.26) | 5.82 ± 0.22 (14) (5.12–6.02) | 6.17 ± 0.28 (23) (5.47–6.85) | 6.32 ± 0.17 (7) (6.11–6.58) |
| MXTR | 9.15 ± 0.20 (13) (8.72–9.45) | 7.77 ± 0.08 (3) (7.71–7.86) | 6.89 ± 0.28 (38) (6.39–7.61) | 6.90 ± 0.17 (15) (6.64–7.24) | 6.68 ± 0.39 (25) (5.95–7.70) | 7.54 ± 0.20 (7) (7.29–7.89) |
| ML | 15.45 ± 0.35 (13) (14.85–16.05) | 13.22 ± 0.28 (3) (13.04–13.54) | 11.75 ± 0.43 (37) (10.99–12.77) | 11.64 ± 0.38 (16) (10.88–12.24) | 11.50 ± 0.72 (25) (10.81–13.67) | 12.94 ± 0.52 (7) (12.25–13.58) |
| MTL | 10.00 ± 0.19 (13) (9.66–10.25) | 8.60 ± 0.18 (3) (8.39–8.73) | 7.52 ± 0.32 (37) (6.58–8.13) | 7.42 ± 0.29 (16) (6.77–7.82) | 7.26 ± 0.40 (25) (6.56–8.21) | 8.20 ± 0.29 (7) (7.83–8.63) |

Cranial measurements of males

| | <i>M. hirsuta</i> | <i>M. matus</i> | <i>M. megalotis</i> | <i>M. microtis</i> | <i>M. minuta</i> | <i>M. schmidtorum</i> |
|------|------------------------------------|-----------------------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| GSL | 24.19 ± 0.59 (15) (23.44–25.21) | 20.50 ± 0.23 (3) (20.27–20.73) | 18.43 ± 0.62 (57) (17.07–20.03) | 18.15 ± 0.56 (16) (17.19–19.10) | 18.80 ± 0.93 (19) (17.35–21.92) | 19.65 ± 0.56 (10) (18.77–20.44) |
| BH | 9.79 ± 0.37 (16) (8.92–10.28) | 8.24 ± 0.08 (3) (8.17–8.32) | 7.76 ± 0.35 (57) (6.93–8.56) | 7.63 ± 0.30 (18) (7.25–8.24) | 7.71 ± 0.30 (19) (7.08–8.19) | 8.00 ± 0.22 (10) (7.54–8.32) |
| BW | 9.28 ± 0.23 (15) (8.91–9.58) | 8.26 ± 0.07 (3) (8.20–8.34) | 7.42 ± 0.29 (57) (7.03–8.28) | 7.37 ± 0.27 (18) (6.93–7.79) | 7.61 ± 0.26 (19) (7.31–8.42) | 7.90 ± 0.21 (10) (7.54–8.18) |
| CPL | 5.92 ± 0.18 (16) (5.63–6.23) | 4.38 ± 0.11 (2) (4.30–4.45) | 3.80 ± 0.24 (59) (3.31–4.47) | 3.72 ± 0.22 (18) (3.30–4.21) | 3.58 ± 0.33 (19) (3.24–4.84) | 4.27 ± 0.32 (10) (3.92–4.77) |
| CL | 21.22 ± 0.49 (15) (20.62–22.63) | 18.11 ± 0.27 (3) (17.81–18.34) | 16.33 ± 0.62 (56) (15.34–18.08) | 15.86 ± 0.54 (16) (15.17–17.15) | 16.72 ± 0.93 (19) (15.26–20.04) | 17.38 ± 0.57 (10) (16.48–18.34) |
| MB | 10.26 ± 0.32 (15) (9.81–10.79) | 9.24 ± 0.30 (3) (9.01–9.58) | 8.24 ± 0.36 (56) (7.35–8.98) | 8.09 ± 0.24 (18) (7.75–8.67) | 8.63 ± 0.28 (19) (7.98–9.08) | 8.72 ± 0.25 (10) (8.31–9.19) |
| ZB | 11.52 ± 0.36 (15) (10.56–12.05) | 9.97 ± 0.22 (3) (9.77–10.21) | 8.68 ± 0.40 (58) (7.79–9.72) | 8.54 ± 0.40 (17) (7.77–9.38) | 8.60 ± 0.32 (19) (7.99–9.53) | 9.17 ± 0.33 (10) (8.80–9.76) |
| POW | 4.93 ± 0.15 (16) (4.67–5.23) | 4.48 ± 0.23 (3) (4.30–4.74) | 3.94 ± 0.18 (59) (3.49–4.39) | 3.83 ± 0.20 (18) (3.33–4.14) | 4.17 ± 0.15 (19) (3.87–4.47) | 4.19 ± 0.11 (10) (4.05–4.34) |
| IW | 5.36 ± 0.25 (16) (5.04–5.99) | 4.74 ± 0.11 (3) (4.62–4.82) | 4.38 ± 0.18 (58) (4.03–4.72) | 4.24 ± 0.18 (18) (3.86–4.62) | 4.40 ± 0.20 (19) (4.01–4.86) | 4.72 ± 0.30 (10) (4.40–5.18) |
| C1C1 | 4.16 ± 0.18 (16) (3.80–4.54) | 3.71 ± 0.05 (3) (3.66–3.75) | 3.23 ± 0.21 (58) (2.79–3.72) | 3.23 ± 0.14 (18) (3.04–3.59) | 3.20 ± 0.12 (19) (2.96–3.41) | 3.35 ± 0.19 (10) (3.05–3.66) |
| GBM | 7.45 ± 0.18 (16) (7.16–7.79) | 6.74 ± 0.05 (3) (6.68–6.78) | 5.93 ± 0.27 (59) (5.43–6.57) | 5.84 ± 0.23 (18) (5.43–6.32) | 5.80 ± 0.25 (19) (5.28–6.54) | 6.24 ± 0.29 (10) (5.95–6.96) |
| PL | 11.48 ± 0.53 (16) (10.55–12.89) | 9.77 ± 0.09 (3) (9.66–9.84) | 8.49 ± 0.42 (58) (7.78–9.86) | 8.26 ± 0.31 (18) (7.76–8.92) | 8.28 ± 0.69 (19) (7.14–10.59) | 8.97 ± 0.45 (10) (8.37–9.56) |
| PPL | 7.16 ± 0.45 (14) (6.07–7.91) | 6.07 ± 0.18 (3) (5.94–6.27) | 5.64 ± 0.29 (54) (5.03–6.42) | 5.75 ± 0.25 (17) (5.30–6.22) | 6.26 ± 0.28 (19) (5.72–6.73) | 6.39 ± 0.19 (9) (6.17–6.75) |
| MXTR | 9.22 ± 0.24 (16) (8.81–9.61) | 7.92 ± 0.03 (3) (7.88–7.94) | 6.89 ± 0.29 (59) (6.29–7.50) | 6.77 ± 0.23 (18) (6.40–7.21) | 6.64 ± 0.36 (19) (5.99–7.77) | 7.40 ± 0.22 (10) (7.12–7.76) |
| ML | 15.67 ± 0.40 (16) (15.16–16.49) | 13.14 ± 0.12 (3) (13.03–13.26) | 11.62 ± 0.41 (59) (10.84–12.48) | 11.45 ± 0.39 (17) (10.91–12.22) | 11.49 ± 0.73 (19) (10.33–14.14) | 12.60 ± 0.72 (10) (11.81–13.72) |
| MTL | 10.10 ± 0.27 (16) (9.41–10.51) | 8.50 ± 0.43 (3) (8.02–8.87) | 7.52 ± 0.29 (59) (6.45–8.10) | 7.37 ± 0.24 (17) (6.95–7.75) | 7.23 ± 0.42 (19) (6.57–8.43) | 8.11 ± 0.35 (10) (7.68–8.76) |

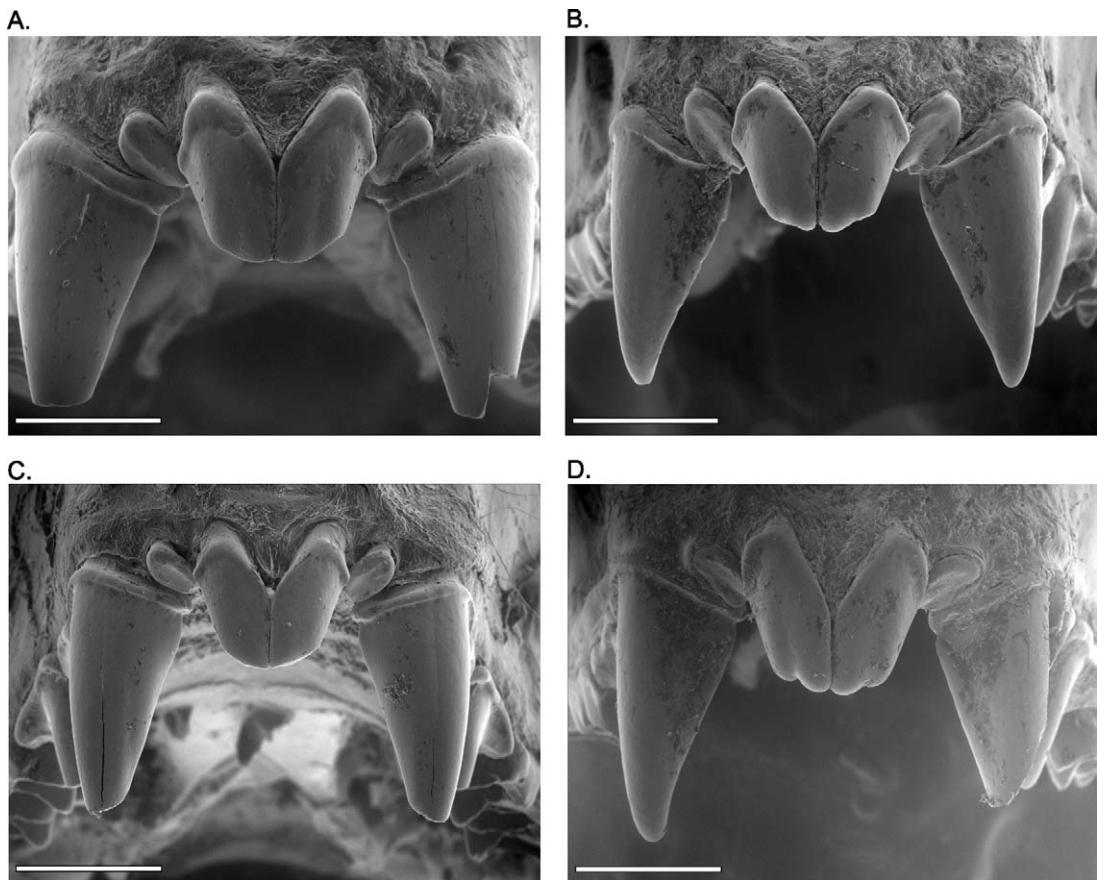


Plate 1. Anterior view of the upper incisors and canines. (A) *Micronycteris buriri* (TTU 105773); (B) *M. megalotis* (Tobago; TTU 43944); (C) *M. megalotis* (Venezuela; TTU 33276); (D) *M. megalotis* (western Ecuador; TTU 103439).

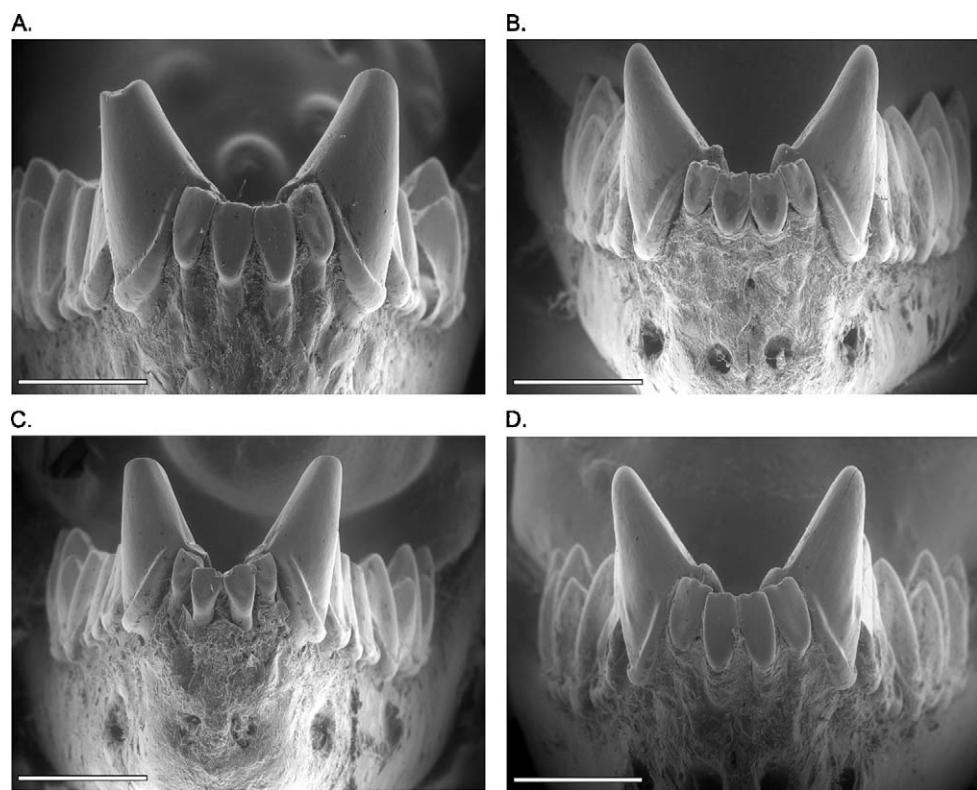


Plate 2. Anterior view of the lower incisors and canines. (A) *Micronycteris buriri* (TTU 105773); (B) *M. megalotis* (Tobago; TTU 43944); (C) *M. megalotis* (Venezuela; TTU 33276); (D) *M. megalotis* (western Ecuador; TTU 103439).

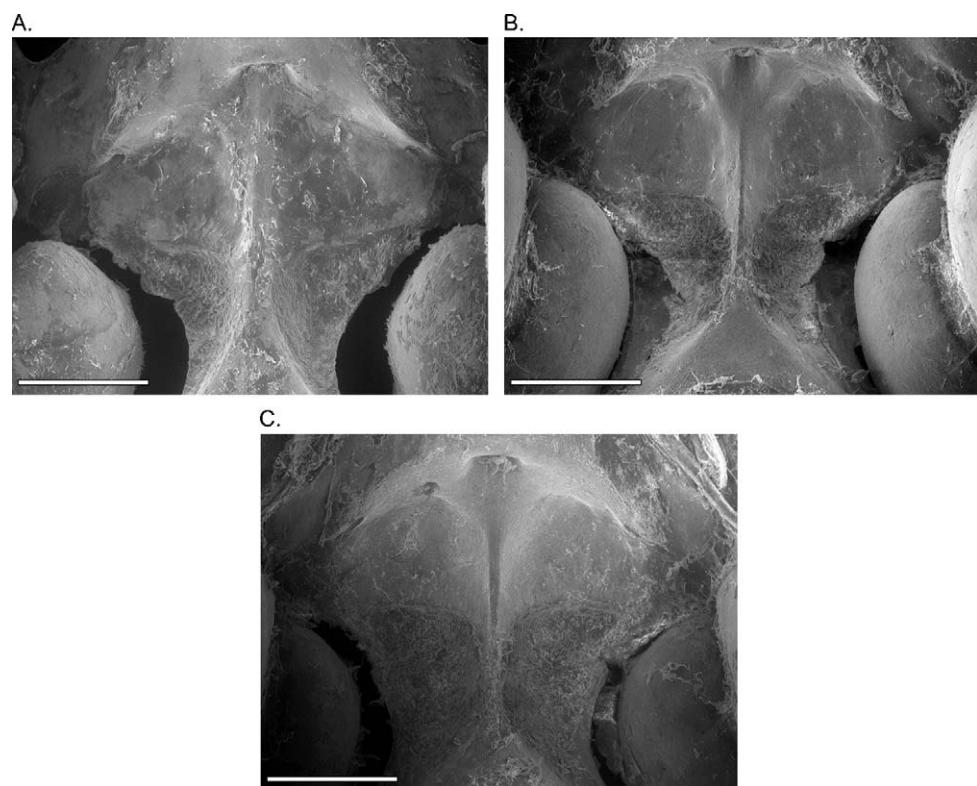


Plate 3. Basal view of the basicranium showing the basisphenoid pits (as defined in Fonseca et al., 2007). (A) *Micronycteris buriri* (TTU 105773); (B) *M. megalotis* (Tobago; TTU 43944); (C) *M. megalotis* (western Ecuador; TTU 103439). The basisphenoid bone of the Venezuelan specimen of *M. megalotis* (TTU 33276) was damaged and was unavailable for comparison.

Appendix C.

Scanning electron micrographs of upper and lower incisors and upper and lower canines (Plates 1 and 2) and basisphenoid bone (Plate 3) of the holotype of *Micronycteris buriri* (TTU 105773) and three specimens of *M. megalotis* from Tobago (TTU 43944; Clade 4 in Fig. 3), Venezuela (TTU 33276; Clade 3 in Fig. 3) and western Ecuador (TTU 103439; Clade 2 in Fig. 3). White bar in lower left portion of each image indicates 1 mm. Electron micrographs were produced at 35× magnification.

Appendix D. Supplementary information

Supplementary information associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2011.01.006.

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