



## Caribbean *Myotis* (Chiroptera, Vespertilionidae), with description of a new species from Trinidad and Tobago

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We describe a new species of *Myotis* (Vespertilionidae, Myotinae) from the Republic of Trinidad and Tobago, Tobago Island. The new species (*Myotis attenboroughi* sp. nov.) can be distinguished from all other Neotropical congeners by cranial features and cytochrome-*b* gene sequences. *Myotis attenboroughi* sp. nov. is allied morphologically with species in the *albescens* group (like *M. nigricans*), and is sister to a clade including *M. cf. handleyi*, *M. nesopolus*, and 3 possibly undescribed species from Central and South America. A review of *Myotis* collections from the Caribbean confirms *M. nyctor* for Barbados and Grenada; *M. dominicensis* for Dominica and Guadeloupe; *M. martiniquensis* for Martinique; *M. pilosatibialis* and *M. riparius* for Trinidad; and *M. attenboroughi* for Tobago. The occurrence of *M. attenboroughi* on Trinidad is still an open question.

Describimos una nueva especie de *Myotis* (Vespertilionidae, Myotinae) de la República de Trinidad y Tobago, isla de Tobago. La nueva especie (*Myotis attenboroughi* sp. nov.) se distingue de otros congéneres Neotropicales en sus rasgos craneanos y secuencias del gen citocromo *b*. *Myotis attenboroughi* sp. nov. es morfológicamente similar a especies del grupo *albescens* (tal como *M. nigricans*) y es hermana de un clado que incluye a *M. cf. handleyi*, *M. nesopolus*, y tres especies, posiblemente no descritas, de Centro y Sud América. Una revisión de las series de *Myotis* del Caribe confirma a *M. nyctor* para Barbados y Granada; *M. dominicensis* para Dominica y Guadalupe; *M. martiniquensis* para Martinica; *M. pilosatibialis* y *M. riparius* para Trinidad; y *M. attenboroughi* para Tobago. La presencia de *M. attenboroughi* en Trinidad sigue siendo hoy un enigma.

Key words: Caribbean, Lesser Antilles, *Myotis attenboroughi*, *Myotis nigricans*, Neotropics, Sir David Attenborough's *Myotis*

*Myotis* Kaup, 1829 (Vespertilionidae, Myotinae) comprises more than 110 species (Simmons 2005). The genus originated in the early Miocene in eastern Asia, with subsequent divergence of a New World clade that comprises all Nearctic and Neotropical lineages (Ruedi et al. 2013). Twenty-five Neotropical species currently are recognized (Wilson 2008; Moratelli et al. 2011, 2013, 2016; Moratelli and Wilson 2011, 2014; Larsen et al. 2012a; Mantilla-Meluk and Muñoz-Garay 2014). However, morphological and molecular evidence indicate that this number represents only a fraction of the real diversity (Larsen et al. 2012b), with some highly variable

species—e.g., *Myotis nigricans* (Schinz, 1821) and *M. riparius* Handley, 1960—potentially hiding undescribed forms (LaVal 1973; Stadelmann et al. 2007; Moratelli et al. 2011, 2013, 2016; Larsen et al. 2012a, 2012b).

*Myotis nigricans* traditionally has been regarded as widely distributed in the Neotropics, occurring from southern Mexico southward to the Republic of Trinidad and Tobago and all mainland South American countries (Wilson and LaVal 1974; Wilson 2008; Moratelli et al. 2011). In contrast, Larsen et al. (2012a, 2012b) raised evidence that *M. nigricans*, as traditionally understood, could be a complex of undescribed species.

In their assessments of the evolutionary history of Caribbean *Myotis* (Larsen et al. 2012a) and the genetic diversity of New World species of that genus (Larsen et al. 2012b), cytochrome-*b* (CYTb) gene sequences from specimens previously assigned to *M. nigricans*, from Tobago, were recovered in a well-supported haplogroup sister to other such haplogroup containing sequences from specimens from northern South America and the Caribbean. However, sequences of specimens whose geographic provenances are closer (Bolivia and Paraguay) to the type locality of *M. nigricans* (southeastern Brazil) were retrieved in another well-supported haplogroup, confirming that *M. nigricans*, as currently understood, is polyphyletic (Larsen et al. 2012b; Moratelli et al. 2016). In parallel, morphological analyses revealed that material from Tobago previously assigned to *M. nigricans* has a peculiar cranial morphology that distinguishes it from representatives of all other Neotropical species in the genus, including the *M. nigricans* complex.

The taxonomic status of *M. nigricans* from Tobago is the primary focus of this research. We conducted molecular, morphological, and morphometric analyses comparing *Myotis* “*nigricans*” from Tobago with samples that morphologically match *M. nigricans* (sensu Moratelli et al. 2011, 2013), and representatives of all other Neotropical species of *Myotis*, with special attention to those from northern South America. Our findings support the hypothesis that black *Myotis* from Tobago, previously assigned to *M. nigricans* (see Wilson 2008), represents an unknown species that we name and describe herein. The occurrence of the new species on Trinidad is still an open question. Additionally, based on critical and extensive review of specimens in collections, we comment on the distribution of other Caribbean *Myotis*.

## MATERIALS AND METHODS

*Specimens examined.*—Specimens directly examined ( $n = 377$ ) for this research include representatives of all Caribbean species of *Myotis* and their primary types, as well as representatives of species from northern South America in the *albescens* group (Appendix I). They comprise fluid-preserved specimens, stuffed skins, and skulls deposited in the American Museum of Natural History (AMNH, New York, New York); Carnegie Museum of Natural History (CM, Pittsburgh, Pennsylvania); Louisiana State University, Museum of Zoology (LSUMZ, Baton Rouge, Louisiana); Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil); Museum of Texas Tech University (TTU, Lubbock, Texas); Museum of Vertebrate Zoology, University of California (MVZ, Berkeley, California); National Museum of Natural History, Smithsonian Institution (USNM, Washington, D.C.); Natural History Museum of Los Angeles County (LACM, Los Angeles, California); Natural History Museum, University of Kansas (KU, Lawrence, Kansas); Royal Ontario Museum (ROM, Toronto, Canada); and Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Brazil). These specimens were identified according to Wilson (2008) and Moratelli et al. (2013), and their

examination is part of a broader, critical review of collections of Neotropical *Myotis*. In this review, representatives of all Neotropical species have been examined (> 3,800 vouchers), including primary types and geographic samples covering the entire distribution of many species.

*Phylogenetic analyses.*—Phylogenetic analyses of cytochrome-*b* gene (CYTb) sequences retrieved from GenBank were conducted for Neotropical species of *Myotis*, previously found to form a monophyletic group (Ruedi et al. 2013). These analyses included 116 CYTb sequences for species in this clade, and 4 and 7 sequences for *Myotis brandtii* and *M. gracilis*, respectively (Appendix II). These latter 2 species were designated as outgroups as a previous study found them to form a monophyletic group sister to the Neotropical clade (Ruedi et al. 2013). Sequences were aligned using default options of MAFFT v.7.017 (Katoh and Standley 2013) as implemented in Geneious v.7.1.5 (Kearse et al. 2012). Subsequently, the Bayesian Information Criterion (BIC), as implemented in PartitionFinder ver. 1.0.1 (Lanfear et al. 2012), was used to determine both the most suitable partition scheme and the best-fit models of nucleotide substitution. This analysis only considered models that can be applied in MrBayes.

Maximum likelihood (ML) and Bayesian inference (BI) were used as optimality criteria. The ML analysis consisted of 20 independent searches in the Genetic Algorithm for Rapid Likelihood Inference (GARLI 2.0—Zwickl 2006) applying the best-fit model and the best partitioning scheme (see “Results”) and default settings. The Bayesian analysis was conducted in MrBayes v. 3.2 (Ronquist et al. 2012). The search started with a random tree. The Markov chains were run for 100 million generations, and trees were sampled every 1,000 generations. Default values were kept for the “relburnin” and “burninfrac” options in MrBayes; therefore, the 1st 25,000,000 generations (25,000 trees) were discarded as burn-in, and posterior probability estimates of all model parameters were based on the remaining (75,000) trees. Convergence and stationarity were assessed in the Bayesian analyses by plotting likelihood values in Tracer 1.5 (Rambaut and Drummond 2007).

Nonparametric bootstrapping (Felsenstein 1985) for the ML analysis and posterior probabilities for the BI analysis (Ronquist et al. 2012) were used to assess nodal support. ML bootstrap analysis was performed in GARLI 2.0 using 100 pseudoreplicated data matrices, with 10 searches performed on each. Bayesian posterior probabilities were calculated simultaneously with the search for the best Bayesian topology conducted as described earlier. We refer to different degrees of nodal support for the ML bootstrap analysis using the following categories: strong support, for bootstrap values  $\geq 75\%$ ; moderate support, for bootstrap values  $> 50\%$  and  $< 75\%$ ; negligible support for values  $\leq 50\%$ . For the BI analysis, we refer to degrees of nodal support with 2 categories, significant or strong in cases in which a node’s posterior probability was  $\geq 0.95$ , and insignificant or negligible for posterior probability values  $< 0.95$ .

*Morphology and morphometrics.*—Measurements were recorded from adults only, and are reported in millimeters (mm), and body mass in grams (g). The head and body (HB)

length (HB), tail length, hind foot length, ear length, and body mass were recorded from museum skin labels, and are reported to the nearest millimeter and to the nearest gram. Fourteen cranial, 2 mandibular, and 4 external dimensions (Table 1) were determined under binocular microscopes with low magnification (usually 6×), and recorded and analyzed to the nearest 0.01 mm, but values were rounded to 0.1 mm throughout the text. Descriptive statistics (mean, range, and sample size) were calculated for all dimensions. The cranial index (CRI =  $((IOB + BCB) \times GLS)/2$ ) and the maxillary index (MXI =  $((BAC + BAM) \times MTL)/2$ ), as used by Moratelli and Wilson (2011, 2015), were used herein to summarize the shape of the skull (i.e., to compare broad differences in skull proportions).

A discriminant function analysis (DFA), with a priori identified samples, was used to compare skull shape between species groups and to assess craniometric characters that best discriminate among samples (Neff and Marcus 1980; Manly 1994; Strauss 2010). The DFA was run in R software (R Development Core Team 2012), using the MASS and Lattice packages. We selected a subset of the cranial dimensions (GLS, CIL, MAB, BCB, IOB, POB, BAC, BAM, MTL, M1–3, MAL, MAN) representing different axes of length and width of skull, rostrum, and mandible. As multivariate procedures require complete data sets, missing values (5% of total data set) were estimated from the existing raw data using the Amelia II package (Honaker et al. 2011) implemented in R software. Measurements were transformed to natural logs and covariance matrices were computed considering all variables. We contrasted the skull size and shape of *Myotis* sp. from Tobago ( $n = 10$ ) with specimens from Trinidad that externally match *M. nigricans* (referred as *M. cf. nigricans* from Trinidad;  $n = 4$ ); topotypes of *M. nigricans* from southeastern Brazil ( $n = 10$ ); material that morphologically matches *M. nigricans* from Carabobo, Venezuela (referred as *M. cf. nigricans* from Venezuela;  $n = 10$ ); *M. handleyi* Moratelli et al., 2013 from

Monagas, Venezuela ( $n = 10$ ); and *M. diminutus* Moratelli and Wilson, 2011 from Ecuador and Colombia ( $n = 2$ ). We included *M. diminutus* (the smallest Neotropical species of *Myotis* in skull measurements) due to its similar external size to specimens of *Myotis* sp. from Tobago. Similarly, we included *M. cf. nigricans* and *M. handleyi*, both from Venezuela, due to their resemblance in fur color or skull shape with the Tobagonian samples, and their geographic closeness and phylogenetic proximity recovered in our analyses. Due to their geographic proximity, we included our few specimens from Trinidad to test their morphometric relationship with *Myotis* sp. from Tobago. However, we examined these specimens before finding evidence that black *Myotis* from Tobago represent a new species, which prevents any taxonomic assignment for these specimens.

Qualitative traits employed here to characterize and distinguish species follow Moratelli et al. (2013). Capitalized color nomenclature follows Ridgway (1912).

*Identifications.*—Identifications of terminals in the gene tree are based on morphological comparisons. Most vouchers that were sources for CYTb sequences retrieved from GenBank were identified based on comparisons with type series, mostly primary types, as well as original species descriptions or descriptions provided by LaVal (1973), Wilson (2008), and Moratelli et al. (2011, 2013). Specimens that we were unable to confidently identify and those retrieved as polyphyletic (probably representing undescribed species) have a “cf.” (Latin, *confer*) preceding the specific epithet. Terminals whose vouchers we did not examine or we were not able to identify at all are reported as “sp.”

## RESULTS

*Phylogenetic analyses.*—The CYTb alignment contained ca. 8% of missing data (character states coded as unknown

**Table 1.**—Description of cranial, mandibular, and external dimensions (and their abbreviations) used in this study. Lengths were measured from the anteriormost point or surface of the 1st structure to the posteriormost point or surface of the 2nd structure, except as specified.

Measurements	Acronyms	Descriptions
Greatest length of skull	GLS	From the apex of the upper internal incisors, to the occiput.
Condylacanine length	CCL	From the anterior surface of the upper canines to a line connecting the occipital condyles.
Condylobasal length	CBL	From the premaxillae to a line connecting the occipital condyles.
Condylol-incisive length	CIL	From the apex of upper internal incisors to a line connecting the occipital condyles.
Basal length	BAL	Least distance from the apex of upper internal incisors to the ventral margin of the foramen magnum.
Zygomatic breadth	ZB	Greatest breadth across the outer margins of the zygomatic arches.
Mastoid breadth	MAB	Greatest breadth across the mastoid region.
Braincase breadth	BCB	Greatest breadth of the globular part of the braincase.
Interorbital breadth	IOB	Least breadth between the orbits.
Postorbital breadth	POB	Least breadth across frontals posterior to the postorbital bulges.
Breadth across canines	BAC	Greatest breadth across outer edges of the crowns of upper canines, including cingulae.
Breadth across molars	BAM	Greatest breadth across outer edges of the crowns of upper molars.
Maxillary tooththrow length	MTL	From the upper canine to M3.
Molariform tooththrow length	M1–3	From M1 to M3.
Mandibular length	MAL	From the mandibular symphysis to the condyloid process.
Mandibular tooththrow length	MAN	From the lower canine to m3.
Forearm length	FA	From the elbow to the distal end of the forearm including carpals.
Third metacarpal length	3ML	From the distal end of the forearm including carpals to the distal end of the 3rd metacarpal.
Length of the dorsal hairs	LDH	From the base to the tip of the hair in fur between scapulae.
Length of the ventral hairs	LVH	From the base to the tip of the hair in fur at mid-thorax.



[?]). PartitionFinder found that the most suitable partitioning scheme was not to use subsets, and that the best-fit model of nucleotide substitution was the Hasegawa, Kishino, and Yano model, with gamma-distributed rate heterogeneity and a proportion of invariant sites (HKY +  $\Gamma$  + I).

In the phylogenetic analyses, sequences from specimens that morphologically match *M. nigricans*, as currently recognized (sensu Moratelli et al. 2011, 2013), were recovered in 5 distinct, strongly supported haplogroups (Fig. 1). Among them, a haplogroup containing samples from Bolivia and Paraguay is geographically closer than the remaining haplogroups to the type locality of *M. nigricans* (Rio de Janeiro, eastern Brazil; see Moratelli et al. 2011), so we follow Moratelli et al. (2016) in referring to this clade as *M. nigricans*. This haplogroup was recovered as sister to *M. clydejonesei* Moratelli et al., 2016. Hereafter, other haplogroups comprising material morphologically similar to *M. nigricans* are referred to as *M. cf. nigricans*, except for the haplogroup formed by samples from Tobago, to which we refer to as “*Myotis* sp. n. from Tobago.” This haplogroup was recovered sister, with strong support, to a clade that included 3 haplogroups within it: 1 comprised by *M. cf. handleyi* and *Myotis* sp. from Honduras; 1 of *M. cf. nigricans* from western Ecuador; and 1 comprised by *M. cf. nigricans* from eastern Peru and *M. nesopolus*. The relationships among these 3 haplogroups were not resolved (Fig. 1).

*Morphological and morphometric analyses.*—*Myotis* sp. n. from Tobago differs from all South American and Caribbean congeners except *M. oxyotus* (Peters, 1866) by its steeply sloping frontals (Fig. 2). *Myotis* sp. n. from Tobago differs from *M. oxyotus* by its much smaller skull and external measurements (sp. n. from Tobago: GLS 12.5–13.1, FA 31.4–33.3; *oxyotus*: GLS 14.2–14.7, FA 34.0–37.7 [in mm]).

Apart from the steeply sloping frontals, *Myotis* sp. n. from Tobago morphologically closely resembles *M. diminutus*, *M. nigricans* (sensu lato; including samples from Trinidad and Venezuela), and *M. handleyi* in pelage texture and color, general size, or skull morphology, or a combination of these aspects. Due to this similarity, we compared their cranial shape in a DFA.

In the DFA (Fig. 3), the 1st 2 discriminant functions (DF1, DF2) represent 47.9% and 35.7% of the skull variation, respectively. Along these axes, *Myotis* sp. n. from Tobago is fully distinct from all analyzed species, except *Myotis cf. nigricans* from Trinidad. Measurements associated with the skull length (GLS, CIL, MAL) and width (IOB) were the best to discriminate samples (Fig. 3; Table 2). Considering skull axes represented by the set of measurements used in the discriminant analysis, these results reveal that *Myotis* sp. n. from Tobago and *M. cf. nigricans* from Trinidad have similar skull morphologies, which are distinct from the ones from mainland samples of *M. nigricans* (sensu lato [including *M. cf. nigricans* from Venezuela and *M. nigricans* from the type locality]) and other similar species from northern South America.

Considering the linear measurements (Table 3), *Myotis* sp. n. from Tobago is similar in external size to *M. diminutus*. Comparing ranges of variation reported for external and

cranial measurements of *Myotis* sp. n. from Tobago with those from the 2 known specimens of *M. diminutus* (USNM 528569, LACM 18761), *Myotis* sp. n. from Tobago is larger in all variables except for forearm length (FA) and postorbital breadth (POB; Table 3). The cranial and maxillary indices are useful to distinguish these 2 species (Table 3). Compared with *M. cf. nigricans* from Venezuela, *Myotis* sp. n. from Tobago is significantly smaller in 11 of 23 skull measurements (Fig. 2; Table 3). Compared with *M. cf. nigricans* from Trinidad, *Myotis* sp. n. from Tobago is significantly smaller in 2 of 15 skull measurements (MAB, MAL; Table 3). Based on results of the uni- and multivariate analyses, population samples of the black *Myotis* from Trinidad and Tobago seem to represent the same species. However, USNM 347150 from Trinidad—the only specimen we critically compared with *Myotis* sp. n. from Tobago—does not have the steeply sloping frontals, which is a trait we have identified as diagnostic for the new species. Because we are not able to confidently identify these specimens from Trinidad based uniquely on morphology, we postpone any decision on the taxonomic status of this population until we can critically compare specimens from Trinidad with those from Tobago.

The molecular, morphological, and morphometric evidence presented strongly support our hypothesis that specimens previously assigned to *M. nigricans* from Tobago represent an undescribed species that we name here as:

*Myotis attenboroughi* sp. n.  
Sir David Attenborough's *Myotis*

*Myotis nigricans nigricans*: Miller and Allen, 1928:177, part.

*Myotis nigricans nigricans*: Goodwin and Greenhall, 1961:276.

*Myotis* sp.: Larsen et al., 2012a, part.

*Myotis nigricans*: Larsen et al., 2012b, part.

M[*Myotis*]. *cf. nigricans*: Moratelli et al., 2016, part.

*Holotype.*—The holotype consists of the stuffed skin and skull, including mandible, of an adult male (USNM 540693 [field number GSM 651]), collected on 4 April 1981 by G. S. Morgan, L. K. Gordon, and F. A. Harrington (Figs. 4 and 5).

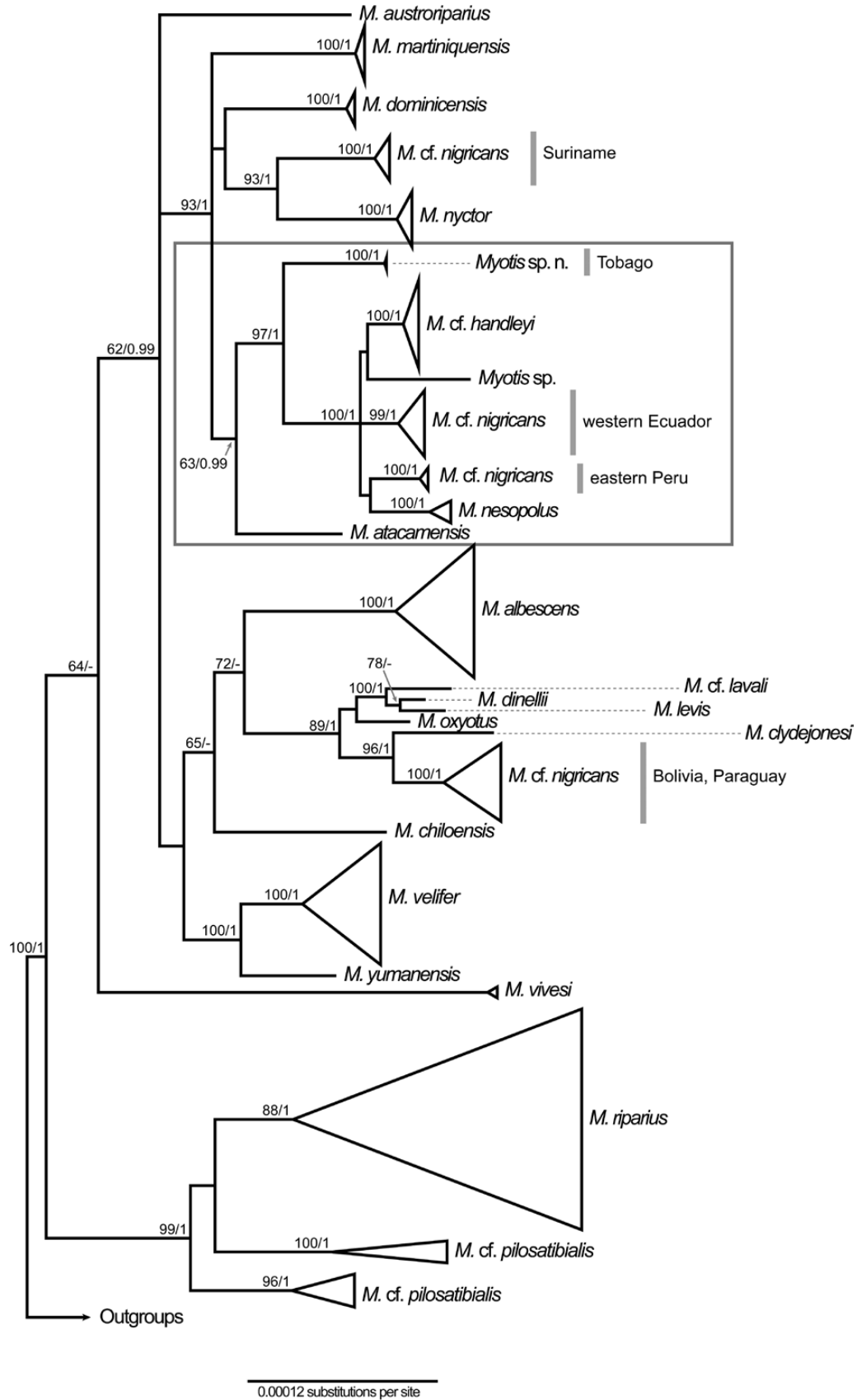
*Type locality.*—Charlottesville, 1 km N of Pirate's Bay, ca. 11°19'N, 60°33'W, Saint John Parish, Tobago Island, Republic of Trinidad and Tobago, sea level.

*Paratypes.*—All from Tobago ( $n = 9$ ), collected in Hillsborough Reservoir (USNM 538064, 538065, 538067–538069, 540619, 540694, 540695), and Charlottesville Village (USNM 540692). External and cranial measurements of the type series are in Table 4.

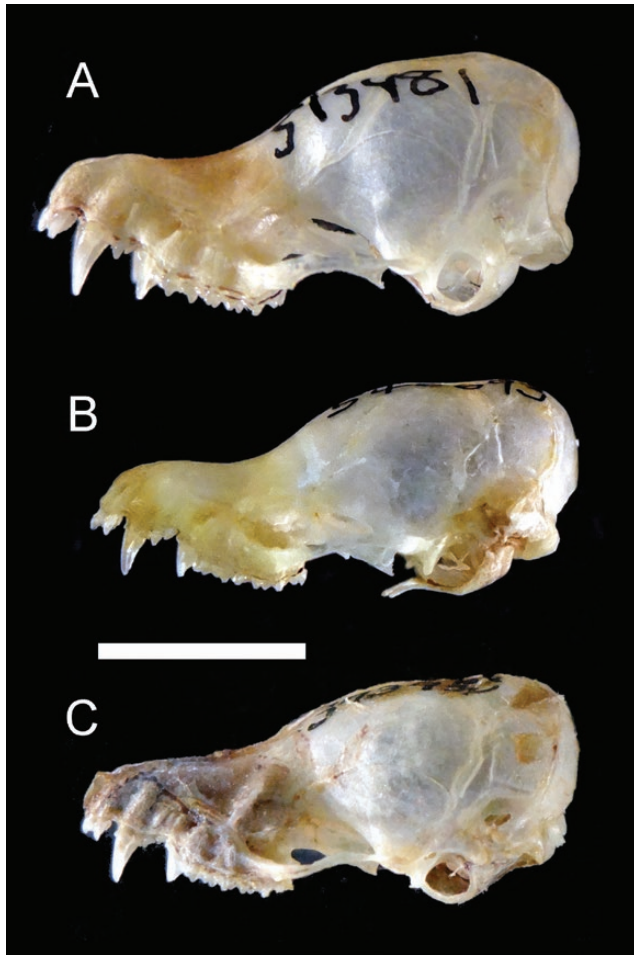
*Other specimens.*—Skulls of 3 other specimens from Tobago (USNM 538066, 540620, 540621) were not examined. They possibly represent *M. attenboroughi*, but we opted to not include them in the type series.

*Distribution.*—Museum records analyzed here confirm *M. attenboroughi* on the island of Tobago. The occurrence of the species in Trinidad is still an open question.

*Diagnosis.*—*Myotis attenboroughi* can be distinguished from all other South American and Caribbean congeners by the



**Fig. 1.**—Phylogenetic tree resulting from the Bayesian inference analysis of the cytochrome-*b* sequence data of species of the genus *Myotis*. The rectangle encloses a lineage that we describe herein as a new species of *Myotis* and haplogroups of 5 more closely related species and candidate species. Nodal support from both the Bayesian inference and the maximum likelihood analyses are shown right and left of slashes (“/”), respectively. Both phylogenetic analyses were conducted using the HKY +  $\Gamma$  + I model.

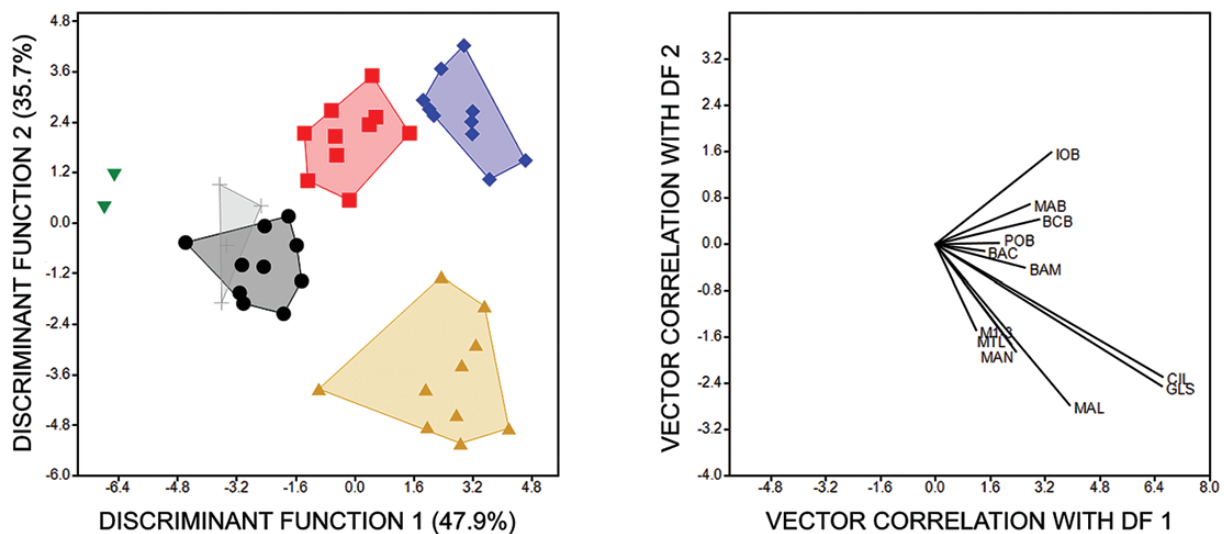


**Fig. 2.**—Lateral views of skulls of *Myotis oxyotus* (A; USNM 513481), *M. sp. n.* from Tobago (B; USNM 540693), and *M. cf. nigricans* (C; USNM 373953). Scale bar = 5 mm.

combination of a small skull (GLS 12.5–13.1 mm) and frontals steeply sloping.

*Description and comparisons.*—*Myotis attenboroughi* is among the smallest South American and Caribbean species in the genus (FA 31.4–33.3 mm, body mass 3.9–4.5 g; other measurements in Tables 3 and 4), with medium-sized ears (12–16 mm) and relatively medium, silky fur (LDH 6–8 mm, LVH 5–6 mm). The ventral pelage is strongly bicolored, with black bases (ca. 2/3 of the hair length) and Light-Buff tips (1/3). Bases and tips of the dorsal fur contrast weakly, with black bases (ca. 2/3 of the hair length) and Mummy-Brown tips (1/3). Membranes are Mummy-Brown. The plagiopatagium is attached to the foot at the level of the toes by a broad band of membrane (see López-González et al. 2001:141, figure 1a). The dorsal surfaces of elbow and tibia are naked or nearly naked. The uropatagium lacks the fringe of hairs along the trailing edge. Like most *Myotis*, its dental formula is 2/3, 1/1, 3/3, 3/3 = 38. The skull is small in length and width (GLS 12.5–13.1 mm, BCB 5.9–6.2 mm). The 2nd upper premolar (P3) is aligned in the tooththrow, being smaller than P2 and P4 and visible in labial view. The sagittal crest is generally absent, but present and low in USNM 540619. Lambdoidal crests are generally present and low, but absent in USNM 538065. Parietals are slightly inclined. The occipital region is rounded, projecting behind the posterior surfaces of occipital condyles.

*Myotis attenboroughi* differs from all South American and Caribbean species except *M. oxyotus* (Peters) by its steeply sloping frontals. It differs from *M. oxyotus* by its much smaller skull and external measurements (*attenboroughi*: GLS 12.5–13.1, FA 31.4–33.3; *oxyotus*: GLS 14.2–14.7, FA 34.0–37.7 mm [in mm]; Table 3). Besides the steeply sloping frontals, *M. attenboroughi* differs from *M. dominicensis* Miller, *M. keaysi* J. A. Allen, *M. riparius* Handley,



**Fig. 3.**—Plots of multivariate individual scores in the 1st 2 discriminant axes (left). Corresponding vector correlations of craniometric characters with the 1st 2 eigenvectors (right). Samples: *Myotis sp. n.* from Tobago (black circles); *M. cf. nigricans* from Trinidad (gray crosses); *M. cf. nigricans* from Venezuela (red squares), *M. nigricans* (blue diamonds [topotypes]), *M. handleyi* (pumpkin triangles), and *M. diminutus* (green inverted triangles). See Table 2 for vector correlation coefficients between original variables and discriminant functions (DF1, DF2).

*M. ruber* (É. Geoffroy), and *M. simus* Thomas by its silky fur, rounded occipital region, and either absence of or low, weakly developed sagittal crest. *Myotis attenboroughi* shares these traits with *M. aelleni* Baud, *M. albescens* (É. Geoffroy),

**Table 2.**—Vector correlation coefficients between original variables and discriminant functions (DF1 and DF2) for selected samples of *Myotis* sp. n. from Tobago, *M. cf. nigricans* from Trinidad, *M. cf. nigricans* from Venezuela, *M. nigricans* from Brazil, which includes topotypes, and *M. diminutus* from Ecuador. See Table 1 for variable abbreviations.

Measurements	DF1 (47.9%)	DF2 (35.7%)
GLS	2.277	0.654
CIL	5.043	-0.551
MAB	-2.805	-4.745
BCB	4.813	-0.561
IOB	4.486	-5.557
POB	1.075	3.993
BAC	-0.869	-4.278
BAM	-5.328	-2.468
MTL	3.359	7.156
M1-3	-0.618	13.001
MAL	-1.961	1.758
MAN	-3.782	-0.067

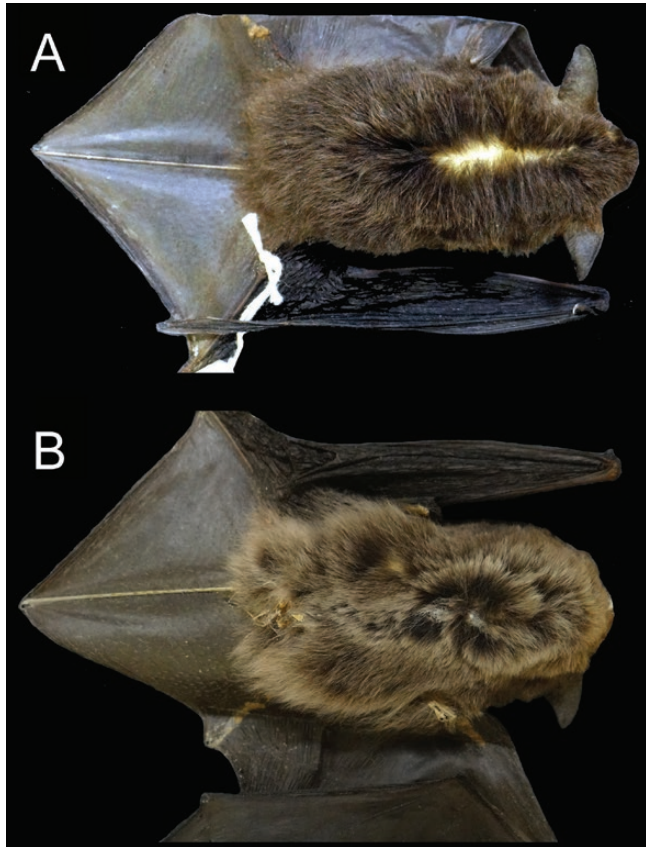
*M. atacamensis* (Lataste), *M. caucensis* LaVal, *M. chiloensis* (Waterhouse), *M. diminutus* Moratelli and Wilson, *M. dinellii* Thomas, *M. handleyi* Moratelli et al., *M. izecksohni* Moratelli et al., *M. lavalii* Moratelli et al., *M. levis* (I. Geoffroy), *M. martiniquensis* LaVal, *M. nesopolus* Miller, *M. nigricans* (Schinz), *M. nyctor* LaVal and Schwartz, *M. oxyotus*, and *Myotis clydejonesi* Moratelli et al., 2016. It differs from *M. albescens*, *M. dinellii*, and *M. levis* by the absence of a fringe of hairs along the trailing edge of the uropatagium; also distinguished from *M. dinellii* and *M. levis* by its shorter ears. *Myotis attenboroughi* differs from *M. aelleni*, *M. chiloensis*, *M. dinellii*, *M. lavalii*, and *M. nesopolus* by its darker and less-contrasting dorsal fur and smaller skull. *Myotis attenboroughi* differs from *M. izecksohni* by its shorter dorsal fur and smaller skull. *Myotis attenboroughi* differs from *M. handleyi*, *M. martiniquensis*, *M. nyctor*, *M. nigricans*, and *M. clydejonesi* by its smaller skull; also distinguished from *M. handleyi* by its bicolored dorsal fur, from *M. nigricans* sensu lato by its lighter ventral fur, and from *M. clydejonesi* by its inflated braincase.

**Etymology.**—We describe *M. attenboroughi* in honor of Sir David Frederick Attenborough. His pioneering and tireless work has been a great contribution to the diffusion of knowledge of the natural world and natural sciences, and has inspired

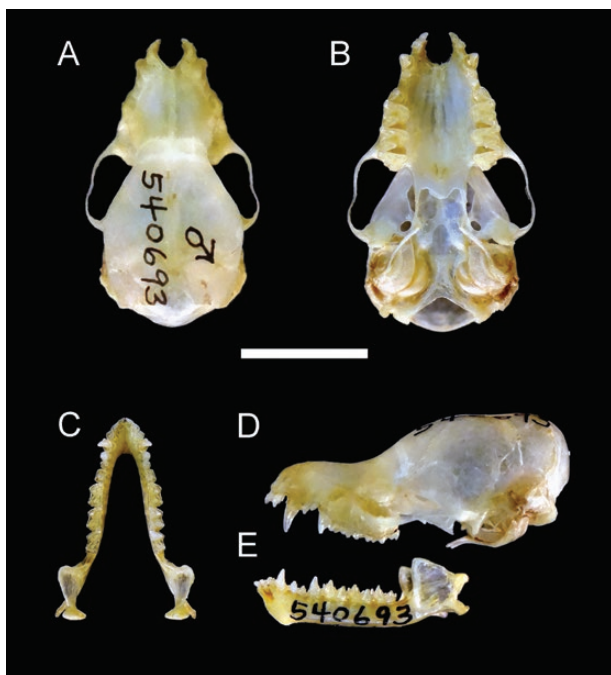
**Table 3.**—Selected measurements (mm) and body mass (g) of *Myotis* sp. n. from Tobago and other morphologically closer species—*M. cf. nigricans* from Trinidad, *M. cf. nigricans* from Venezuela, *M. oxyotus*, and *M. diminutus*—in external (size or pelage color) or cranial features. One-way ANOVA ( $F$  values [ $*P \leq 0.05$ ,  $**P \leq 0.01$ ,  $***P \leq 0.001$ ]) was used to compare external and cranial measurements of *M. sp. n.* from Tobago with *Myotis cf. nigricans* from Venezuela ( $F_a$ ), and with *M. cf. nigricans* from Trinidad ( $F_b$ ). Descriptive statistics include the mean, range (in parentheses), and sample size ( $n$ ). External measurements, except forearm length and 3rd metacarpal length, are rounded to the nearest 1 mm; other measurements are rounded to the nearest 0.1 mm. See Table 1 for variable abbreviations.

Measurements	<i>M. sp. n.</i> from Tobago	<i>M. cf. nigricans</i> from Trinidad	<i>M. cf. nigricans</i> from Venezuela	<i>M. oxyotus</i>	<i>M. diminutus</i>	$F_a$	$F_b$
	Mean (range), $n$	Mean (range), $n$	Mean (range), $n$	Mean (range), $n$	$n = 2$		
Body mass	4.1 (3.9–4.5), 9			5.5 (5.0–6.0), 5	3.5, –		
HB	74 (70–78), 4		77 (74–81), 15	88 (82–94), 6	77, 77	8.59*	
Tail	34 (32–35), 4		37 (34–39), 15	40 (37–44), 6	33, 33	19.10***	
Foot	7 (6–8), 4		8 (8–8), 15	9 (8–9), 6	6, –	16.07***	
Ear	14 (12–16), 4		12 (11–13), 15	14 (13–15), 6	11, –	2.26	
LDF	7 (6–8), 4		7 (6–7), 9	8 (7–10), 6	7, 5		
LVF	5 (5–6), 4		5 (5–6), 9	6 (5–7), 6	6, 6	1.26	
FA	32.3 (31.4–33.3), 5		33.5 (32.3–34.3), 15	36.5 (34.0–37.7), 6	33.3, 33.4	0.77	
3MC	29.5 (28.5–30.3), 4		31.4 (31.1–31.7), 3	34.2 (33.0–35.2), 6	30.0, 30.6	0.46	
GLS	12.9 (12.5–13.1), 10	13.2 (12.6–13.6), 4	13.2 (12.9–13.4), 15	14.4 (14.2–14.7), 6	12.0, 12.4	19.83***	0.12
CCL	11.5 (11.1–11.7), 10	11.6 (11.2–12.0), 4	11.7 (11.5–11.9), 15	12.8 (12.6–13.0), 6	10.6, 11.0	14.82*	3.84
CBL	12.1 (11.8–12.4), 10	12.1 (11.8–12.5), 4	12.4 (12.1–12.6), 15	13.4 (13.1–13.7), 6	11.2, 11.5	17.24***	1.86
CIL	12.3 (12.0–12.6), 10	12.3 (12.0–12.7), 4	12.5 (12.3–12.8), 15	13.7 (13.4–13.9), 6	11.4, –	15.72***	2.56
BAL	11.0 (10.8–11.4), 10	11.1 (10.5–11.4), 4	11.2 (11.0–11.4), 15	12.1 (11.9–12.3), 6	10.2, –	7.75**	1.90
ZB	7.9 (7.8–8.1), 6	8.2 (7.9–8.4), 2	7.9 (7.6–8.1), 8	9.0 (9.0–9.1), 4	–, –	0.48	
MAB	6.5 (6.4–6.7), 10	6.8 (6.5–7.2), 4	6.7 (6.6–7.1), 14	7.2 (6.8–7.5), 6	6.0, 6.5	3.15	7.56*
BCB	6.0 (5.9–6.2), 10	6.1 (6.0–6.2), 4	6.2 (6.0–6.5), 15	6.7 (6.5–7.0), 6	5.7, 6.0	7.39*	2.68
IOB	4.2 (4.1–4.3), 10	4.2 (4.0–4.4), 4	4.4 (4.2–4.6), 15	4.8 (4.7–4.9), 6	3.9, 4.1	6.44*	0.16
POB	3.3 (3.2–3.3), 10	3.3 (3.2–3.5), 4	3.3 (3.1–3.5), 15	3.6 (3.4–3.8), 6	3.2, 3.3	0.35	1.03
BAC	3.3 (3.2–3.3), 10	3.3 (3.1–3.6), 4	3.3 (3.2–3.4), 13	3.7 (3.6–3.9), 6	3.0, 3.4	1.81	1.77
BAM	5.2 (5.1–5.3), 10	5.2 (4.8–5.5), 4	5.2 (5.0–5.4), 15	5.8 (5.7–5.9), 6	4.8, 5.2	0.01	1.72
MTL	4.9 (4.8–5.0), 10	4.9 (4.6–5.2), 4	4.8 (4.7–4.9), 15	5.4 (5.3–5.6), 6	4.4, 4.8	2.09	0.79
M1-3	2.8 (2.8–2.8), 10	2.8 (2.6–3.0), 4	2.7 (2.7–2.8), 15	3.1 (3.0–3.1), 6	2.6, 2.7	10.32**	0.12
MAL	9.2 (8.9–9.5), 10	9.5 (9.3–9.9), 3	9.3 (9.0–9.5), 12	10.4 (10.3–10.7), 6	8.6, 8.9	0.82	7.18*
MAN	5.2 (5.1–5.3), 10	5.2 (4.8–5.6), 4	5.2 (5.0–5.3), 15	5.9 (5.7–6.1), 6	4.7, 5.0	0.09	1.12
CRI	67.3 (64.7–70.0), 10	67.5 (63.2–18.2), 4	71.2 (68.1–75.6), 15	84.4 (79.8–89.8), 6	59.2, 63.8		
MIX	20.4 (19.4–21.5), 10	23.8 (71.9–23.8), 4	20.4 (19.5–21.3), 13	25.9 (25.4–27.1), 6	17.2, 20.5		





**Fig. 4.**—Dorsal (A) and ventral (B) views of the skin of the holotype of *Myotis attenboroughi* sp. n. (USNM 540693). Scale bar = 10 mm. See [Table 3](#) for measurements.



**Fig. 5.**—Dorsal (A) and ventral (B) views of the cranium, dorsal view of the mandible (C), and lateral views of cranium (D) and mandible (E) of the holotype of *Myotis attenboroughi* sp. n. (USNM 540693). Scale bar = 5 mm. See [Table 3](#) for measurements.

generations of wildlife biologists, naturalists, and filmmakers interested in the natural world. We suggest the vernacular name “Sir David Attenborough’s *Myotis*.”

*Nomenclatural statement.*—A life number was obtained for the new species *M. attenboroughi*: urn:lsid:zoobank.org:pub:FCBB13D4-2A83-4B09-9D67-ED275AE2A36B.

*Natural history.*—According to labels of museum specimens, in April 1981, 2 females, 1 pregnant (USNM 540695) and 1 lactating (USNM 540694), were collected with “mist net on top of dam.” Two males (USNM 540692, 540693) were caught in a mist net over a small stream, near the ocean (1 km N of Pirate’s bay), on the island of Tobago. In July 1979, 5 females (USNM 538065–538069) and 1 male (USNM 538064) were “collected in large group of same species in dam house” in the Hillsborough Reservoir.

*Remarks.*—The taxonomic status and phylogenetic relationships of *Myotis* “*nigricans*” from Trinidad remain to be determined.

## DISCUSSION

In an attempt to identify the Lesser Antillean *Myotis*, [Miller and Allen \(1928\)](#) recognized only *M. nigricans*, with 3 subspecies for the islands. They assigned populations from Grenada, and Trinidad and Tobago to the nominate subspecies; those from Dominica to *M. nigricans dominicensis* Miller, 1902; and those from Curaçao to *M. nigricans nesopolus* Miller, 1900. Later, [LaVal \(1973\)](#) elevated *dominicensis* to the species level; reported *M. riparius* and *M. keaysi pilosatibialis* from Trinidad; and described *M. martiniquensis* from Martinique and Barbados. These actions were followed by the recognition of Barbados’ populations as a distinct subspecies—*M. martiniquensis nyctor* LaVal and Schwartz, 1974. [Genoways and Williams \(1979\)](#) elevated *nesopolus* to the species level, and [Genoways et al. \(1998\)](#) reported *M. nigricans* from Grenada. [Larsen et al. \(2012a\)](#) raised *M. martiniquensis nyctor* to the species level. According to [Larsen et al. \(2012a\)](#), *M. nyctor* occurs in Barbados, with 3 pending records from Grenada. We examined this material from Grenada: USNM 254717 is *Peropteryx* (Emballonuridae); and USNM 252600 and CM 83427 are *M. nyctor*, confirming the occurrence of *M. nyctor*, and rejecting the occurrence of *M. cf. nigricans* on Grenada.

We confirmed *M. nyctor* for Barbados, *M. dominicensis* for Dominica and Guadeloupe, *M. martiniquensis* for Martinique, and *M. attenboroughi* for Tobago. Based on molecular evidence, *M. nigricans* seems to be restricted to southern South America ([Larsen et al. 2012b](#); [Moratelli et al. 2016](#)), with a cryptic and undescribed species in northern South America ([Moratelli et al. 2016](#)). Other records of *Myotis* species from Trinidad include *M. pilosatibialis* and *M. riparius* (see [Wilson 2008](#)).

Although the uni- and multivariate analyses revealed similar skull morphology of Trinidadian and Tobagonian samples, we were not able to confidently attribute specimens from Trinidad to *M. attenboroughi* based on morphological comparison. Thus, the taxonomic identity and phylogenetic positioning of



**Table 4.**—Selected measurements (mm) and body mass (g) of the holotype (USNM 540693) and adult females and males of *Myotis attenboroughi* sp. n. from Tobago. Descriptive statistics include the mean, range (in parentheses), and sample size (*n*). External measurements, except forearm length and 3rd metacarpal length, are rounded to the nearest 1 mm; other measurements are rounded to the nearest 0.1 mm. See Table 1 for variable abbreviations.

Measurements	Holotype (male)	Females	Males
	USNM 540693	Mean (range), <i>n</i>	Mean (range), <i>n</i>
Body mass	4.1	4.0 (3.5–5.0), 7	4.0 (3.9–4.1), 3
HB	78	74 (73–75), 3	(70, 78), 2
Tail	35	33 (32–34), 3	(35, 35), 2
Foot	6	8 (7–8), 3	(6, 6), 2
Ear	12	14 (11–16), 3	(12, 12), 2
LDF	7	(7, 8), 2	(6, 7), 2
LVF	5	(5, 6), 2	(5, 6), 2
FA	33.3	32.1 (31.4–33.0), 3	(32.6, 33.3), 2
3MC	30.3	(28.5, 29.6), 2	(29.5, 30.3), 2
GLS	13.5	12.7 (12.4–13.0), 7	13.1 (12.7–13.4), 3
CCL	11.7	11.1 (10.9–11.5), 7	11.5 (11.4–11.6), 3
CBL	12.4	11.7 (11.4–12.1), 7	12.1 (11.9–12.3), 3
CIL	12.6	11.9 (11.6–12.2), 7	12.2 (12.0–12.5), 3
BAL	11.4	10.6 (10.4–11.1), 7	11.1 (10.8–11.4), 3
ZB	8.1	7.7 (7.7–7.8), 3	7.7 (7.5–8.0), 3
MAB	6.7	6.4 (6.2–6.6), 7	6.4 (6.3–6.6), 3
BCB	6.2	6.0 (5.9–6.0), 7	6.0 (5.8–6.1), 3
IOB	4.2	4.1 (3.9–4.3), 7	4.2 (4.2–4.3), 3
POB	3.2	3.2 (3.2–3.3), 7	3.2 (3.2–3.3), 3
BAC	3.3	3.1 (2.8–3.2), 7	3.2 (3.1–3.3), 3
BAM	5.3	4.8 (4.6–5.1), 7	5.1 (4.9–5.2), 3
MTL	5.0	4.7 (4.6–4.8), 7	4.9 (4.8–4.9), 3
M1–3	2.8	2.7 (2.6–2.7), 7	2.8 (2.7–2.8), 3
MAL	9.5	8.9 (8.7–9.3), 7	9.2 (8.9–9.4), 3
MAN	5.3	5.0 (4.8–5.2), 7	5.1 (5.0–5.3), 3

Trinidadian populations previously assigned to *M. nigricans* are open questions.

There is no extant or fossil record of *Myotis* for the Greater Antilles. Only 1 fossil record has been recorded for the Bahamas, in the Lucayan Archipelago (Morgan 2001; Simmons 2005; Morgan and Czaplewski 2012). This fossil has been treated as *M. cf. austroriparius*—a member of the Nearctic group of this genus (see Stadelmann et al. 2007).

*Myotis attenboroughi* is the 26th species of Neotropical *Myotis* and the only mammal species endemic to both the island of Tobago and the Republic of Trinidad and Tobago. Whereas premodern taxonomists described mammalian species that were only known from Trinidad, Tobago, or both islands—e.g., *Marmosa tobagi* (Didelphimorphia, Didelphidae), *Peropteryx trinitatis* (Chiroptera, Emballonuridae), *Proechimys trinitatis* (Rodentia, Echimyidae; see Allen and Chapman 1893; Miller 1899; Thomas 1911)—modern studies either have rendered such species invalid or documented their presence in mainland South America (Simmons and Voss 1998; Voss et al. 2014; Patton and Leite 2015). A recent phylogeographic study focused on the didelphid marsupial *Marmosa robinsoni* proposed that the effect of the Last Glacial Maxima lowering sea levels exposed land masses that connected Tobago to Trinidad and the latter to mainland South America, thus explaining low levels of differentiation between the insular populations and those from the adjacent mainland (Gutiérrez et al. 2014). The endemic nature of *M. attenboroughi*—herein documented on the basis

of morphological and molecular data—represents a notable deviation from this notion, and suggests that the landmasses that connected the islands and the mainland during the Last Glacial Maxima did not harbor suitable habitat for the dispersal of this bat species. Other similar instances are likely to be determined by future research, considering that the degree of differentiation of some proposed insular endemics—e.g., *Mazama trinitatis* Allen, 1915, which is currently considered a junior synonym of *Mazama americana* (Erxleben, 1777), but see Groves and Grubb (2011)—is yet to be assessed with modern approaches.

*Myotis attenboroughi* merits special attention from the conservation point of view. By being endemic to the island of Tobago, whose area is of only about 300 km<sup>2</sup>, and only known from a few localities and a handful of specimens, it is clear that the species faces a higher risk of extinction than most other species of mammals. We hope that by documenting its taxonomic singularity, this article will prompt scientific, institutional, and governmental efforts for the conservation (Gutiérrez and Helgen 2013) and study of *M. attenboroughi*.

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## APPENDIX I

*Specimens examined in morphological and morphometric analyses.*—Specimens examined are organized according to the taxa herein recognized. These vouchers consist of fluid-preserved specimens, stuffed skins, and skulls deposited in the American Museum of Natural History (AMNH, New York, United States); Carnegie Museum of Natural History (CM, Pittsburgh, United States); Louisiana State University, Museum of Zoology (LSUMZ, Baton Rouge, United States); Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil); Museum of Texas Tech University (TTU, Lubbock, United States); Museum of Vertebrate Zoology, University of California (MVZ, Berkeley, United States); National Museum of Natural History, Smithsonian Institution (USNM, Washington, D.C., United States); Natural History Museum of Los Angeles County (LACM, Los Angeles, United States); Natural History Museum, University of Kansas (KU, Lawrence, United States); Royal Ontario Museum (ROM, Toronto, Canada); and Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Brazil). Localities are arranged alphabetically by species and major political units. Specimens marked with asterisks were included in the discriminant analysis.

*Myotis attenboroughi* sp. n.—TRINIDAD AND TOBAGO ( $n = 13$ ): Tobago Island, Charlottetown, 1 km N of Pirate's Bay, Saint John Parish (USNM 540692\* [paratype], 540693\* [holotype]); Tobago Island, St. Mary Parish, Hillsborough Reservoir (USNM 538064\*, 538065\*, 538066, 538067\*, 538068\*, 538069\*, 540619\*, 540620, 540621, 540694\*, 540695\* [paratypes]). Tobago Island, St. Mary Parish, Hillsborough Reservoir (USNM).

*Myotis caucensis*.—COLOMBIA (11): Valle del Cauca, Cauca river (AMNH 32787 [holotype]); Valle del Cauca, Candelaria, Ingenio Mayanguez (USNM 461858–461867). PERU (10): Cuzco, Madre de Dios, 15 km E Puerto Maldonado, Reserva Cuzco Amazonico (KU 144288–144291); Loreto, Yarinacocha (LSUMZ 12252, 12254–12258).

*Myotis clydejonessi*.—SURINAME ( $n = 1$ ): Sipaliwini, Raleigh Falls (TTU 109227 [holotype]).

*Myotis diminutus*.—ECUADOR ( $n = 1$ ): Pichincha, Santo Domingo, 47 Km S (By Road), Rio Palenque Science Center (USNM 528569\* [holotype]). COLOMBIA ( $n = 1$ ): Nariño, La Guayacana (LACM 18761\*).

*Myotis dominicensis*.—DOMINICA ( $n = 41$ ): St. Joseph Parish (AMNH 237395, 237396, KU 104931–104934, 104949–104958, 104960–104964, 104969–104971, MVZ 173791, TTU 31487, 31489, 31490, 31494, 31499, 31500, 31502, 31503, 31505, 31511, 31513, 31516–31519); St. Andrews Parish, NE border of the N Forest Reserve, Never Fail (MVZ 173793). GUADALOUPE ( $n = 2$ ): Parque Nacional de Guadeloupe (CM 112378, 112381).

*Myotis handleyi*.—VENEZUELA ( $n = 27$ ): Aragua, Rancho Grande Biological Station, 13 km NW Maracay (USNM 517503\*, 562923\*, 562924, 562925\*, 562926–562933\*, 562934, 562935\*, 562936, 562937\*); Distrito Federal, Pico Ávila, 5 km NE Caracas, near Hotel Humboldt (USNM 370932\* [holotype]); Distrito Federal, Pico Ávila, 5 km NE Caracas, near Hotel Humboldt (USNM 370891 [paratype]);

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Miranda, Curupao, 5 km NW Guarenas (USNM 387723); Monagas, 3 km NW Caripe, near San Agustín (USNM 409391, 409429–409431, 409433\*, 409435\*, 409437, 409438\*).

*Myotis keaysi*.—VENEZUELA ( $n = 45$ ): Aragua, Rancho Grande Biological Station, 13 km NW Maracay (USNM 370893–370895, 370898–370902, 370911–370913, 370915–370922, 370924, 370926, 370929); Aragua, Rancho Grande Biological Station, 13 km NW Maracay (USNM 370927, 370928, 370930, 370931); Aragua, Pico Guayamayo, 13 km NW Maracay (USNM 521564); Aragua, Rancho Grande, Portachuelo (USNM 562920, 563005, 563006); Aragua, Rancho Grande (USNM 562921); Bolívar, Gran Sabana (USNM 130625, 130626); Carabobo, Montalban, 4 km NW Montalban, La Copa (USNM 441741, 441742); Distrito Federal, Los Venados, 4 km NW Caracas (USNM 370889); Distrito Federal, Pico Ávila, 5 km NNE Caracas, near Hotel Humboldt (USNM 370890); Distrito Federal, junction Puerto Cruz Highway and Colonia Tovar Highway, 0.5 km W (USNM 562984); Guarico, Hacienda El Vira, 10 km NE Altigracia (USNM 387707); Miranda, San Andres, 16 km SE Caracas (USNM 373920); Miranda, Curupao, 5 km NW Guarenas (USNM 387714–387716, 387718); Monagas, Caripe (USNM 534265).

*Myotis martiniquensis*.—MARTINIQUE (24): Tartame, ca. 6 km E, La Trinite (AMNH 214061, 214064–214068); Sten Thermale Dabsalon (CM 112382); Presquile La Caravelle, 2.3 km W Tartane, long RT D2 (CM 112383–112397, 112398, 112399).

*Myotis nesopolus*.—CURAÇAO ( $n = 1$ ): Punda area, Willemstad (USNM 101849 [holotype of *M. nesopolus*]). VENEZUELA ( $n = 9$ ): Falcón, Capatarida (USNM 441710, 441735–441737, 441740); Falcón, 6 km SW Capatarida (USNM 441711); Falcón, Capatarida (USNM 441728); Lara, Río Tucuyo (AMNH 130709 [holotype of *M. larensis*]); Zulia, Near Cojoro, 35 km NNE Paraguaipoa (USNM 441721).

*Myotis nigricans*.—BRAZIL ( $n = 10$ ): Rio de Janeiro, Seropédica, UFRRJ campus (ALP 588\*, 589\*, 625\*, 626\*, 627\*, 628\*, 629\*, 630\*, 631\*, 635\*). PARAGUAY (54): Presidente Hayes, 227 km NW Villa Hayes by road (MVZ 144707, 144708, 144710, 144711, 144713–144717, 144719, 144720, 144722, 144726–144732, 144735, 144738, 144739, 144741, 144743, 144744, 144746–144750, 144752, 144753, 144755–144757, 144761–144764, 144766–144780).

*Myotis cf. nigricans*.—SURINAME ( $n = 3$ ): Para, Zanderij (CM 63933, 69053, 77699). VENEZUELA (20): Carabobo, Urama, 10 Km NW Urama, El Central (USNM 140447, 373921\*, 373922\*, 373923\*, 373924\*, 373926\*, 373929\*, 373932\*, 373933, 373935\*, 373936, 373942\*, 373943, 373946, 373947, 373948\*, 373949, 373950, 441741, 441742).

*Myotis nyctor*.—BARBADOS ( $n = 8$ ): St. Thomas Parish, Cole's cave (KU 151761–151766, 109473 [paratype]); St. Thomas, Near Cole's cave (AMNH 213926). GRENADA (2): Grenada Island, St. David (USNM 25260, CM 83427).

*Myotis oxyotus*.—VENEZUELA ( $n = 9$ ): Amazonas, Cerro Duida, Cano Culebra, 50 km NW Esmeralda (USNM 405799); Amazonas, Cerro Neblina, Camp VII (USNM 560809–560811); Bolívar, Km. 125, 85 km SE El Dorado (USNM

387712); Bolívar, El Pauji, 21 km NE Icabaru, El Pauji (USNM 441750); Distrito Federal, Alto Ño León, 33 km SW Caracas (USNM 409427); Merida, La Mucuy, 4 km E Tabay (USNM 373919, 387705).

*Myotis pilosatibialis*.—TRINIDAD AND TOBAGO ( $n = 1$ ): Trinidad Island, St. George (TTU 5441).

*Myotis riparius*.—COSTA RICA ( $n = 2$ ): Puntarenas, 5.3 km S (by road) San Vito (CM 92491); Limon, Fila La Maquina (LSUMZ 12928). FRENCH GUIANA ( $n = 2$ ): Paracou, near Sinnamary (AMNH 266376, 268591). GUYANA ( $n = 7$ ): Barima-Waini, North West District (USNM 568021); Potaro-Siparuni, Iwokrama Field Station, Iwokrama Forest (ROM 112049); Potaro-Siparuni, Iwokrama Reserve, Burro Burro River, 25 km WNW of Kurupukari (ROM 107278, 114620); Potaro-Siparuni, Mount Ayanganna, First Plateau Camp (ROM 114688, 114689); Upper Takutu-Upper Essequibo, Gunn's Strip (ROM 106773). NICARAGUA ( $n = 1$ ): Chontales (KU 11228). PANAMA ( $n = 8$ ): Darién, Tacarcuna Village Camp, Río Pucro (USNM 310255 [holotype], 310254, 310256, 310257 [paratypes]); Darién, Río Paya, Mouth (USNM 306798); Panama, Cerro Azul (USNM 306795); Chiriqui (USNM 331916); Bocas del Toro, Isla Popa, 1 Km SE Deer Island Channel (USNM 464368). TRINIDAD AND TOBAGO ( $n = 1$ ): Trinidad Island, St. George (TTU 5467). VENEZUELA ( $n = 12$ ): Amazonas, Boca Mavaca, 84 km SSE Esmeralda, 7 km up Río Mavaca (USNM 405803, 405804); Amazonas, Capibara, 106 km SW Esmeralda, Brazo Casiquiare (USNM 409457); Amazonas, ca. 2 km SE Cerro Neblina Base Camp (USNM 560625); Amazonas, Tamatama, Río Orinoco (USNM 405806); Apure, Nulita, 29 km SW Santo Domingo, Selvas de San Camilo (USNM 416584, 441746, 441748); Aragua, Rancho Grande (USNM 562940); Barinas, 7 km NE Altamira (USNM 441743); Bolívar, Río Supamo, 50 km SE El Manteco (USNM 387721); Bolívar, San Ignacio de Yhuruani (USNM 448544).

*Myotis simus*.—BRAZIL ( $n = 56$ ): Amazonas, Borba (AMNH 91886–91892, 94224, 94225, 94227, 94230–94234); Amazonas, Itacoatiara (MZUSP 4372); Amazonas, Manaus (AMNH 79534, 91472–91478, 91500); Amazonas, Parintins (AMNH 92983, 93489–93497, 93922–93925); Amazonas, Rio Juruá (MZUSP 638, 1074).

*Myotis* sp.—TRINIDAD AND TOBAGO ( $n = 4$ ): Trinidad Island, Saint George (AMNH 175725\*, 175726\*, 179964\*); Trinidad Island, Saint Patrick (USNM 347150).

## APPENDIX II

*Specimens used in cytochrome-b analyses*.—Terminals (focal and putative species of the genus *Myotis*), GenBank accession numbers of sequences, vouchers, provenance, and authors. Information presented herein for terminal taxonomic identifications results from re-identification of vouchers (see “Materials and Methods”), and do not necessarily match those identifications assigned by researchers that generated the corresponding sequence(s) available at GenBank. Acronyms for institutional collections are as follows: American Museum of Natural History (AMNH, New York, United States); Carnegie

Museum of Natural History (CM, Pittsburg, United States); Field Museum of Natural History (FMNH, Chicago, United States); Museum of Natural History, University of Kansas (KU, Lawrence, United States); Natural History Museum of Los Angeles County (LACM, Los Angeles, United States); Louisiana State University, Museum of Zoology (LSUMZ, Baton Rouge, United States); Museum of Vertebrate

Zoology, University of California (MVZ, Berkeley, United States); Národní Muzeum (NMP, Prague, Czech); Pontificia Universidad Católica del Ecuador (QCAZ, Quito, Ecuador); Royal Ontario Museum (ROM, Toronto, Canada); Universidad Autónoma Metropolitana (UAMI, Iztapalapa, Mexico); and University of Nebraska State Museum (UNSM, Lincoln, United States).

Terminal	GenBank	Voucher	Locality	Source
<i>M. albescens</i>	JX130444	CM 63920	Nickerie, Suriname	Larsen et al. (2012b)
<i>M. albescens</i>	JX130463	TTU 85088	Pastaza, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130464	TTU 85089	Pastaza, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130465	TTU 85094	Pastaza, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130522	TTU 85091	Pastaza, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130472	TTU 102363	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130500	TTU 102348	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130501	TTU 103744	Guayas, Ecuador	Larsen et al. (2012b)
<i>M. albescens</i>	JX130445	TTU 46343	Huánuco, Peru	Larsen et al. (2012b)
<i>M. albescens</i>	AF376839	FMNH 162543	Tarija, Bolivia	Ruedi and Mayer (2001)
<i>M. albescens</i>	JX130503	TTU 99124	Boquerón, Paraguay	Larsen et al. (2012b)
<i>M. albescens</i>	JX130502	TTU 99801	Ñeembucú, Paraguay	Larsen et al. (2012b)
<i>M. albescens</i>	JX130504	TTU 99818	Ñeembucú, Paraguay	Larsen et al. (2012b)
<i>M. atacamensis</i>	AM261882	MVZ 168933	Olmos, Peru	Stadelmann et al. (2007)
<i>M. attenboroughi</i>	JN020573	UNSM ZM-29470	St. George Parish, Tobago	Larsen et al. (2012a)
<i>M. attenboroughi</i>	JN020574	UNSM ZM-29483	St. George Parish, Tobago	Larsen et al. (2012a)
<i>M. austroriparius</i>	AM261885		Tennessee, United States	Stadelmann et al. (2007)
<i>M. chiloensis</i>	AM261888		Santiago, Chile	Stadelmann et al. (2007)
<i>M. clydejonesi</i>	JX130520	TTU 109227	Sipaliwini, Suriname	Larsen et al. (2012b)
<i>M. dinellii</i>	JX130475	TTU 66489	Córdoba, Argentina	Larsen et al. (2012b)
<i>M. dominicensis</i>	AF376848		St. Joseph's Parish, Dominica	Ruedi and Mayer (2001)
<i>M. dominicensis</i>	JN020554	TTU 31519	St. Joseph's Parish, Dominica	Larsen et al. (2012a)
<i>M. dominicensis</i>	JN020555	TTU 31507	St. Joseph's Parish, Dominica	Larsen et al. (2012a)
<i>M. dominicensis</i>	JN020556	TTU 31508	St. Joseph's Parish, Dominica	Larsen et al. (2012a)
<i>M. handleyi</i>	JN020569	TTU 48161	Guárico, Venezuela	Larsen et al. (2012a)
<i>M. handleyi</i>	JX130529	TTU 48162	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130530		Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130531	TTU 48163	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130532	TTU 48164	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130533	TTU 48168	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130535	CM 78645	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130543	TTU 48169	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. handleyi</i>	JX130543	TTU 48169	Guárico, Venezuela	Larsen et al. (2012b)
<i>M. cf. lavalii</i>	AF376864	MVZ AD50	Paraíba, Brazil	Ruedi and Mayer (2001)
<i>M. levis</i>	AF376853	FMNH 141600	São Paulo, Brazil	Ruedi and Mayer (2001)
<i>M. martiniquensis</i>	AM262332		Martinique	Stadelmann et al. (2007)
<i>M. martiniquensis</i>	JN020558	MNHN:2005-896	Le Morne-Rouge, Martinique	Larsen et al. (2012a)
<i>M. martiniquensis</i>	JN020557	MNHN:2005-895	Grand'Rivière, Martinique	Larsen et al. (2012a)
<i>M. martiniquensis</i>	JN020559		Grand'Rivière, Martinique	Larsen et al. (2012a)
<i>M. martiniquensis</i>	JN020560	MNHN:2008-974	Grand'Rivière, Martinique	Larsen et al. (2012a)
<i>M. martiniquensis</i>	JN020561		Grand'Rivière, Martinique	Larsen et al. (2012a)
<i>M. nesopolus</i>	JN020575		Bonaire, Netherlands Antilles	Larsen et al. (2012a)
<i>M. nesopolus</i>	JN020576		Bonaire, Netherlands Antilles	Larsen et al. (2012a)
<i>M. nesopolus</i>	JN020577		Bonaire, Netherlands Antilles	Larsen et al. (2012a)
<i>M. nigricans</i>	JX130450	TTU 34952	La Paz, Bolivia	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130528	TTU 34953	La Paz, Bolivia	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130455	TTU 95992	San Pedro, Paraguay	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130496	TTU 99743	Presidente Hayes, Paraguay	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130498	TTU 99046	Alto Paraguai, Paraguay	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130499	TTU 99802	Ñeembucú, Paraguay	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130539	TTU 99516	Concepción, Paraguay	Larsen et al. (2012b)
<i>M. nigricans</i>	JX130540	TTU 99151	Boquerón, Paraguay	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JN020570	CM 63933	Nickerie, Suriname	Larsen et al. (2012a)

APPENDIX II. *Continued*

Terminal	GenBank	Voucher	Locality	Source
<i>M. cf. nigricans</i>	JN020571	CM 69053	Para, Suriname	Larsen et al. (2012a)
<i>M. cf. nigricans</i>	JN020572	CM 77699	Para, Suriname	Larsen et al. (2012a)
<i>M. cf. nigricans</i>	JX130523	TTU 103803	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130541	TTU 103751	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130546	TTU 102760	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130547	TTU 102765	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130548	TTU 102487	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130549	TTU 102489	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130550	TTU 102490	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130452	TTU 46347	Huánuco, Peru	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130537	TTU 46344	Huánuco, Peru	Larsen et al. (2012b)
<i>M. cf. nigricans</i>	JX130538	TTU 46346	Huánuco, Peru	Larsen et al. (2012b)
<i>M. nyctor</i>	JN020562	CM 83427	St. David Parish, Grenada	Larsen et al. (2012a)
<i>M. nyctor</i>	JN020563	TTU 109225	St. Thomas Parish, Barbados	Larsen et al. (2012a)
<i>M. nyctor</i>	JN020564	TTU 109226	St. Thomas Parish, Barbados	Larsen et al. (2012a)
<i>M. nyctor</i>	JN020565	TTU 109229	St. Thomas Parish, Barbados	Larsen et al. (2012a)
<i>M. nyctor</i>	JN020566	TTU 109224	St. Thomas Parish, Barbados	Larsen et al. (2012a)
<i>M. nyctor</i>	JN020567	TTU 109230	St. Thomas Parish, Barbados	Larsen et al. (2012a)
<i>M. oxyotus</i>	AF376865	FMNH 129208	Lima, Peru	Ruedi and Mayer (2001)
<i>M. cf. pilosatibialis</i>	JX130526	TTU 35360	San Luis Potosi, Mexico	Larsen et al. (2012b)
<i>M. cf. pilosatibialis</i>	JX130449	TTU 47514	Yucatán, Mexico	Larsen et al. (2012b)
<i>M. cf. pilosatibialis</i>	JX130525		Yucatán, Mexico	Larsen et al. (2012b)
<i>M. cf. pilosatibialis</i>	AF376852		Yucatán, Mexico	Ruedi and Mayer (2001)
<i>M. cf. pilosatibialis</i>	JX130489	CM 55764	Vera Cruz, Mexico	Larsen et al. (2012b)
<i>M. cf. pilosatibialis</i>	JX130514	TTU 85060	Tungurahua, Ecuador	Larsen et al. (2012b)
<i>M. cf. pilosatibialis</i>	JX130519	TTU 60891	Santa Ana, El Salvador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130479	TTU 84380	Atlantida, Honduras	Larsen et al. (2012b)
<i>M. riparius</i>	JX130480	TTU 84138	Atlantida, Honduras	Larsen et al. (2012b)
<i>M. riparius</i>	AM261891		La Selva, Costa Rica	Stadelmann et al. (2007)
<i>M. riparius</i>	JX130474	CM 78659	Bolívar, Venezuela	Larsen et al. (2012b)
<i>M. riparius</i>	JX130473	CM 68443	Para, Suriname	Larsen et al. (2012b)
<i>M. riparius</i>	JX130469	TTU 85344	Esmeraldas, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130515	TTU 85345	Esmeraldas, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130572	TTU 102681	Esmeraldas, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130492	TTU 102883	Esmeraldas, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130513	TTU 84870	Pastaza, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130506	TTU 85090	El Oro, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130516	QCAZ 11380	Chimborazo, Ecuador	Larsen et al. (2012b)
<i>M. riparius</i>	JX130436		Huánuco, Peru	Larsen et al. (2012b)
<i>M. riparius</i>	JX130481	TTU 46348	Huánuco, Peru	Larsen et al. (2012b)
<i>M. riparius</i>	AF376866	MVZ AD119*	Pernambuco, Brazil	Ruedi and Mayer (2001)
<i>M. riparius</i>	AF376867	MVZ AD472*	São Paulo, Brazil	Ruedi and Mayer (2001)
<i>M. riparius</i>	AM262336		São Paulo, Brazil	Stadelmann et al. (2007)
<i>M. riparius</i>	JX130485	TTU 99645	Paraguari, Paraguai	Larsen et al. (2012b)
<i>M. riparius</i>	JX130486	TTU 94912	Canindeyu, Paraguai	Larsen et al. (2012b)
<i>M. riparius</i>	JX130488		Canindeyu, Paraguai	Larsen et al. (2012b)
<i>M. riparius</i>	JX130491	TTU 99378	Canindeyu, Paraguai	Larsen et al. (2012b)
<i>M. velifer</i>	AY460343		Oklahoma, United States	Rodriguez and Ammerman (2004)
<i>M. velifer</i>	EF222340		Texas, United States	Unpublished
<i>M. velifer</i>	EU680298		Texas, United States	Unpublished
<i>M. velifer</i>	EU680299		Texas, United States	Unpublished
<i>M. velifer</i>	JX130468	TTU 109261	Texas, United States	Larsen et al. (2012b)
<i>M. velifer</i>	AF376870	MVZ 146766	Sonora, Mexico	Ruedi and Mayer (2001)
<i>M. velifer</i>	JX130478	TTU 44816	Tamaulipas, Mexico	Larsen et al. (2012b)
<i>M. velifer</i>	JX130438	UAMI 15306	Michoacán, Mexico	Larsen et al. (2012b)
<i>M. velifer</i>	JX130462	UAMI 15304	Michoacán, Mexico	Larsen et al. (2012b)
<i>M. velifer</i>	JX130589	UAMI 15305	Michoacán, Mexico	Larsen et al. (2012b)
<i>M. velifer</i>	JX130592		Michoacán, Mexico	Larsen et al. (2012b)
<i>M. velifer</i>	JX130477	TTU 6098	Santa Ana, El Salvador	Larsen et al. (2012b)
<i>M. vivesi</i>	AJ504406		Gulf of California, Mexico	Stadelmann et al. (2004)
<i>M. vivesi</i>	AJ504407		Gulf of California, Mexico	Stadelmann et al. (2004)



APPENDIX II. *Continued*

Terminal	GenBank	Voucher	Locality	Source
<i>M. yumanensis</i>	AF376875	MVZ 15585	California, United States	Ruedi and Mayer (2001)
<i>Myotis</i> sp.	JX130493	TTU 61228	Valle, Honduras	Larsen et al. (2012b)
Outgroup				
<i>M. brandtii</i>	AF376844		Neuhaus, Germany	Ruedi and Mayer (2001)
<i>M. brandtii</i>	AM261886	NMP PB 916	North west, Russia	Stadelmann et al. (2007)
<i>M. brandtii</i>	AY665139		Moscow, Russia	Tsytsulina et al. (2012)
<i>M. brandtii</i>	AY665168		Znojmo, Czech Republic	Tsytsulina et al. (2012)
<i>M. gracilis</i>	AB106609		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243025		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243026		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243027		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243028		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243029		Hokkaido, Japan	Kawai et al. (2003)
<i>M. gracilis</i>	AB243030		Hokkaido, Japan	Kawai et al. (2003)