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Review of *Myotis* (Chiroptera, Vespertilionidae) from northern South America, including description of a new species

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ABSTRACT

We describe a new species of bat in the genus *Myotis* (Vespertilionidae, Myotinae) from the coastal mountains of Venezuela. The new species (*Myotis handleyi*, sp. nov.) can be distinguished from other South American congeners by the following set of traits: dorsal fur long, silky, and bicolored with burnished tips; skull long; rostrum long and broad; frontals moderately to steeply sloping; sagittal crest absent or very low; plagiopatagium broadly attached to the foot at the level of the base of the toes; fringe of hairs along the trailing edge of uropatagium absent; and fur on uropatagium not reaching knees. We review Colombian and Venezuelan samples of *Myotis*, covering all of the currently recognized species known from these countries. Based on our analyses, we provide a sketch of the taxonomic diversity of the genus in Colombia and Venezuela, along with a key to their identification. Among other conclusions, we elevate *M. nigricans caucensis* to the species level; confirm that populations of *M. nigricans* from the opposite sides of the Andes represent the same taxon; retain J.A. Allen's names *M. esmeraldae*, *M. bondae*, and *M. maripensis* in the synonymy of *M. nigricans*; and document clinal variation in size along an altitudinal gradient for *M. nigricans*, with larger specimens from higher elevations. This research, based on museum and field collections, is one of a series of studies by the senior author re-evaluating species limits among Neotropical *Myotis*.

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INTRODUCTION

Taxonomic revisions that include South American *Myotis* have been published by Miller and Allen (1928), LaVal (1973) and Wilson (2008). Recently, several new species have been described, most of them within the *M. nigricans* (Schinz, 1821) complex (Moratelli and Wilson, 2011a; Moratelli et al., 2011a; Larsen et al., 2012a). Nevertheless, even after the removal of these species, *M. nigricans* remains one of the most widely distributed New World myotine bats. The species is recorded from Mexico south into northern Argentina, including a 2600 m altitudinal gradient in the Andes (LaVal, 1973; Wilson and LaVal, 1974; Simmons, 2005; Wilson, 2008). Although a cohesive morphometric pattern is evident for the species as currently recognized, *M. nigricans* remains a composite (Moratelli et al., 2011a). Morphometric analyses on *M. nigricans* carried out by Moratelli et al. (2011a) revealed a Venezuelan population, which they suggested represented a new species distinguishable from *M. nigricans* by its larger cranium and longer rostrum (see Moratelli et al., 2011a: 595, fig. 2). The primary focus of our report is on the taxonomic status of Venezuelan populations currently recognized as *M. nigricans*.

In addition to *M. nigricans,* five other species of *Myotis* are known from Venezuela (Sánchez and Lew, 2012): *M. albescens* (É. Geoffroy, 1806), *M. keaysi* J.A. Allen, 1914, *M. nesopolus* Miller, 1900, *M. oxyotus* (Peters, 1866), and *M. riparius* Handley, 1960. Linares (1998) reported on the possible occurrence of a seventh species, *M. simus* Thomas, 1901, in the lowlands of the state of Amazonas, a hypothesis not rejected by Moratelli et al. (2011b). A similar assemblage of *Myotis* occurs in Colombia comprising *M. albescens*, *M. keaysi*, *M. nesopolus*, *M. nigricans*, *M. oxyotus*, *M. riparius*, and *M. simus* (Eisenberg, 1989; Muñoz-Arango, 2001; Wilson, 2008; Muñoz-Garay and Mantilla-Meluk, 2012). Among Venezuelan and Colombian species, four are currently considered polytypic, with three (*M. nigricans*, *M. keaysi*, and *M. nesopolus*) represented by at least two subspecies in one or both countries and on the adjacent island of Trinidad (Trinidad and Tobago) and the Netherlands Antilles islands of Curaçao and Bonaire (LaVal, 1973; Wilson, 2008). LaVal (1973) recognized several populations of *M. nigricans* from upper elevations and on both sides of the Andes in Ecuador and Colombia as distinct subspecies; a taxonomic arrangement partially countered by Bogan (1978) who did not recognize populations from the opposite sides of the Andes as different.

Based primarily on the large samples of Venezuelan *Myotis* available in the National Museum of Natural History (USNM), we provide an outline of the taxonomic diversity in Colombia and Venezuela. Initially we examined samples from Venezuela that matched LaVal's (1973) description of *M. nigricans*, and compared these with other South American samples of this species. This comparison further emphasized the distinctiveness of the highland (1100–2100 m) populations from Venezuela and led to a more thorough evaluation of the taxonomic status of populations from all elevations on both sides of the Andes. Herein, we describe a new species from Venezuela and provide taxonomic notes on the other Venezuelan and Colombian *Myotis*, along with a key for identification.

MATERIALS AND METHODS

Specimens examined from Colombia and Venezuela consisted mainly of skins and skulls housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and the American Museum of Natural History, New York (AMNH). Our analyses included 378 specimens, most of them adults (based on closed epiphyses), 229 of which are from Colombia and Venezuela, covering all species currently reported for these countries, except *M. nesopolus*—whose sample is restricted to Curaçao ($N = 9$). The remaining specimens are from different parts of South America and were included to assess geographic variation in the *M. nigricans* complex ($N = 67$) and to assess morphological variation in *M. simus* ($N = 73$). A complete list of specimens used in the analyses is in the appendix.

Fourteen cranial, two mandibular, and four external dimensions (in mm) were measured on adult specimens using a digital caliper accurate to 0.02 mm. The measurements and their abbreviations are defined as follows (lengths were measured from the anteriormost point or surface of the first structure to the posteriormost point or surface of the second structure, except as specified): greatest length of skull (GLS), from the apex of the upper internal incisors, to the occiput; condylocanine 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; condylo-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 toothrow length (MTL), from the upper canine to M3; molariform toothrow length (M13), from M1 to M3; mandibular length (MAL), from the mandibular symphysis to the condyloid process; mandibular toothrow 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 third metacarpal; length of the dorsal hairs (LDH), from the base to the tip of the hair in fur between scapulae; and length of the ventral hairs (LVH) in fur at mid thorax. The length of ear (EL) and body weight (mass) were recorded from skin labels. Descriptive statistics (mean, range, and standard deviation) were calculated for all dimensions. The cranial index (CRI = (((IOB + BCB) × GLS)/2)) and a modification of the maxillary index (MXI = (((BAC + BAM) × MTL)/2)) used by Baud and Menu (1993) and López-González et al. (2001), were used here to summarize the shape of the skull. The same set of qualitative characters used by Moratelli et al. (2011a) was employed here to characterize and distinguish species. Capitalized color nomenclature is based on Ridgway (1912).

Principal component (PCA) and discriminant function (DFA) analyses were used to search for patterns of skull size and shape variation among populations in the *M. nigricans* complex. For these analyses, we selected a subset of the cranial dimensions (GLS, CIL, MAB, BCB, IOB, POB, BAC, BAM, MTL, M13, MAN, MAL), representing different axes of length and width of skull, rostrum, and mandible. To obtain a more balanced sampling design for multivariate analyses, each sample was limited to a minimum of two and a maximum of 15 adult specimens randomly selected, totaling 120 specimens divided into 16 geographical groups, with males and females pooled to enhance sample sizes (fig. 1). PCA was used to summarize trends of size and shape variation (with the total dataset treated as a unique sample), and DFA was used to assess craniometric characters that best discriminate among samples (with a priori identified samples—Neff and Marcus, 1980; Manly, 1994; Strauss, 2010). Mahalanobis distances between samples were portrayed in an UPGMA (unweighted pair-group method using arithmetic averages) dendrogram. To better evaluate craniometric similarity between lower and upper elevation samples from Venezuela and Colombia, we performed a discriminant analysis including only those samples, with groups reclassified. To confirm identifications of other specimens not included in the geographical groups, and the identifications of type specimens that fix names currently in the synonymy of *M. nigricans* (*M. bondae*, *M. maripensis*, *M. esmeraldae*, and *M. caucensis*), we assigned these specimens a posteriori to the larger samples on the basis of least Mahalanobis distances to the centroids of the population samples in 1,000 bootstrap iterations. As multivariate procedures require complete datasets, we estimated missing values (5.4% of total dataset) from the existing raw data using the expectation-maximization algorithm (E-M algorithm; Little and Rubin, 1987; Strauss et al., 2003). Then, measurements and estimated values were log-transformed and covariance matrices computed considering all variables. The statistical significance of differences among samples was assessed by single and multivariate analyses of variance (one-way ANOVA and MANOVA, respectively). To test whether the model of isolation by distance adequately described the pattern of variation revealed for *M. nigricans*, we compared geographic and morphological distance matrices using the nonparametric Mantel's test (Mantel, 1967). Statistical procedures were performed in MATLAB (MathWorks, Inc.) using functions written by R. Strauss and available from http://www.faculty.biol.ttu.edu/Strauss/Matlab/matlab.htm (Strauss, 2012).

Samples included in the morphometric analyses are as follows (fig. 1): Cochabamba, Bolivia, 2000 m (group 1); Mato Grosso do Sul, Brazil, 10 m (group 2); Paraná, Brazil, sea level (group 3); Seropédica, Rio de Janeiro, Brazil, 33 m (group 4); Tinguá, Rio de Janeiro, Brazil, 33–100 m (group 5); São Paulo, Brazil, sea level (group 6); Valle del Cauca, Colombia, 975 m (group 7); Nariño, Colombia, 250 m (group 8); Esmeraldas, Ecuador, 18 m (group 9); Zamora-Chinchipe, Ecuador, ca. 850–915 m (group 10); Amazonas, Peru, 665 m (group 11); Amazonas, Venezuela, ca. 100 m (group 12); Aragua, Venezuela, ca. 1100 m (group 13); Carabobo, Venezuela, 25 m (group 14); Distrito Federal, Venezuela, ca. 2100 m (group 15); and Monagas, Venezuela, 1190 m (group 16). Group 4, from Seropédica, Rio de Janeiro, represents a topotypical series of *M. nigricans*. Groups 8 and 9, from lowland Colombia and Ecuador, include specimens assigned to *M. n. punensis* by LaVal (1973). A complete list of specimens used in the geographic analyses is in the appendix.

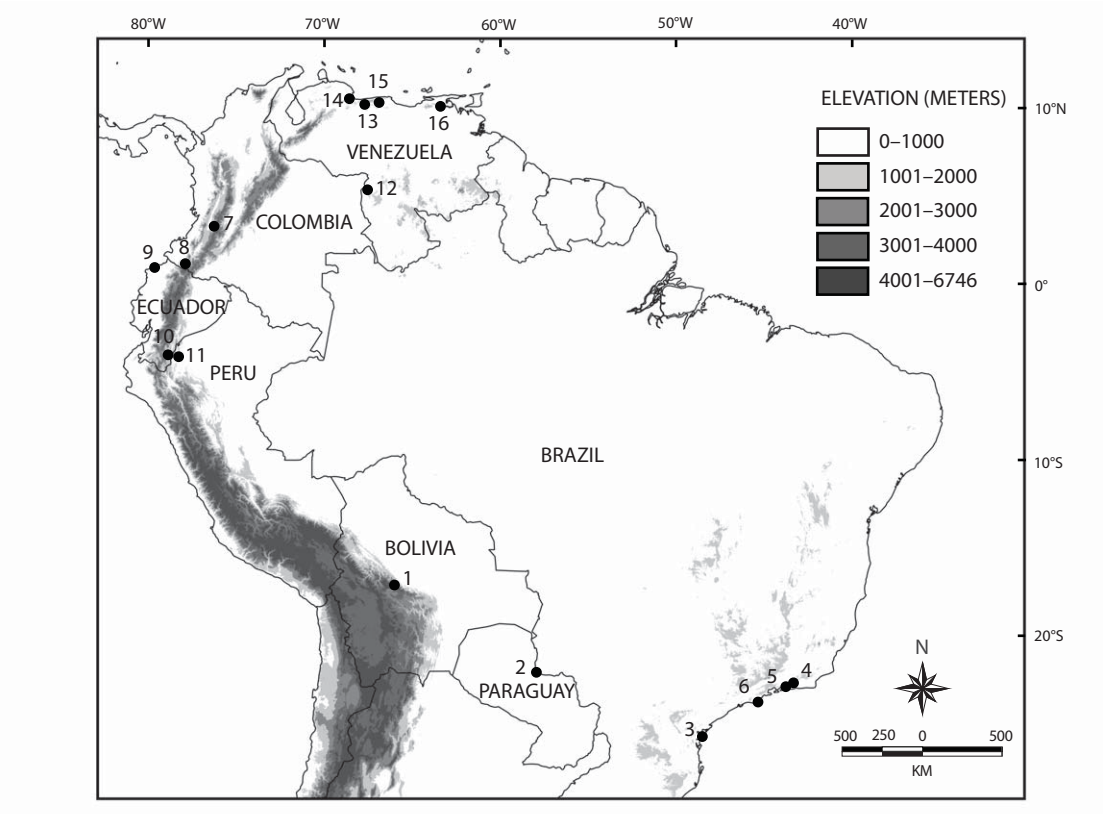

FIG. 1. Map of part of South America illustrating localities of *Myotis nigricans* samples (sensu LaVal, 1973) used in morphometric analyses. Samples: (1) Cochabamba, Bolivia, 2000 m; (2) Mato Grosso do Sul, Brazil, 10 m; (3) Paraná, Brazil, sea level; (4) Seropédica, Rio de Janeiro, Brazil, 33 m; (5) Tinguá, Rio de Janeiro, Brazil, 33–100 m; (6) São Paulo, Brazil, sea level; (7) Valle del Cauca, Colombia, 975 m; (8) Nariño, Colombia, 250 m; (9) Esmeraldas, Ecuador, 18 m; (10) Zamora-Chinchipe, Ecuador, ca. 850–915 m; (11) Amazonas, Peru, 665 m; (12) Amazonas, Venezuela, ca. 100 m; (13) Aragua, Venezuela, ca. 1100 m; (14) Carabobo, Venezuela, 25 m; (15) Distrito Federal, Venezuela, ca. 2100 m; and (16) Monagas, Venezuela, 1190 m.

We also examined and commented on names currently in the synonymy of *Myotis nigricans* (see Wilson, 2008), including evaluations of identifications and validity of names represented by the holotypes of *M. bondae* J.A. Allen, 1914; *M. maripensis* J.A. Allen, 1914; *M. esmeraldae* J.A. Allen, 1914; and *M. caucensis* J.A. Allen, 1914. These holotypes were assigned a posteriori to samples of *M. nigricans* following the same procedure reported above to classify single specimens.

RESULTS

The first principal component (PC1) accounted for 52% of the total craniometric variation and represents overall skull size (table 1). Among Venezuelan groups, PC1 centroids revealed that the lower-elevation samples from Amazonas (group 12) and Carabobo (group 14), and the upper-elevation sample from Monagas (group 16) have smaller skulls than upper-elevation

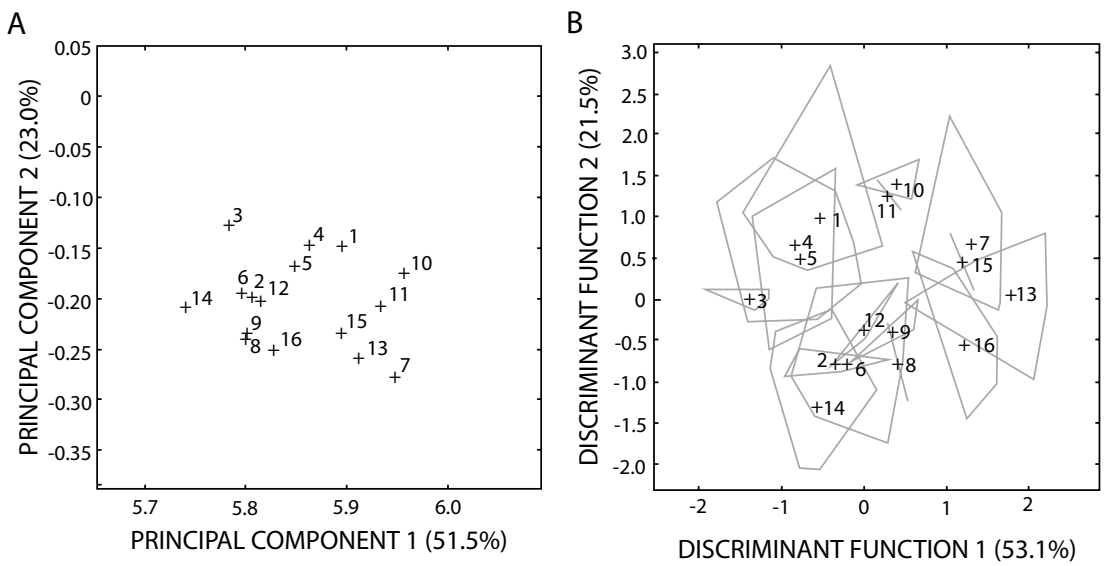

FIG. 2. **A.** Plots of centroid and group labels in the first two principal components. **B.** Plots of centroid and group labels, with groups delimited by convex hulls, in the first two discriminant axes. Samples: (1) Cochabamba, Bolivia, 2000 m; (2) Mato Grosso do Sul, Brazil, 10 m; (3) Paraná, Brazil, sea level; (4) Seropédica, Rio de Janeiro, Brazil, 33 m; (5) Tinguá, Rio de Janeiro, Brazil, 33–100 m; (6) São Paulo, Brazil, sea level; (7) Valle del Cauca, Colombia, 975 m; (8) Nariño, Colombia, 250 m; (9) Esmeraldas, Ecuador, 18 m; (10) Zamora-Chinchipe, Ecuador, ca. 850–915 m; (11) Amazonas, Peru, 665 m; (12) Amazonas, Venezuela, ca. 100 m; (13) Aragua, Venezuela, ca. 1100 m; (14) Carabobo, Venezuela, 25 m; (15) Distrito Federal, Venezuela, ca. 2100 m; and (16) Monagas, Venezuela, 1190 m.

samples from Aragua (group 13) and Distrito Federal (group 15, fig. 2A). Excluding the Monagas sample, Venezuelan samples from upper elevations overlap in size with samples from mid to high elevations in Bolivia (group 1), Peru (group 11), Colombia (group 7), and Ecuador (group 10), all of which are represented by specimens with larger skulls. The Monagas sample is more similar in size to lower-elevation samples from different areas in South America (fig. 2A), all generally having smaller skulls.

The first two discriminant functions (DF1 and DF2) summarize 75% of the among-group craniometric variation (table 1). DF1, which accounts for 53% of the total variation, revealed two major clusters (table 1; figs. 2B and 3) that are significantly distinct (MANOVA: Wilks' lambda = 0.0073, F = 3.21, $p < 0.0001$). Lower-elevation samples from Colombia (group 8) and Venezuela (groups 12, 14) had either negative or low positive values along DF1, similar to samples from Bolivia (group 1), Brazil (groups 2–6), Ecuador (groups 9, 10), and Peru (group 11—table 1; fig. 2B). This cluster is here assigned to *M. nigricans* based on similarity with the topotypical sample of this species (group 4). The other cluster, mainly represented by individuals with higher positive values along DF1, includes samples from upper elevations in Venezuela (Aragua, Distrito Federal, and Monagas [groups 13, 15, 16]) and Colombia (Valle del Cauca [group 7]—fig. 2B). In the graphic representation of the discriminant analysis, groups 10 and 11 (Ecuador [850–915 m] and Peru [665 m]) are intermediate between the two clusters recognized above, but in the multivariate space their centroids are closer to the centroid of group 1

TABLE 1. Vector correlation coefficients (loadings) between original variables and principal components (PC1 and PC2) and between original variables and discriminant functions (DF1 and DF2) for South American samples tentatively assigned to *Myotis nigricans*.
Values in **boldface** indicate vector correlations with magnitudes > ±0.29.

	Loadings of PCA and DFA					
	All samples combined				Venezuelan and Colombian samples	
	PC1	PC2	DF1	DF2	DF1	DF2
Characters	51.5%	23.0%	53.1%	21.5%	78.8%	8.9%
GLS	**0.87**	**- 0.31**	**0.41**	**0.39**	**0.74**	**0.67**
CIL	**0.82**	- 0.28	**- 0.43**	- 0.04	**- 0.46**	0.01
MAB	**0.65**	**0.41**	- 0.22	0.10	- 0.11	0.11
BCB	**0.67**	**0.54**	- 0.10	**0.41**	- 0.04	- 0.12
IOB	**0.54**	**0.58**	- 0.13	0.16	- 0.03	0.01
POB	**0.59**	**0.59**	0.08	0.11	0.07	- 0.14
BAC	**0.79**	- 0.19	- 0.06	0.26	- 0.05	0.04
BAM	**0.85**	- 0.04	- 0.09	**- 0.32**	- 0.18	0.12
MTL	**0.80**	**- 0.50**	- 0.20	**0.32**	**0.36**	**0.41**
M13	**0.72**	**- 0.59**	**0.46**	- 0.28	0.24	**- 0.44**
MAN	**0.81**	**- 0.42**	**0.52**	- 0.28	0.06	**- 0.35**
MAL	**0.77**	**- 0.54**	0.18	**0.45**	- 0.02	- 0.07

(Bolivia [2000 m]—assigned to *nigricans*) than to any centroid in the other cluster (fig. 3); a similarity that indicates altitudinal variation within the cluster recognized as *M. nigricans*.

Results of classification analyses are in table 2. The holotypes of *M. bondae* (AMNH 14587), *M. maripensis* (AMNH 17069), and *M. esmeraldae* (AMNH 33239) were mainly classified with different samples of *M. nigricans*. The holotype of *M. caucensis* (AMNH 32787) was assigned to the Valle del Cauca sample (group 7). USNM 387723 from Miranda, Venezuela (elevation of 1180 m) was grouped with the two specimens from Distrito Federal (group 15). A specimen (USNM 309020) from Ricuarte, Nariño, Colombia (1500 m) was mainly classified with a sample from Esmeraldas, Esmeraldas, Ecuador (18 m), assigned to *M. nigricans*. Two specimens from lowland localities in the Venezuelan states of Trujillo (USNM 387708) and Apure (USNM 441722) were assigned to different samples of *M. nigricans*. The classification analysis confirmed (1) the identification of the holotypes of *M. bondae*, *M. maripensis*, and *M. esmeraldae* as representatives of *M. nigricans*, and (2) the occurrence of *M. nigricans* at 1500 m elevation in Colombia, and (3) at other Venezuelan lowland localities (Trujillo and Apure) in addition to those in Carabobo and Amazonas.

In a separate discriminant analysis limited to Venezuelan and Colombian samples, DF1 and DF2 accounted for 62% of the total craniometric variation (table 1). This analysis reveals three clusters (fig. 4A)—cluster 1: upper-elevation sample from Colombia (Valle del Cauca [group 1]); cluster 2: lowland samples from Colombia (Nariño [group 2]) and Venezuela (Carabobo, and Amazonas [groups 3 and 4]); cluster 3: upper-elevation samples from Venezuela

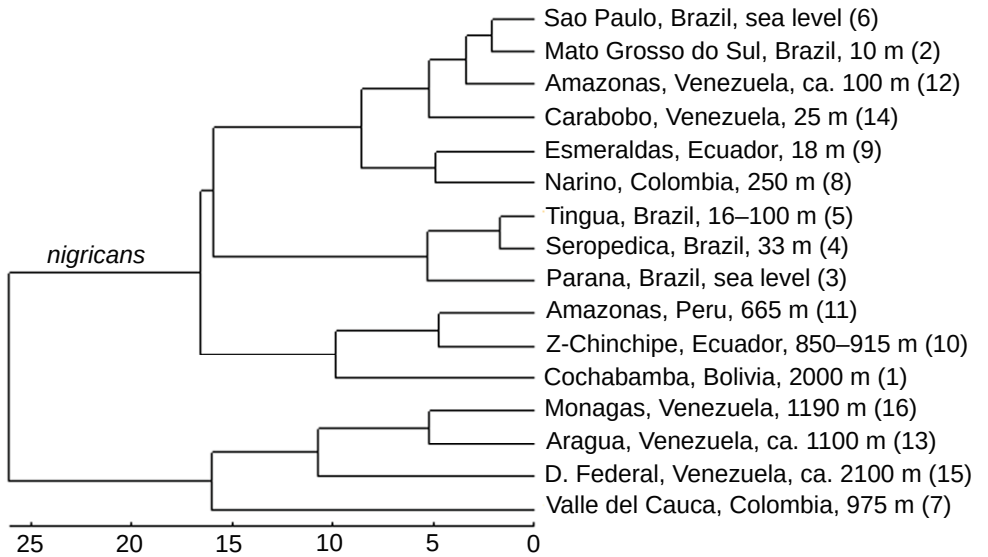

FIG. 3. UPGMA dendrogram of Mahalanobis distances between samples analyzed (localities in parentheses) in the present study. See methodology for description of localities.

TABLE 2. Frequency distribution of classification of single specimens using the minimum Mahalanobis distance to the centroids of selected samples based on 1000 bootstrap iterations. Values in **boldface** correspond to higher affinity and dashes (—) correspond to zero.

	Groups																
Specimens	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Classification
AMNH 14587	—	—	—	—	0.24	—	—	0.12	0.07	—	**0.40**	0.09	—	0.02	—	0.05	*M. nigricans*
AMNH 17069	—	—	—	—	—	—	—	**0.98**	—	—	—	0.01	0.01	—	—	—	*M. nigricans*
AMNH 33239	—	—	—	—	—	—	—	**0.35**	0.27	—	—	0.30	—	0.08	—	—	*M. nigricans*
AMNH 32787	—	—	—	—	—	—	**0.95**	—	—	—	0.04	—	0.01	—	—	—	Valle del Cauca
USNM 387723	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**1.0**	—	Distrito Federal
USNM 309020	—	—	—	—	—	0.05	—	0.07	**0.48**	0.01	0.01	0.04	—	0.34	—	—	*M. nigricans*
USNM 387708	—	—	—	—	—	**0.77**	0.02	0.06	0.07	—	—	—	—	0.08	—	—	*M. nigricans*
USNM 441722	—	0.21	0.01	—	—	0.04	—	—	—	—	—	0.01	—	**0.72**	—	—	*M. nigricans*

Groups: (1) Cochabamba, Bolivia, 2000 m; (2) Mato Grosso do Sul, Brazil, 10 m; (3) Paraná, Brazil, sea level; (4) Serópédica, Rio de Janeiro, Brazil, 33 m; (5) Tinguá, Rio de Janeiro, Brazil, 33–100 m; (6) São Paulo, Brazil, sea level; (7) Valle del Cauca, Colombia, 975 m; (8) Nariño, Colombia, 250 m; (9) Esmeraldas, Ecuador, 18 m; (10) Zamora-Chinchipe, Ecuador, ca. 850–915 m; (11) Amazonas, Peru, 665 m; (12) Amazonas, Venezuela, ca. 100 m; (13) Aragua, Venezuela, ca. 1100 m; (14) Carabobo, Venezuela, 25 m; (15) Distrito Federal, Venezuela, ca. 2100 m; and (16) Monagas, Venezuela, 1190 m.

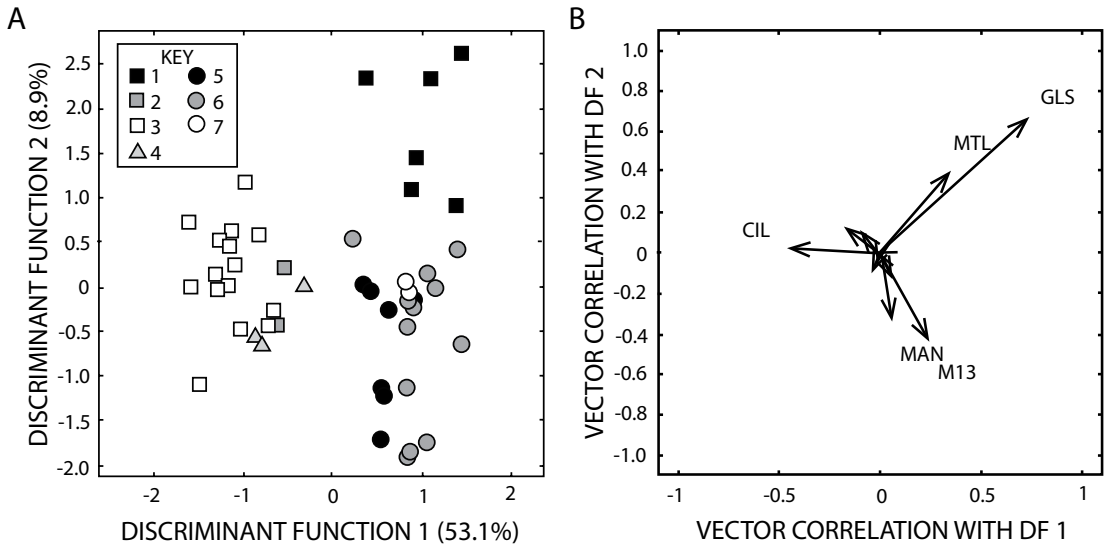

FIG. 4. **A.** Plots of multivariate individual scores in the first two discriminant functions. **B.** Corresponding vector correlations (> ±0.29) of craniometric characters with the first two eigenvectors. Samples: (1) Valle del Cauca, Colombia, 975 m; (2) Nariño, Colombia, 250 m; (3) Carabobo, Venezuela, 25 m; (4) Amazonas, Venezuela, ca. 100 m; (5) Monagas, Venezuela, 1190 m; (6) Aragua, Venezuela, ca. 1100 m; and (7) Distrito Federal, Venezuela, ca. 2100 m. See Materials and Methods for variable abbreviations.

TABLE 3. Results of MANOVA and Mantel test for comparisons of lower and upper elevation samples from Colombia and Venezuela.

	MANOVA			Mantel test	
	Wilks' lambda	F	*p*	r	*p*
Clusters 1 vs. 2	0.0116	3.23	< 0.0001	0.03	0.42
Clusters 1 vs. 3	0.0418	1.93	0.02	- 0.67	0.83
Clusters 2 vs. 3	0.0114	3.09	< 0.0001	0.56	0.08

Cluster 1: upper elevation sample from Valle del Cauca, Colombia (975 m; group 1); cluster 2: lowland samples from Nariño, Colombia (250 m; group 2), and Carabobo (25 m) and Amazonas (ca. 100 m), Venezuela (groups 3 and 4); and cluster 3: upper elevation samples from Monagas (1190 m), Aragua (ca. 1100 m), and Distrito Federal (ca. 2100 m), Venezuela (groups 5, 6, and 7).

(Monagas, Aragua, and Distrito Federal [groups 5, 6 and 7]). These clusters are significantly distinct from each other; and the Mantel test did not detect significant correlation between geographic and morphological distance matrices (table 3), suggesting that the morphometric divergence between samples cannot be explained by their geographic distances. The sample from Valle del Cauca (group 7) is distinct from the remaining samples by having higher values for the greatest length of skull on both axes (fig. 4).

Comparisons among Venezuelan *Myotis nigricans* (sensu LaVal, 1973), reveal that upper-elevation samples are, on average, cranially and externally larger than lower elevation samples, but partially overlap in all measurements (table 4). In addition to external dimensions (EL, FA, 3MC, LDH, LVH), differences in characters related to length of skull (GLS, CCL, CBL, CIL, BAL) and

TABLE 4. Selected measurements (mm) and weight (g) of lower (Carabobo and Amazonas) and upper (Aragua, Monagas, and Distrito Federal) elevation samples of *Myotis nigricans* (sensu LaVal, 1973) from Venezuela, and F values (one-way ANOVA: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

	Lower elevation samples (25–100 m)				Upper elevation samples (1100–2100 m)				
	Mean	Range	SD	*N*	Mean	Range	SD	*N*	F
Weight	3.8	2.9–4.6	—	2	4.7	3.5–6.0	0.65	20	—
EL	12	11–14	0.70	18	13	12–15	0.81	22	7.71**
FA	33.5	32.3–34.3	0.62	17	35.4	33.7–37.3	0.89	20	7.60**
3MC	31.4	31.1–31.7	—	3	32.4	31.3–33.6	0.90	11	55.21***
LDH	6.7	5.9–7.6	0.43	18	7.2	5.9–8.7	0.76	20	6.45*
LVH	5.3	4.7–5.8	0.31	18	5.8	4.8–6.1	0.31	20	9.93**
GLS	13.4	13.2–13.8	0.15	21	13.9	13.5–14.2	0.21	22	54.83***
CCL	11.7	11.5–12.1	0.14	21	12.1	11.7–12.5	0.23	22	28.76***
CBL	12.4	12.1–12.7	0.16	21	12.8	12. 5–13.2	0.25	22	40.72***
CIL	12.6	12.3–12.9	0.15	21	12.9	11.7–13.4	0.36	22	16.89***
BAL	11.2	11.0–11.5	0.16	21	11.6	11.2–12.0	0.23	22	29.41***
ZB	8.0	7.6–8.3	0.19	9	8.3	8.0–8.6	0.14	13	31.88***
MAB	6.7	6.6–7.1	0.14	19	6.8	6.5–7.1	0.15	21	0
BCB	6.3	6.0–6.5	0.13	21	6.3	6.1–6.6	0.14	21	3.56
IOB	4.4	4.0–4.6	0.15	21	4.4	4.0–4.7	0.19	22	0.39
POB	3.3	3.1–3.5	0.11	21	3.5	3.3–4.0	0.15	22	14.51***
BAC	3.3	3.2–3.5	0.11	18	3.4	3.2–3.7	0.11	22	8.08**
BAM	5.2	4.8–5.7	0.19	21	5.4	5.0–5.8	0.17	22	9.17**
MTL	4.9	4.7–5.1	0.09	21	5.1	5.0–5.3	0.10	22	78.27***
M13	2.8	2.7–2.9	0.07	20	3.0	2.8–3.1	0.07	22	108.10***
MAL	9.3	9.0–9.7	0.18	15	9.8	9.4–10.0	0.19	19	38.79***
MAN	5.2	5.0–5.5	0.10	19	5.5	5.4–5.7	0.10	20	76.75***

Summary statistics: SD = Standard deviation (calculated for samples larger than 5 specimens); *N* = sample size (adults only). See Materials and Methods for variable abbreviations.

rostrum (MTL, M13, MAL, MAN), width of rostrum (BAC, BAM), and postorbital and zygomatic widths (POB, ZB) were statistically significant; whereas other dimensions related to width of cranium (MAB), braincase (BCB) and rostrum (IOB) were not (table 4). These results indicate that specimens from upper elevations in northern Venezuela have proportionally longer skulls and longer and broader rostra, whereas the cranium and braincase are proportionally narrower (fig. 5). These specimens also have longer, darker, and more contrasting dorsal fur with burnished tips (fig. 6). These samples from upper elevations in Venezuela can be distinguished from Valle del Cauca specimens by their comparatively smaller skulls, more steeply sloping frontals (but not as steep as in *M. oxyotus*), shorter braincases (fig. 5), and tricolored dorsal fur (fig. 6).

Based on congruence with the topotypes, specimens from lower elevations in Venezuela were classed as representatives of *M. nigricans* (figs. 2B and 3). Against that background, we recognize upper elevation samples from Venezuela and Colombia as distinct from each other

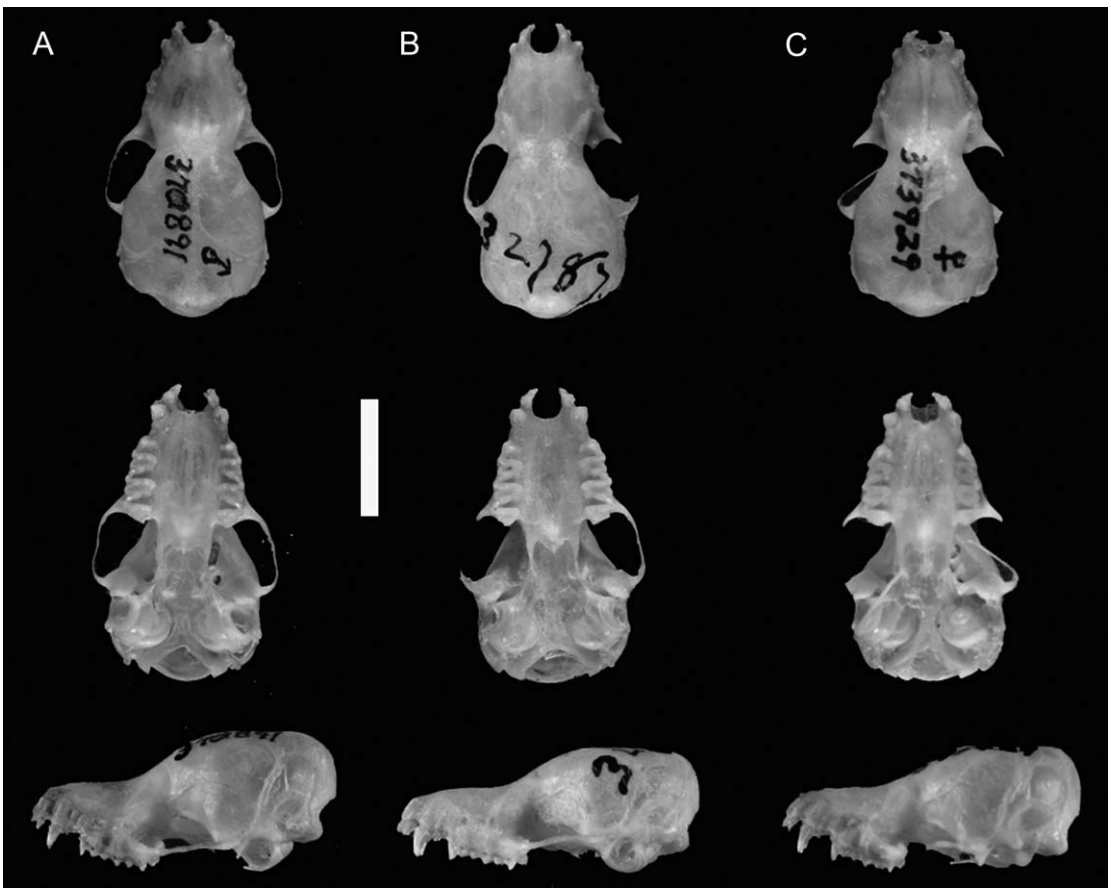

FIG. 5. Dorsal, ventral, and lateral views (scale bar = 5 mm) of skulls of specimens from **A,** upper elevations in Venezuela (USNM 370891; subsequently assigned to *M. handleyi*); **B,** Colombia (AMNH 32787; subsequently assigned to *M. caucensis*); and **C,** lower elevation in Venezuela (USNM 373929; *M. nigricans*). See table 4 for measurements.

and from *M. nigricans*. The taxonomic status of the Valle del Cauca sample is discussed under the Taxonomic Notes section on other Venezuelan and Colombian *Myotis*. Based on our results, we recognize the Venezuelan populations from Monagas, Aragua, Miranda, and Distrito Federal as an undescribed taxon we name here as:

Myotis handleyi, sp. nov.

Handley's Myotis

Figures 5–8; tables 5, 6

Myotis nigricans nigricans: LaVal, 1973:7, part.
Myotis nigricans: Handley, 1976:36, part.

Holotype: An adult male, USNM 370932, with skin and skull, including mandible (figs. 7 and 8), collected by the Smithsonian Venezuelan Project team (Mammals Field Number 753),

FIG. 6. Dorsal (**A–C**) and ventral (**D–F**) views of skins of specimens from upper elevations in Venezuela (**A** and **D**—USNM 370891; subsequently assigned to *M. handleyi*), and Colombia (**B** and **E**—AMNH 461860; subsequently assigned to *M. caucensis*), and lower elevation in Venezuela (**C** and **F**—USNM 373925; *M. nigricans*). See table 4 for measurements.

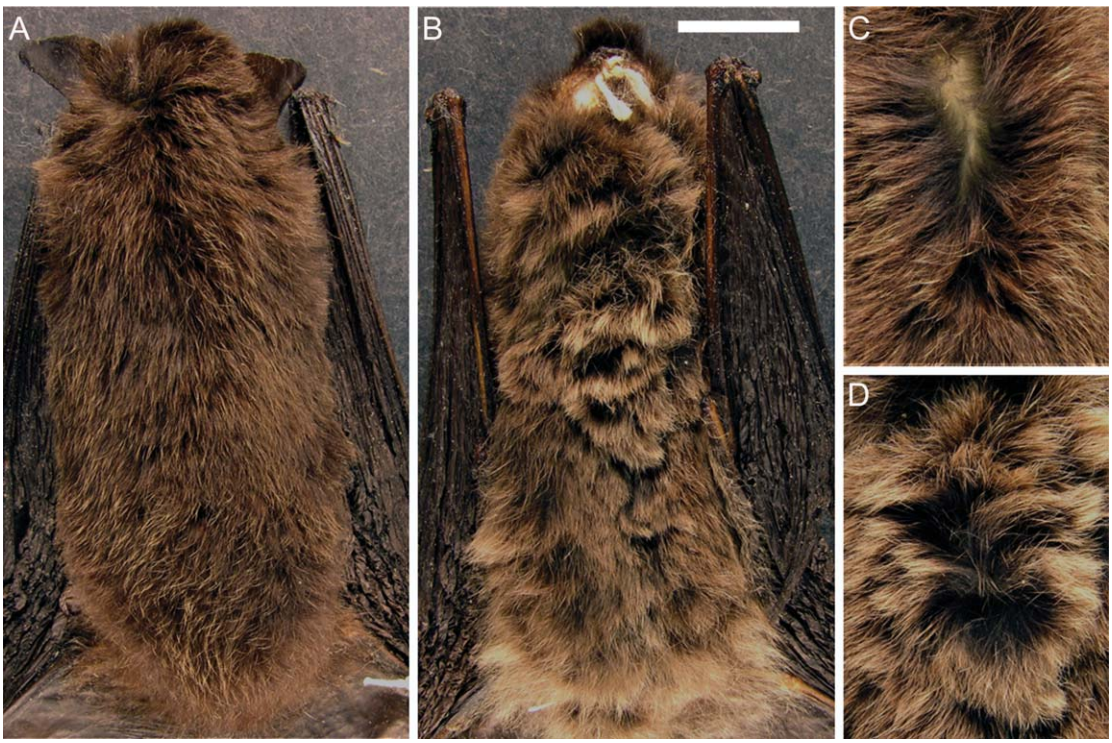

FIG. 7. Dorsal (**A**) and ventral (**B**) views of the skin of the holotype of *Myotis handleyi* (USNM 370932; scale bar = 10 mm). On the right side enlarged views of the dorsal (**C**) and ventral (**D**) pelage, highlighting the contrast between bases and tips. See table 5 for measurements.

elevation 2092 m, on 19 August 1965. External and craniodental measurements for the type series and other specimens are provided in table 5.

Type Locality: Pico Ávila, 5 km northeast of Caracas, ca. 10.33°N, 66.52°W, Distrito Federal, Venezuela, elevation 2092 m.

Paratype: Adult male, USNM 370891, collected by the Smithsonian Venezuelan Project team (Mammals Field Number 928), at the same locality as the holotype, elevation 2150 m, on 29 August 1965. The paratype consists of skin and cranium (mandible missing).

Other Specimens: Additional specimens were collected in Venezuela from 1966 to 1986 by the Smithsonian Venezuelan Project in Monagas (USNM 409391, USNM 409429–409431, 409433, 409435, 409437, 409438) and Miranda (USNM 387723), and by C.O. Handley, Jr., and D.I. Rhymer (USNM 517503) and A.L. Gardner and M. Candee, (USNM 562923–562937) in Aragua.

Distribution: *Myotis handleyi* is known from two cordilleras in northern Venezuela. We have examined specimens from Distrito Federal (2092–2150 m) and the states of Monagas (1190 m), Aragua (1050–1100 m), and Miranda (1180 m). The Distrito Federal, Miranda, and Aragua localities are in the Cordillera de la Costa, and the Monagas locality is in the Macizo Oriental (fig. 9). We expect this species to be found in adjacent mountains such as the Serranía del Interior, Sierra de Aroa, Serranía de San Luis, and the Cordillera de Mérida

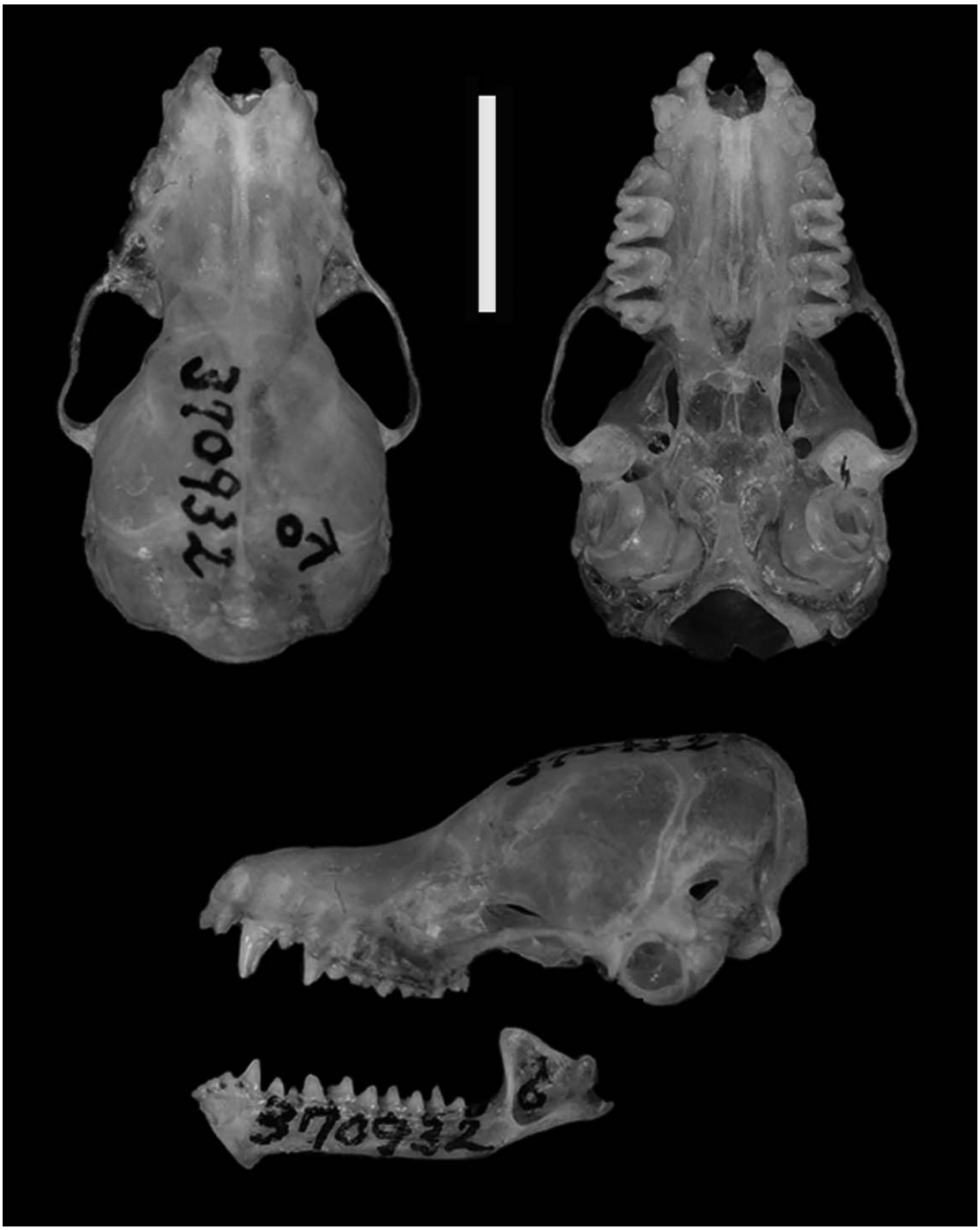

FIG. 8. Dorsal, ventral and lateral views (scale bar = 5 mm) of the cranium and lateral view of the mandible of the holotype of *Myotis handleyi* (USNM 370932). See table 5 for measurements.

TABLE 5. Selected measurements (mm) of the holotype (USNM 370932) and paratype (USNM 370891) of *Myotis handleyi*, and selected measurements and weight (g) of other specimens from Aragua, Monagas and Miranda assigned to *M. handleyi*.

	Type-specimens		Other specimens							
	USNM	USNM	Females				Males			
	370932	370891	Mean	Range	SD	*N*	Mean	Range	SD	*N*
Weight	—	—	4.5	3.5–6.0	0.72	12	5.0	4.6–5.6	0.38	10
EL	12	12	13	13–14	0.45	12	13	12–15	1.01	9
FA	35.2	37.3	35.6	33.7–36.5	0.79	11	35.1	34.0–36.1	0.82	10
3MC	31.7	34.1	32.4	31.3–33.6	0.90	11	32.3	31.0–34.1	1.00	9
LDH	8.0	8.7	6.8	6.1–7.6	0.50	8	7.5	6.5–8.4	0.58	8
LVH	6.4	5.9	5.5	4.8–6.1	0.50	8	6.0	5.1–7.1	0.70	8
GLS	13.9	14.0	14.0	13.5–14.2	0.24	12	13.8	13.6–13. 9	0.13	10
CCL	12.1	12.2	12.2	11.7–12.5	0.26	12	11.9	11.7–12.1	0.12	10
CBL	12.9	12.9	12.9	12.5–13.2	0.26	12	12.6	12.5–12.9	0.14	10
CIL	13.0	13.1	13.0	11.7–13.4	0.46	12	12. 8	12.6–13.0	0.14	10
BAL	11.5	11.8	11.7	11.4–12.0	0.22	12	11.4	11.2–11.6	0.13	10
ZB	8.3	8.3	8.3	8.0–8.6	0.22	6	8.3	8.3–8.4	0.05	7
MAB	6.6	6.8	6.8	6.6–7.1	0.13	12	6.7	6.5–6.9	0.17	9
BCB	6.2	6.4	6.4	6.2–6.6	0.11	12	6.3	6.1–6.6	0.18	9
IOB	4.7	4.7	4.4	4.0–4.6	0.17	12	4.4	4.1–4.6	0.20	10
POB	3.4	3.5	3.6	3.4–4.0	0.16	12	3.5	3.3–3.7	0.14	10
BAC	3.4	3.4	3.5	3.3–3.7	0.09	12	3.3	3.2–3.4	0.11	10
BAM	5.3	5.3	5.5	5.3–5.8	0.13	12	5.2	5.0–5.4	0.17	10
MTL	5.1	5.1	5.2	5.0–5.3	0.10	12	5.0	5.0–5.2	0.07	10
M13	2.9	2.9	3.0	2.9–3.1	0.07	12	2.9	2.8–3.0	0.06	10
MAL	9.7	—	9.8	9.5–10.1	0.18	12	9.6	9.4–9.7	0.14	8
MAN	5.5	—	5.5	5.4–5.7	0.10	12	5.4	5.4–5.5	0.05	9

Summary statistics: SD = Standard deviation; N = sample size (adults only). See Materials and Methods for variable abbreviations.

(fig. 9). Anderson and Gutiérrez (2009) and Quiroga-Carmona and Molinari (2012) provide detailed descriptions of mountain ranges in northern Venezuela.

Diagnosis: The following set of traits distinguishes *M. handleyi* from all other South American congeners: dorsal fur long, silky, and bicolored with burnished tips; skull long, rostrum long and broad, and frontals moderately to steeply sloping; sagittal crest very low or absent; plagiopatagium broadly attached to the foot at the level of the base of the toes; fringe of hairs along the trailing edge of uropatagium absent; and fur on uropatagium not reaching knees.

Description: A medium-sized species of South American *Myotis* (FA 33.7–37.3 mm, weight 3.5–6.0 g; table 5); with medium-sized ears (ear length 12–15 mm); relatively long, silky fur (LDH: 6–9 mm, LVH: 5–7 mm); ventral fur strongly bicolored, with black bases (ca. 3/4 of the hair length) and Light-Buff tips (1/4); and dorsal fur moderately tricolored, with black bases

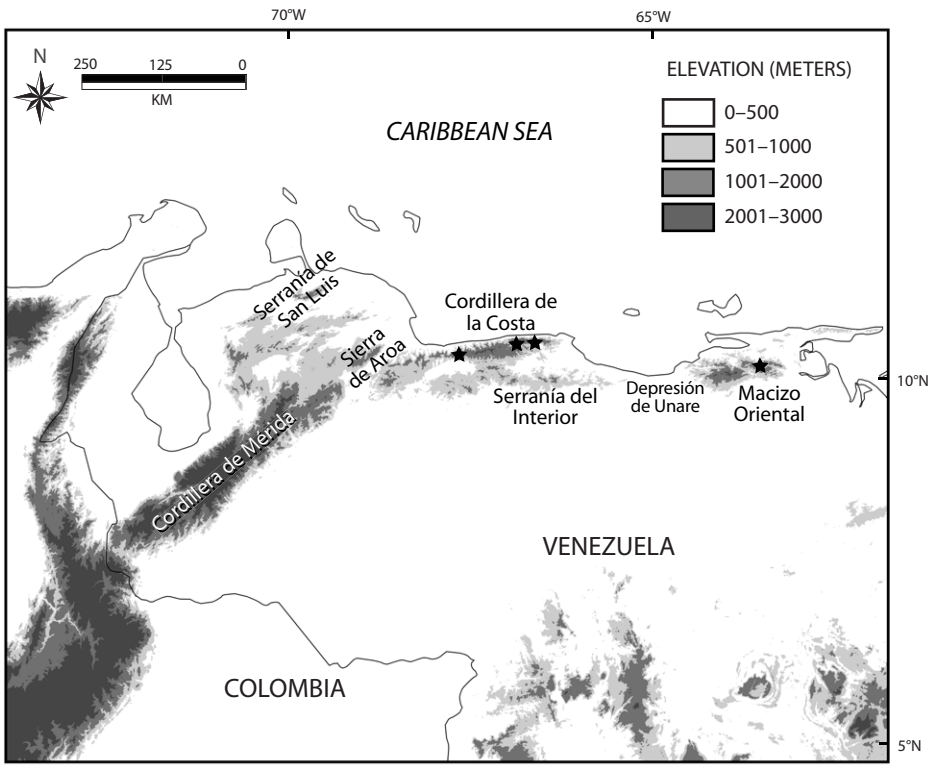

FIG. 9. Map of northeastern Colombia and northern Venezuela showing known distribution of *Myotis handleyi* (stars).

(ca. 3/6 of the hair length), a central Mummy Brown band (ca. 2/6), and Antimony Yellow tips (ca. 1/6). This third (terminal) band is well defined in most individuals (e.g., USNM 370891, 409434, 409439), but can be difficult to see in others (e.g., USNM 409435, 409437, 409438). Membranes are Mummy-Brown. Skull small to moderate in size (GLS 13.5–14.2 mm; BCB 6.1–6.6 mm); with the second upper premolar (P3) aligned in toothrow, smaller than P2 and P4, and visible in labial view, but crowded to the lingual side and barely visible in USNM 562934; sagittal crest usually absent, but low and weakly developed in USNM 562927; lambdoidal crests absent or when present, varying from very low to moderate in development; and occipital rounded and projecting behind the posterior surfaces of occipital condyles. External and cranial measurements are in tables 5 and 6.

Variation: Populations of *M. handleyi* apparently are confined to the Cordillera de la Costa (Aragua, Miranda, and Distrito Federal) and the Macizo Oriental (Monagas). Specimens from the Macizo Oriental are smaller than those from Cordillera de la Costa (table 6). Measurements related to length of cranium (GLS, CCL, CBL, BAL) and rostrum (MTL, M13), and width of rostrum (BAC, BAM) prove statistically significant; whereas others related to cranial breadth (ZB, MAB, BCB, IOB, POB) were not. The Cordillera de la Costa is separated from the Macizo Oriental by the Depresión de Unare, a gap of ca. 200 km of lowland dry forests. If *M. handleyi* proves to be restricted to the upper elevations, these differences may be indicative of distinct subspecies. Their relationship will be assessed when additional specimens become available.

TABLE 6. Selected measurements (mm) and weight (g) of samples of *Myotis handleyi* from Cordillera de la Costa (Aragua, Miranda, and Distrito Federal) and from the Macizo Oriental (Monagas), and F values (one-way ANOVA: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

	Cordillera de la Costa				Macizo Oriental				
	Mean	Range	SD	N	Mean	Range	SD	N	F
Weight	4.5	3.5–6.0	0.69	13	5.05	4.6–5.6	0.35	8	4.79*
EL	13	12–15	0.65	15	13	12–15	0.89	8	0.02
FA	35.6	33.7–37.3	0.82	14	34.9	34.0–35.9	0.83	7	2.59
3MC	32.5	31.3–34.1	0.90	13	32.1	31.0–33.5	0.82	7	0.94
LDH	7.1	6.1–8.7	0.50	10	7.5	6.5–8.4	0.63	7	0.98
LVH	5.6	4.8–6.4	0.50	10	6.1	5.1–7.1	0.71	7	3.19
GLS	14.0	13.5–14.2	0.23	15	13.7	13.6–13. 9	0.14	8	7.90*
CCL	12.2	11.7–12.5	0.25	15	11.9	11.7–12.1	0.11	8	8.68**
CBL	12.9	12.5–13.2	0.25	15	12.6	12.5–12.9	0.13	8	11.95**
CIL	13.0	11.7–13.4	0.44	15	12. 8	12.6–13.0	0.13	8	2.30
BAL	11.7	11.4–12.0	0.22	15	11.4	11.2–11.6	0.12	8	14.34**
ZB	8.3	8.0–8.6	0.20	9	8.3	8.1–8.4	0.12	5	0.12
MAB	6.8	6.6–7.1	0.14	15	6. 7	6.5–6.9	0.17	7	3.31
BCB	6.4	6.2–6.6	0.12	15	6.3	6.1–6.6	0.17	7	1.07
IOB	4.5	4.0–4.7	0.18	15	4.4	4.1–4.6	0.18	8	0.90
POB	3.5	3.4–4.0	0.16	15	3.4	3.3–3.7	0.13	8	1.90
BAC	3.4	3.3–3.7	0.09	15	3.3	3.2–3.4	0.10	8	15.24***
BAM	5.4	5.3–5.8	0.14	15	5.3	5.0–5.4	0.16	8	7.76*
MTL	5.2	5.0–5.3	0.10	15	5.0	5.0–5.2	0.07	8	24.87***
M13	3.0	2.9–3.1	0.07	15	2.9	2.8–3.0	0.05	8	4.11*
MAL	9.8	9.5–10.0	0.17	14	9.6	9.4–9.7	0.14	5	0.02
MAN	5.5	5.4–5.7	0.10	14	5.4	5.4–5.5	0.05	6	3.91

Summary statistics: SD = Standard deviation (calculated for samples larger than 5 specimens); N = sample size (adults only). See Materials and Methods for variable abbreviations.

Comparisons: *Myotis handleyi* can be distinguished from South American congeners by qualitative and quantitative traits. It differs from *M. albescens* and *M. levis* (I. Geoffroy, 1824) by the absence of a fringe of hairs along the trailing edge of the uropatagium; from *M. keaysi*, *M. riparius*, *M. ruber* (É. Geoffroy, 1806), and *M. simus* by the silky dorsal fur and absence of sagittal crest. *Myotis handleyi* is also distinguished from *M. keaysi* by the fur on uropatagium not reaching the knees, and from *M. simus* by the plagiopatagium broadly attached at base of toes. *Myotis handleyi* can be distinguished from *M. nesopolus*, *M. chiloensis* (Waterhouse, 1840), and *M. lavali* Moratelli et al., 2011a, by its less contrasting dorsal fur; also distinguished from *M. nesopolus* by its shorter dorsal fur and longer forearm, and from *M. chiloensis* and *M. lavali* by the darker dorsal fur and absence of sagittal crest. *Myotis handleyi* differs from *M. oxyotus* and *M. izecksohni* Moratelli et al., 2011a, by having shorter dorsal fur and a smaller skull; it is also distinguishable from *M. oxyotus* by its less steeply sloping frontals. *Myotis handleyi* can be distinguished from *M. aelleni* Baud, 1979, by its smaller external and cranial dimensions; from *M. atacamensis* (Lataste,

1892) and *M. diminutus* Moratelli and Wilson, 2011a, by its larger external and cranial dimensions; also distinguished from *M. atacamensis* by having a nearly naked dorsal surface of the uropatagium, and from *M. diminutus* by its broader skull (*M. handleyi*: cranial index 70–85, maxillary index 22–25; *M. diminutus*: cranial index 59, maxillary index 17). *Myotis handleyi* can be distinguished from *M. nigricans* by the longer skull and broader rostrum, moderately sloping frontals, longer and darker dorsal fur with burnished tips, and whitish tips on the ventral fur (Light-Buff), in contrast to yellowish tips (Ochraceous-Buff) in *M. nigricans*.

The forearm and third metacarpal lengths, and the length and color of dorsal fur are the most useful traits when distinguishing *M. handleyi* from *M. nigricans* in the field. The absence of a fringe of hairs along the trailing edge of uropatagium, the silky, long (> 5 mm), and tricolored dorsal fur with burnished tips, and the forearm length (> 33 mm) are the most useful field traits for identifying *M. handleyi* from the remaining Venezuelan and Colombian species. Nevertheless, we recommend examination of skulls for unequivocal identification.

Etymology: *Myotis handleyi* honors the late Charles O. Handley, Jr., in recognition of his outstanding contributions to South American chiropterology. Handley, with V.J. Tipton, coordinated the consortium of scientists who studied the distribution and ecology of mammalian ectoparasites, arboviruses, and their hosts in Venezuela from 1965 to 1968, in an initiative called the Smithsonian Venezuelan Project. These collections are the basis for more than 50 papers on Venezuelan mammals and their parasites (Handley, 1976).

Natural History: One pregnant, nine lactating, and one postlactating females were caught in May 1986 as they emerged from crevasses in an outside wall at the Rancho Grande Biological Station, which is located in humid forest. Specimens from Distrito Federal and Monagas also were caught in humid forest habitat.

TAXONOMIC NOTES ON OTHER VENEZUELAN AND COLOMBIAN *MYOTIS*

Koopman (1994) divided the tribe Myotini into species groups. According to his assessment, four groups are represented in the fauna of Venezuela and Colombia, as follows: *nigricans* group (*M. nigricans*, *M. nesopolus,* and *M. keaysi*), *ruber* group (*M. simus* and *M. riparius*), *levis* group (*M. oxyotus*), and *albescens* group (*M. albescens*). However, neither phylogenetic relationships (Ruedi and Mayer, 2001; Stadelmann et al., 2007) nor the distribution of qualitative characters traditionally used in the taxonomy of Neotropical species (e.g., Thomas, 1901, 1902; Miller and Allen, 1928; Handley, 1960; LaVal, 1973; Baud and Menu, 1993; López-González et al., 2001; Wilson, 2008) provide support for these groups. In an attempt to reconcile molecular and morphological information, we propose arranging the Venezuelan and Colombian species into the *albescens* and *ruber* groups (using the oldest available names for each clade), each one sharing evolutionary affinities and diagnostic traits, and separated from each other since at least mid-to-late Miocene (ca. 7–8 mya; Stadelmann et al., 2007). Morphologically, species in the *albescens* group—*M. albescens*, *M. nesopolus*, *M. nigricans,* and *M. oxyotus*—can be characterized by silky fur, rounded occipital region, and by either the absence of or a low, weakly developed sagittal crest. Species in the *ruber* group—*M. keaysi*, *M. riparius,* and *M. simus*—are

characterized by woolly fur, generally flattened occipital region, and the presence of a sagittal crest, which usually varies from moderately developed to high. Based on these traits, *M. handleyi* is unquestionably allied with the *albescens* group. The following comments pertain to the remaining species currently recognized as occurring in Colombia and Venezuela. All measurements and observations are from adult individuals, except as specified. Specimens examined are listed in the appendix.

Myotis albescens (É. Geoffroy, 1806)

Currently this species is treated as monotypic and occurs from southern Veracruz, Mexico, southward through Central America into Uruguay and Argentina (Simmons, 2005; Wilson, 2008; Braun et al., 2009; Moratelli and Oliveira, 2011). South American populations show a trend toward increasing size southward, with smaller specimens found in the north. Venezuelan and Brazilian Amazon basin specimens are similar in size (Moratelli and Oliveira, 2011).

We examined 49 specimens from lowland Venezuela (sea level to 195 m) and three from Colombia. Based on the list of Colombian specimens examined by LaVal (1973), one is from lowland Colombia (USNM 483946 [Arata and Thomas' field number 484]; 75 m of elevation), and two are from the highlands (USNM 433354, 433355; 1500 m). LaVal (1973) reported a specimen from highland Venezuela (USNM 409391; ca. 1190 m) and two from lowland Colombia (Arata and Thomas' field numbers 698, 699 [catalog numbers unknown]) that we could not locate. Based on these records the species occurs at upper elevations in both Colombia and Venezuela. In comparison with other Colombian and Venezuelan species, *M. albescens* is small to medium sized in its external dimensions (FA 32.0–37.7 mm, weight 4–8 g). All specimens have silky, moderately long fur (LDH 5–7 mm, LVH 4–5 mm). Most dorsal hairs vary from black (e.g., USNM 387697) to Mummy Brown (e.g., USNM 373914, 370933) from the base almost to the tip (ca. 4/5 of the hair length); the tips (ca. 1/5) are Antimony Yellow and usually contrast strongly with the basal color, a pattern similar to that in *M. handleyi*. The yellowish tips are less evident in a few specimens (e.g., USNM 374008) in which the dorsal fur can be nearly unicolored. The ventral fur is strongly bicolored, with blackish bases (2/3 hair length) and generally whitish tips (1/3 length). The ventral fur often becomes progressively paler (whiter) from the upper thorax to the pelvic region. Membranes are Mummy Brown. A fringe of hairs along the trailing edge of the uropatagium is always present. The plagiopatagium is broadly attached to the foot to the level of the base of the toes. The skull is moderate in size (GLS 13.8–14.6 mm, BCB 6.5–7.0 mm), and the rostrum is comparatively short (MTL 4.9–5.1 mm) and broad (BAM 5.2–5.8 mm). The P3 usually is aligned in the toothrow and visible in labial view, but in USNM 373913, the tooth is slightly displaced lingually and not easily seen from the side. A sagittal crest is absent; lambdoidal crests are usually present and vary from low to well developed. The parietals slope anteriorly; the occipital region projects posteriorly behind the occipital condyles. The braincase is globular in dorsal view; the postorbital and interorbital constrictions are comparatively wide. *Myotis albescens* can be distinguished easily from other Venezuelan and

Colombian species by the fringe of hairs on the uropatagium, Antimony Yellow tips on the dorsal fur, short and broad rostrum, globular braincase, broad interorbital and postorbital regions, and the lack of a sagittal crest.

Myotis nigricans (Schinz, 1821)

Myotis nigricans occurs from Mexico through Central America southward into Bolivia, northern Argentina, Paraguay, and southern Brazil (Simmons, 2005). Three subspecies currently are recognized, two of them in South America (Wilson, 2008). The nominate subspecies is widespread on the continent, except along the Andes in Colombia, Ecuador, and Peru where it is largely replaced by *Myotis n. caucensis* Allen, 1914—a name that has been considered a junior synonym of *M. n. osculati* (Cornalia, 1849); we discuss the taxonomic status of *M. n. caucensis* and this nomenclatural question in the next account. Literature records report *M. nigricans* from sea level to highlands in Costa Rica (3150 m—LaVal, 1973). Our results support a correlation between size and elevation, with individuals from higher elevations larger than those from the lowlands (figs. 2A and 3), as previously suggested by LaVal (1973).

Other names applied to populations of *M. nigricans* from northern South America and Panama are *M. chiriquensis* J.A. Allen, 1904, *M. punensis* J.A. Allen, 1914, *M. bondae* J.A. Allen, 1914, *M. maripensis* J.A. Allen, 1914, and *M. esmeraldae* J.A. Allen, 1914. LaVal (1973) relegated the names *M. bondae* and *M. maripensis* to the synonymy of *M. n. nigricans*. The holotype of *M. punensis*, from Isla Puna, Ecuador, was described as similar in color to *M. albescens* (Allen, 1914). Subsequently, Miller and Allen (1928) identified the holotype of *M. punensis* as an individual of *M. nigricans*, and regarded the name as one of several junior synonyms of that taxon. LaVal (1973) applied the name *M. n. punensis* to populations of *M. nigricans* from low to mid-elevations west of the Andes in Colombia, Ecuador, and Peru, and treated *M. esmeraldae* as a synonym. Subsequently, Bogan (1978) found no support for recognizing *M. n. punensis* and recommended that it and *M. esmeraldae* be placed in the synonymy of *M. n. nigricans*, a reasonable conclusion considering that Bogan had not examined the holotype of *M. punensis*. Moratelli and Wilson (2011b) examined the type and concluded that *M. punensis* is a junior synonym of *M. albescens*. According to Moratelli and Wilson (2011b), if populations of *M. nigricans* from the Pacific side of the Andes proved to be distinct from populations currently assigned to *M. n. nigricans*, the name *M. esmeraldae* J.A. Allen, 1914, currently in the synonymy of *M. n. nigricans*, is available. As noted above, the taxonomic status of populations on both sides of the Andes currently assigned to *M. nigricans* is pending. Regarding this question, our multivariate analyses did not detect discontinuities between eastern and western populations (figs. 2 and 3), as evidenced by the results of the MANOVA (Wilks' lambda = 0.0336, F = 1.44, p = 0.17) for samples from eastern Venezuela (Amazonas and Carabobo), western Ecuador (Esmeraldas), and western Colombia (Nariño). Qualitative traits also do not distinguish between eastern and western samples, supporting Bogan's (1978) conclusion that eastern and western populations did not represent separate taxa. Regarding the identities of the holotypes of *M. bondae*, *M. maripensis,* and *M. esmeraldae*, their classification with samples assigned to

M. nigricans instead of to either *M. handleyi* or *M. n. caucensis* supports continuing to treat these names as synonyms of *M. nigricans* (table 2). If future work contradicts our results, the name *M. chiriquensis* J.A. Allen, 1904, also currently in the synonymy of *M. nigricans* (Wilson, 2008), has priority over the three names cited above.

Based on results of morphometric analyses, we restricted our observations on *M. nigricans* to 59 specimens from Venezuela (56 from Carabobo and 3 from Amazonas) and 3 from Colombia (Nariño). Altitudinal records are from lowland localities in Venezuela (states of Amazonas, Apure, Carabobo, and Trujillo [24–138 m]) to lowland and upper elevation localities in the Cordillera Occidental of Colombia (state of Nariño, Colombia [250 m at La Guayacana and 1500 m in Ricuarte]—table 2). Venezuelan and Colombian *M. nigricans* are small (FA 32.2–34.3 mm), with small to medium-sized ears (11–14 mm), and silky, moderately long pelage (LDH 6–7 mm; LVH 5–6 mm). Dorsal fur is bicolored with black bases (2/3) and Prout's Brown tips (1/3). The ventral fur appears yellowish, with individual hairs black basally with Ochraceous-Buff tips. Membranes are Mummy Brown. A distinct fringe of hairs along the trailing edge of the uropatagium is lacking, although a few hairs may be found in some specimens. The plagiopatagium is broadly attached to the feet. The skull is small to moderate in size (GLS 13.2–13.8 mm). The sagittal crest may be present or absent; if present, it is always low. The P3 usually is aligned in the toothrow and visible in labial view, but in USNM 373945, this tooth is displaced lingually and not clearly visible labially. The parietals slope forward in lateral view, and the occipital usually projects well behind the posterior limit of the occipital condyles, except in USNM 373950 and USNM 373952, in which the occipital appears flattened. These specimens from Colombia and Venezuela fit the descriptions of *M. n. nigricans* provided by Moratelli et al. (2011a).

Myotis caucensis Allen, 1914 (? = *Vespertilio osculati* Cornalia, 1849)

Our sample from 975 m in Valle del Cauca, Colombia, matches LaVal's (1973) description of *M. n. caucensis*. However, morphometric results suggest that *caucensis* is not a subspecies of *M. nigricans*, but warrants recognition as a full species inasmuch as it can be distinguished from both *M. nigricans* and *M. handleyi* (figs. 2b–6). Therefore, we recognize the Colombian sample from Valle del Cauca as representing *Myotis caucensis*.

Based on information provided by LaVal (1973) for *M. n. caucensis*, the taxon occurs along the Andes of Colombia, Ecuador, and Peru, including intermontane valleys and adjacent Amazon lowlands of those countries. The elevational range is from ca. 200 m to 2600 m through lowland and mountain-slope forests to scrub-steppe vegetation at the upper extreme of its distribution.

Our assessment is based on seven specimens from Valle del Cauca, Colombia, at elevations between 975 and 1067 m. *Myotis caucensis* is a medium-sized species (FA 36.1–38.4 mm; weight 4.5–6.3 g), with silky, moderately long pelage (LDH 6–8 mm; LVH 5–7 mm). The dorsal fur is nearly unicolored Mummy Brown, but with darker bases weakly contrasting with the paler tips in some individuals (e.g., USNM 461858, 461867). The ventral fur is slightly paler and bicolored, with black bases (2/3) and Ochraceous-Buff tips (1/3) and resembles the ventral fur in *M. handleyi*, but is more yellowish. Membranes are Mummy Brown. A fringe of hairs

along the trailing edge of the uropatagium is absent, although scattered hairs can be seen in a few specimens (e.g., USNM 461861, 461862). The plagiopatagium is attached broadly to the feet at the level of the base of the toes. The skull is moderate in size (GLS 14.1–14.7 mm). The P3 is aligned in the toothrow and visible in labial view. A sagittal crest is lacking; lambdoidal crests are usually lacking, but when present are always low; and the parietals are inclined forward in lateral view. The braincase is elongated and the occipital projects considerably behind the occipital condyles.

A possible earlier name for this taxon is *Myotis osculati* (Cornalia, 1849), which is based on a specimen collected by G. Osculati between 1846 and 1848 in eastern Ecuador and described by Cornalia as *Vespertilio osculati*. Osculati's collection was deposited in the Museo di Storia Naturale di Milano, Italy, in 1848, where it was destroyed during the Second World War (Cagnolaro and Violani, 1988; G. Bardelli, personal commun.). Festa (1906) tentatively assigned the type to *M. nigricans* based on its similarity with Ecuadorian specimens identified as *nigricans* by Knud Andersen of the British Museum. Based on Festa (1906), Cabrera (1917, 1958) also relegated the name to the synonymy of *M. nigricans*, postulating that if animals from Colombia, Ecuador, and northern Peru were determined to represent a separate subspecies, the correct name would be *M. n. osculati*. LaVal (1973) did not treat *M. osculati*, and recognized those populations as *M. nigricans caucensis* J.A. Allen, 1914. Ibáñez (1984a, 1984b) recommended the use of *M. n. osculati* instead of *M. n. caucensis* based on priority; Wilson (2008) recognized *M. n. osculati* as a valid subspecies, listing *M. n. caucensis* as a synonym. We have not critically examined specimens from eastern Ecuador, the source of the type of *M. osculati* (Cornalia, 1849); therefore, we are not able to evaluate *osculati* and its relationship to *caucensis* or to other *Myotis* from western Amazonia that are currently treated as synonyms of *M. nigricans*. If *Myotis* "*nigricans*" from this region prove to be the same species we are calling *M. caucensis*, then this species should bear the name *M. osculati*.

Cornalia (1849) assigned the name *Vespertilio quixensis* Osculati to the synonymy of *Vespertilio osculati*. In an introduction to the facsimile reprint of Cornalia's (1849) rare publication, Cagnolaro and Violani (1988) recommended treating *V. quixensis* as a nomen nudum, but the name became available in the combination *Phyllostomus quixensis* Osculati, 1854 (p. 153). It is possible that the description of *quixensis* appeared in the first edition of the Osculati's work; however, we have not been able to examine that rare publication.

Myotis oxyotus (Peters, 1866)

This species occurs from Costa Rica to southwestern Bolivia (LaVal, 1973; Espinoza, 2007). Two subspecies are recognized, with the nominate form (*M. o. oxyotus*) only in South America (LaVal, 1973; Wilson, 2008), where it has been reported from the Andes of Colombia, Ecuador, Peru, Bolivia, and from the Andes, Cordillera de La Costa, and southern tepui highlands of Venezuela (Wilson, 2008). The other subspecies, *M. o. gardneri* LaVal, 1973, occurs from Panama to Costa Rica (LaVal, 1973; Wilson, 2008).

We examined nine specimens from Venezuela and one from Colombia, all of them from localities from 800 to 2150 m in elevation. Compared to other Venezuelan species, *M. oxyotus*

is medium sized to large in its external dimensions (FA 34.0–40.4 mm, weight 4–6 g). All specimens have long, silky fur (LDH 7–10 mm, LVH 5–7 mm). Dorsal hairs are Mummy Brown with bases sometimes slightly darker. Although LaVal (1973) and Wilson (2008) used the bicolored dorsal fur as a diagnostic trait for the nominate subspecies, the contrast between bases and tips in Venezuelan and Colombian specimens is slight, with the dorsal fur appearing almost unicolored. The ventral fur is strongly bicolored, with blackish bases and Pale Pinkish Buff tips (in USNM 409427 tips are Dresden Brown). Membranes are Mummy Brown or slightly darker. The plagiopatagium is broadly attached to the foot at the level of the toes; the uropatagium lacks a fringe of hairs along the trailing margin. The skull is the largest among Venezuelan and Colombian species (GLS 14.1–15.0 mm, BCB 6.1–7.0 mm). The frontals are comparatively steeply sloping. The P3 is aligned in the toothrow and visible in labial view, but in USNM 560809 is displaced lingually and not easily seen in labial view. The sagittal crest is usually absent; when present, it is always very low. The lambdoidal crests are low and weakly developed. The parietals are inclined forward; and the occipital region is always rounded and projecting behind the posterior surfaces of the occipital condyles. Large cranial size and the steeply sloping frontals are the most useful traits when identifying *M. oxyotus*.

We cannot confidently associate our samples with the nominate subspecies based on LaVal's (1973) descriptions. Therefore, we recommend that samples covering the distributional range of both subspecies be evaluated to review their taxonomic status.

Myotis nesopolus Miller, 1900

This species has been reported from Colombian and Venezuelan Caribbean regions and the Netherlands Antillean Islands of Curaçao and Bonaire (Wilson, 2008; Larsen et al., 2012a; Muñoz-Garay and Mantilla-Meluk, 2012). Two subspecies are recognized, with the nominate form restricted to the islands and *M. n. larensis* LaVal, 1973 on the mainland (Genoways and Williams, 1979; Wilson, 2008).

Myotis nesopolus was described first from Curaçao based on a specimen that resembled *M. nigricans*, but slightly smaller and paler in color, especially on the underparts (Miller, 1900). Subsequently, Miller and Allen (1928) treated *M. nesopolus* as a subspecies of *M. nigricans*. LaVal (1973) did not include *M. nesopolus* in his revision of Neotropical *Myotis*, and described *M. larensis* based on specimens from tropical dry forest habitat along the coast of western Venezuela. Genoways and Williams (1979) determined that mainland and island specimens were morphometrically similar and that the Venezuelan specimens were only slightly smaller than specimens from Curaçao; consequently, they recognized *M. larensis* as a subspecies of *M. nesopolus*, an arrangement followed by subsequent workers (e.g., Simmons, 2005; Wilson, 2008). On the other hand, Larsen et al. (2012a) questioned their subspecific status because a genetic distance of 4.1% between mainland and island populations suggests separate species (see Bradley and Baker, 2001).

We examined 12 specimens from mainland localities not exceeding 55 m in elevation, along with the holotypes of *M. nesopolus* (USNM 101849) and *M. n. larensis* (AMNH 130709). The holotype of *M. n. nesopolus* was the only specimen from Curaçao we examined. The high-

est elevational record we have is 500 m, reported by LaVal (1973) for the holotype of *M. n. larensis*. Based on mainland specimens, *M. nesopolus* is the smallest Venezuelan and Colombian species of *Myotis* in external measurements (FA 31.2–33.2 mm, weight 3–5 g). All specimens have moderate to long silky fur (LDH 6–8 mm, LVH 5–6 mm). The bases of the dorsal hairs are blackish (2/3), and tips are Tawny-Olive (1/3), with obvious contrast in color between bases and tips. The ventral fur is blackish basally and pale (whitish) on the tips. Membranes are Mummy Brown. The fur on the dorsal surface of the uropatagium extends slightly past the knee. The plagiopatagium is broadly attached to the side of the foot at the level of the toes; the uropatagium lacks a fringe of hairs along the trailing edge. The skull is moderate in size (GLS 13.6–14.5 mm, BCB 6.1–6.3 mm), with its dimensions overlapping those of the other *Myotis* we discuss here. The P3 is aligned in the toothrow and visible in labial view. A very low sagittal crest is present; lambdoidal crests may be present or absent, and when present are low and weakly developed. The parietals are inclined forward and the occipital region is always rounded. This species can be distinguished from other Venezuelan *Myotis* by its strongly bicolored dorsal fur, smaller external size, a forearm length 33 mm or less (can overlap with juveniles and smaller adults of *M. nigricans*), and a long third metacarpal relative to forearm (ratio 3MC/FA greater than 0.96). All of our specimens match LaVal's (1973) description of *M. larensis*.

The holotype of *M. nesopolus* has the dorsal fur Dresden Brown, with bases slightly darker. The ventral fur is blackish basally and Light Buff on the tips. Its dorsal fur coloration is much darker than that of mainland specimens examined, and the conspicuous contrast between bases and tips, used by LaVal (1973) and Wilson (2008) to characterize the mainland form, is not evident. However, according to Genoways and Williams (1979) specimens from Bonaire and Curaçao agree in coloration with continental specimens. According to Miller (1900) "the bases of the dorsal hairs [are] just perceptibly darker," but because the specimen was originally preserved in fluid, one cannot exclude the possibility that fur color has been altered. We recommend reexamining and comparing these samples with other mainland and island samples to assess the taxonomic status of these populations.

Myotis keaysi J.A. Allen, 1914

This species occurs from Mexico southward into northern Argentina along the Andes. In northern South America *M. keaysi* occurs in the Cordillera de Mérida and Cordillera de la Costa of Venezuela and is on Trinidad (Simmons, 2005; Wilson, 2008). Wilson (2008) recognized two subspecies. The nominate subspecies is distributed along the Andes of Colombia, Ecuador, Peru, Bolivia, and Argentina, whereas *M. k. pilosatibialis* LaVal, 1973, occurs from Mexico through Central America and across northern South America as far as the island of Trinidad (LaVal, 1973; Wilson, 2008).

We examined 45 specimens from Venezuela. Elevation records range from 630 m in the tropical dry forests of Guárico to ca. 2100 m in the humid mountain forests of Distrito Federal. In comparison with other Colombian and Venezuelan species, *M. keaysi* is moderate to large in its external dimensions (FA 35.7–37.5 mm, weight 5–6 g). All specimens have medium to long, woolly pelage (LDH 6–8 mm, LVH 5–6 mm), although in specimens with longer pelage, the fur

appears to be silky. Specimens from Rancho Grande, Aragua, show two different pelage colors. The dorsal fur of USNM 370929 and USNM 562921 is Antique Brown, and the ventral fur Prout's Brown basally and Antimony Yellow on the tips. The dorsal fur of USNM 370930 and USNM 370937 is Mummy Brown, and the ventral fur blackish basally and Light Buff on the tips. In a specimen from Miranda (USNM 387714), pelage color is mixed: dorsal fur is both Buckthorn Brown and Mummy Brown; and the ventral fur is either Prout's Brown at the base and Antimony Yellow on the tips, or blackish at the base and tipped Light Buff. This variation in the pelage color could be evidence of seasonal variation in color or progressive fading in a closed roost site where ammonia levels are high. Membranes are Mummy Brown. The fur on the uropatagium extends to the foot along the tibia, and sparse fur on the plagiopatagium extends from elbow to tibia. The plagiopatagium is broadly attached to the foot at the level of the toes; the uropatagium lacks a fringe of hairs. The skull is comparatively small to medium in size (GLS 13.4–14.2 mm, BCB 6.2–6.7 mm). The P3 is aligned in the toothrow and visible in labial view, except in USNM 562921 in which the tooth is partially hidden between adjacent teeth. The sagittal crest usually is present, ranging from low to medium in height (absent in USNM 562921). The lambdoidal crests are present, varying from weakly to strongly developed. The parietals are inclined forward, and the occipital region is comparatively flattened posteriorly.

Comprehensive samples representing the entire range of the species must be evaluated to determine the taxonomic status and limits of the two recognized subspecies; Venezuelan specimens we examined match LaVal's (1973) description of *M. k. pilosatibialis*, especially by the furring on the uropatagium along the tibia reaching the foot.

Myotis riparius Handley, 1960

Myotis riparius occurs from Honduras southward into Uruguay, southeastern Brazil, northern Argentina, Paraguay, and Bolivia (Simmons, 2005). Originally described as a subspecies of *M. simus*, *M. riparius* was elevated to the specific level by LaVal (1973). Wilson (2008) treated *M. riparius* as monotypic.

We examined 11 specimens from Venezuela and three from Colombia. Records are from both lowland (50–150 m) and montane localities (1000–1100 m). Based on the samples available to us, *M. riparius* is a small to medium sized *Myotis* (FA 33.6–37.0 mm, weight 4–5 g) with moderately long, woolly fur (LDH 5–8 mm, LVH 4–6 mm). Dorsal hairs are unicolored Mummy Brown (e.g., USNM 448544) or Prout's Brown (e.g., USNM 405803). Ventral hairs are blackish on the bases and strongly contrasting Antimony Yellow on the tips. Membranes are Mummy Brown. The plagiopatagium is broadly attached to the foot at the level of the base of the toes; the uropatagium lacks a trailing fringe of hairs. The skull is small to medium in size (GLS 13.2–14.4 mm, BCB 6.0–7.0 mm). The P3 usually is displaced to the lingual side and not visible in labial view or, less frequently, aligned in the toothrow and visible in labial view. The sagittal crest is present in all specimens examined except in USNM 562940, varying from low to high and well developed, but in USNM 405803 and 405804, the crest is low and weakly developed. The lambdoidal crests are present and vary from low to high. The parietals are inclined forward and the occipital region is flattened posteriorly. *Myotis riparius* can be distin-

guished from all Venezuelan and Colombian species, except *M. simus* and *M. keaysi*, by its woolly pelage. From *M. simus* it can be distinguished by the plagiopatagium broadly attached along the foot, longer fur, and cranial traits discussed below. From *M. keaysi*, *M. riparius* can be distinguished by the fur on the uropatagium not reaching the knee, whereas in Venezuelan specimens of *M. keaysi*, fur extends along the tibia to the foot.

Myotis simus Thomas, 1901

Myotis simus is a South American endemic currently known from Colombia, Ecuador, Peru, Bolivia, Paraguay, northeastern Argentina, and northern and midwestern Brazil (Moratelli, 2012). Although there are no confirmed records for Venezuela, the distribution map proposed by Moratelli et al. (2011c) suggests a high probability that *M. simus* will be found in the southern parts of the country. This species was treated as monotypic by Wilson (2008).

We found only three specimens of *M. simus* from Colombia (LaVal, 1973); all were caught at a locality ca. 100 m in elevation, and are deposited at Texas Tech University (TTU 9073, 9076, 9078). In addition, our observations are based on 73 Amazon basin specimens (10 Ecuadorian, 21 Peruvian, and 42 Brazilian) deposited at USNM, AMNH, and Museu de Zoologia da Universidade de São Paulo (MZUSP). This species appears to be restricted to lowland localities (Moratelli et al., 2011b). *Myotis simus* is a medium-sized species (FA 35.4–39.7 mm, weight 5–8 g [$N = 2$]), with short, woolly fur (LDH 4–6 mm, LVH 3–4 mm). Dorsal hairs are unicolored, and ventral hairs are weakly bicolored. Coloration is variable (may be seasonal), ranging from Tawny, Russet, and Cinnamon-Brown, with or without slightly burnished hair tips dorsally, and Ochraceous-Tawny or Buckthorn-Brown ventrally (Handley, 1960; Moratelli, 2012). The attachment of the plagiopatagium to the foot is variable in this species. We were able to verify the attachment in 53 specimens and found the membrane attached at the ankles in 8 (15%); whereas in 45 (85%), the membrane extends from the ankle as a narrow (< 1.5 mm) band along the foot to the base of the toes (illustrated by López-González, et al. [2001: 141, fig. 1]), but is never broadly attached to the foot at the level of the toes in contrast to all other South American *Myotis*. The skull is comparatively large (GLS 13.6–15.1 mm, BCB 6.6–7.7 mm), with a broad rostrum (BAC 4.1–4.5 mm, IOC 4.8–5.0 mm). The P3 is aligned in the toothrow at its base in 55 individuals (83%), but displaced at the tip or obscured by the cingulum of P4, making the tooth not completely visible in labial view; in four individuals (6%) P4 is displaced lingually and not visible; in seven (11%) it is aligned in the toothrow and visible. In 61of 64 adults (95%), the sagittal crest is present, varying from low to high. Of 20 subadults examined, the crest is present in 13 (65%) and varies from low to high as noted for adults. The lambdoidal crests are present in all adult and subadult individuals, varying from low to high. The parietals are inclined forward, and the occipital region is flattened posteriorly. *Myotis simus* is an easily identified species based on plagiopatagium attachment at the ankle, and its short, plush dorsal fur. Plagiopatagium attachment can be somewhat ambiguous in dry skins. In these cases, the velvety fur distinguishes *M. simus* from most of its Venezuelan and Colombian congeners, except *M. riparius* and *M. keaysi*, from which it can be distinguished by its much shorter fur. In addition, *M. simus* can be distinguished from these two species by the shorter and broader

rostrum and interorbital region (*M. simus*: BAC 4.1–4.5 mm, IOC 4.8–5.0 mm; *M. riparius*: BAC 3.4–3.9 mm, IOC 4.4–4.7 mm; *M. keaysi*: BAC 3.5–3.8 mm, IOC 4.1–4.6 mm).

DISCUSSION

We contend that no species of *Myotis* currently known from Colombia and Venezuela is sufficiently represented by samples covering its entire geographic and altitudinal ranges. This lack of material hinders robust taxonomic analyses. Four species are considered polytypic—*M. keaysi* (*k. keaysi* and *k. pilosatibialis*), *M. nesopolus* (*n. nesopolus* and *n. larensis*), *M. nigricans* (*n. nigricans* and *n. extremus*), and *M. oxyotus* (*o. oxyotus* and *o. gardneri*)—all of them pending revision. LaVal (1973) separated South American populations of *M. nigricans* into three subspecies: *nigricans*—widespread in the continent; *punensis*—restricted to the west side of the Andes; and *caucensis*—occurring in the Andes of Colombia, Ecuador, and Peru and in adjacent Amazon valleys. We refute the distinction between eastern and western populations (in agreement with Bogan, 1978) and recognize populations from the lower Colombian Andes as a distinct species, thus raising *M. n. caucensis* to species rank as originally described in 1914 by J.A. Allen. Therefore, apparently only the nominate subspecies of *M. nigricans* occurs in South America, with *M. n. extremus* restricted to southern Mexico. The same pattern fits *M. oxyotus*, with the nominate subspecies in South America, whereas *M. o. gardneri* is restricted to Central America. However, in *M. keaysi* and *M. nesopolus* both subspecies of each occur in South America, and additional samples from Colombia and Venezuela are needed to reassess their taxonomic status. The nominate subspecies of *M. keaysi* occurs in the Andes of Colombia southward into Argentina, whereas *M. k. pilosatibialis* is found in northern Venezuela and on Trinidad, and northward in Central America into Mexico. There are no available records of these two forms in sympatry, but this scenario may change after careful review of vouchers. In table 7 we summarize records from lowland and highland localities in Colombia and Venezuela for all species and include habitat information along with taxonomic and nomenclatural remarks.

With the description of *M. handleyi* and recognition of *M. caucensis* as a species, we now recognize 17 mainland species of South American *Myotis*. When the Caribbean islands of Dominica, Martinique, and Barbados are included, this number rises to 20 species (Wilson, 2008; Moratelli and Wilson, 2011a; Moratelli et al., 2011a; Larsen et al., 2012a). The species diversity of South American *Myotis* may be further increased following reexamination of available samples deposited in South and North American museum collections, and the reevaluation of the taxonomic and nomenclatural status of forms currently considered synonyms of polytypic species, many of which are pending revision. *Myotis simus* and *M. keaysi*, as currently recognized, appear to be composites (LaVal, 1973; Wilson, 2008; Moratelli et al., 2011c). The taxonomic status of *M. aelleni* also needs to be reevaluated, as it could prove a junior synonym of *M. chiloensis* (see Barquez et al., 1999).

At least seven species of *Myotis* occur in Venezuela and eight in Colombia (table 7). Based on our data and altitudinal records reported by LaVal (1973), this assemblage comprises species restricted to upper elevations (*M. handleyi*, *M. keaysi*, and *M. oxyotus*), species distributed from low to high along an elevational gradient (*M. albescens*, *M. nigricans*, *M. caucensis*, and *M. ripar-*

TABLE 7. Summary of the species accounts including records from lower and upper elevation localities in Colombia and Venezuela, with habitat information (obtained from skin tags and literature) and remarks.

Taxon	Colombian (C) and Venezuelan (V) records followed by references (superscripted)		Habitats	Remarks
	Records below 600 m	Records above 600 m		
M. albescens	C[1,2] V[1,2]	C[1,2] V[2]	LR[1], LDF[1]	Few specimens known from highland Venezuela and lowland and highland Colombia.
M. caucensis	C?[2]	C[1,2]	LR[2], UR[2], ScSt[2]	Occurrence in Ecuador, Peru, and Amazon lowland of Colombia pending confirmation. *Myotis osculati* a possible name for this taxon. Specimens in collections sometimes misidentified as *M. oxyotus*.
M. handleyi	—	V[1]	UR[1]	Individuals from Cordillera de la Costa larger than those from Macizo Oriental—may constitute different subspecies.
M. keaysi keaysi	—	C[2]	UR[2]	Needs revision.
M. keaysi pilosatibialis	—	V[1,2]	UR[1], DF[1] LR[2*], UR[2*], USF[2*], OCF[2*], ScSt[2*]	Needs revision. Specimens in collections sometimes misidentified as *M. riparius*.
M. nesopolus larensis	C[3] V[1,2]	—	ScSt[1,2] DF[4]	The taxonomic status subspecies pending revision.
M. nigricans nigricans	C[1,2] C[1,2]	C[1,2] V[2](?)	All types of habitat (but rare in the Amazon basin) [2*]	The occurrence in Cordillera de la Costa, Serranía del Interior, and Macizo Oriental of northern Venezuela pending confirmation (specimens reported by LaVal, 1973 and Handley, 1976 as *M. nigricans* identified as *M. handleyi*).
M. oxyotus oxyotus	—	C[1,2]	2: UR[1,2]	Needs revision.
M. riparius	C[2] V[1,2]	C[1,2] V[1,2]	LR[1], UR[1] Maybe absent from more xeric areas[2] LR[2*], UR[2*], USF[2*], Sa[2*], Gr[2*]	Specimens in collections possibly misidentified as *M. nigricans* or *M. keaysi*.
M. simus	C[1,2] V[4] (?)	—	LR[1,2]	Occurrence in the Amazon lowlands of Venezuela unconfirmed.

C = Colombia; V = Venezuela; ? = unconfirmed.
Habitat types: LR, lowland rainforest; UR, upland rainforest; USF, upland semideciduous forest; LDF, lowland deciduous forest; DF, upland deciduous forest; OCF, oak-conifer forest; ScSt, scrub-steppe; Sa, savanna; Gr, grassland.
References: [1] This study; [2] LaVal, 1973; [3] Muñoz-Garay and Mantilla-Meluk, 2012; [4] Moratelli et al., 2011b. * Habitat information not restricted to Colombia and Venezuela.

ius), and species apparently restricted to lowland habitats (*M. nesopolus* and *M. simus*). The Andean Cordillera appears to play an important role in this assemblage inasmuch as it connects populations of *M. keaysi* and *M. oxyotus*, separates populations of *M. nigricans*, and is a barrier to *M. simus*. *Myotis albescens*, *M. caucensis*, *M. k. pilosatibialis*, *M. nigricans*, and *M. riparius* occur in a variety of habitat types throughout South and Central America; whereas *M. handleyi*, *M. k. keaysi*, *M. n. larensis*, *M. o. oxyotus,* and *M. simus* are restricted to one or a few habitats (table 7). Carrera et al. (2010) reported the occurrence of *M. simus* west of the Ecuadorian Andes based on 8 specimens; we examined 2 of them (TTU 85090 and 102634), and both represent *M. riparius*. The remaining specimens are deposited in the Museo de Zoologia of the Pontificia Universidad Católica del Ecuador and require examination to confirm identification.

Moratelli et al. (2011a) found a pattern of craniometric cohesion for South American populations of the widespread species *M. nigricans*. We also found this pattern in samples on both sides of the Andes, as previously suggested by Bogan (1978). Based on these results, and our treatment of *M. n. caucensis* as a species, we recognize two subspecies of *M. nigricans*—the nominate form, widespread in South America on both sides of the Andes and in Central America and eastern Mexico as far north as Tamaulipas (Miller and Allen, 1928; Wilson, 2008), and *M. n. extremus*, restricted to southern Mexico (Bogan, 1978). Variation in external and cranial dimensions found in museum specimens identified as *M. nigricans* suggests that the species continues to be composite. The current state of morphological taxonomy does not allow us to distinguish between some of our samples with high confidence despite the fact that we can identify discontinuities between some nearby samples. Perhaps molecular studies will help in evaluating these discontinuities and reveal additional undescribed cryptic species (see Larsen et al., 2012b). We interpret the intraspecific morphological and morphometric pattern found in *M. nigricans* as evidence of demographic interaction among populations. Based on that assumption, we recognize *M. nigricans* as a widespread species distributed on both sides of the Andes.

KEY TO VENEZUELAN AND COLOMBIAN SPECIES OF *MYOTIS*

1a. Fringe of hairs along the trailing edge of uropatagium present . . . . . *M. albescens*
1b. Fringe of hairs along the trailing edge of uropatagium absent 2
2a. Fur on dorsum of uropatagium extending along tibia to foot; fur on plagiopatagium along body distributed from elbow to tibia . . . . . *M. keaysi*
2b. Fur on dorsum of uropatagium reaching knee or below; fur on plagiopatagium along body either absent or extremely sparse 3
3a. Dorsal fur woolly; occipital usually flattened posteriorly 4
3b. Dorsal fur silky; occipital usually rounded posteriorly 5
4a. Plagiopatagium broadly attached to foot at level of toes (> 1.5 mm wide); dorsal fur 5 mm or longer; breadth across canines 3.4–3.9 mm; interorbital breadth 4.4–4.7 mm. . . . . *M. riparius*
4b. Plagiopatagium attached at ankles or extending to base of toes by a narrow band of membrane (< 1.5 mm wide); dorsal fur 4 mm or shorter; breadth across canines 4.1–4.5 mm; interorbital breadth 4.8–5.0 mm . . . . . *M. simus*

5a. Dorsal fur strongly bicolored; forearm length usually 33 mm or shorter; third metacarpal long relative to forearm (ratio 3MC/FA greater than 0.96) . . . . . *M. nesopolus*
5b. Dorsal fur slightly bicolored or unicolored; forearm length usually 33 mm or longer; third metacarpal short relative to forearm (ratio 3MC/FA usually less than 0.95). 6
6a. Frontals steeply sloping; parietals rounded posteriorly in lateral view; greatest length of skull, including incisors, 14.4 mm or more. . . . . *M. oxyotus*
6b. Angle of slope of frontals variable; parietals flattened and dorsal profile inclined forward; greatest length of skull, including incisors, 14.2 mm or less 7
7a. Dorsal pelage bicolored, ranging from dark to medium brown, with burnished tips . . . . . *M. handleyi*
7b. Dorsal pelage unicolored, ranging from medium to pale brown, lacking burnished tips . 8
8a. Forearm length 35.0 mm or less; frontals comparatively steeply sloping . . . . . *M. nigricans*
8b. Forearm length 36.0 mm or more; frontals not steeply sloping . . . . . *M. caucensis*

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APPENDIX

Specimens Examined

The list of specimens is organized in alphabetical order. Specimens assigned to *M. caucensis*, *M. handleyi,* and *M. nigricans* marked with asterisks were included in the multivariate analyses; specimens here assigned to *M. nigricans* marked with a dagger were assigned to *M. n. punensis* by LaVal (1973).

Myotis albescens (*N* = 52): COLOMBIA (adults: 2 females; subadult: 1 male): Cundinamarca, Apulo (USNM 433354, 433355); *Valle del Cauca*, Río Zabaletas, 29 km SE Buenaventura (USNM 483946). VENEZUELA (adults: 29 females, 17 males; young: 2 females, 1 male): *Amazonas*, Belén, 56 km NNW of Esmeralda, Río Cunucunuma, 150 m (USNM 405790, 405794, 405796); *Amazonas*, Belén, 56 km NNW of Esmeralda, Cano Essa, 150 m (USNM 405792); *Amazonas*, Capibara, 106 km SW of Esmeralda, Brazo Casiquiare, 130 m (USNM 409392, 409395, 416579); *Amazonas*, Cerro Neblina Base Camp, 140 m (USNM 560807, 560808); *Amazonas*, Paria, 25 km S of Puerto Ayacucho, 114 m (USNM 409416, 409420, 409422); *Amazonas*, Paria, 25 km S of Puerto Ayacucho, 195 m (USNM 409425); *Amazonas*, Río Mavaca, 108 km SSE Esmeralda (USNM 405798); *Amazonas*, San Juan, 163 km ESE Puerto Ayacucho, Río Manapiare, 155 m (USNM 409403, 409404, 409406–409408, 409410–409415, 409454, 416581); *Amazonas*, San Juan, Río Manapiare, 155 m (USNM 416580, 416582); *Apure*, Río Cinaruco, 38 km NNW Puerto Páez, 76 m (USNM 373909, 373913–373917, 374008); *Apure*, Nulita, 29 km SSW Santo Domingo, Selvas de San Camilo, 24 m (USNM 441714–441716); *Bolívar*, Río Supamo, 50 km SE El Manteco, 150 m (USNM 387693); *Miranda*, 7 km E Río Chico, near Puerto Tuy, sea level (USNM 387697–387701, 387703); *Miranda*, 10 km SE Río Chico, near Tacariquade La Laguna, sea level (USNM 387702); *Trujillo*, Valera, 23 km NW Valera, Río Motatán (USNM 370933); *Zulia*, El Rosario, 42 km NW Encontrados, 24 m (USNM 441718).

Myotis caucensis (*N* = 11): COLOMBIA (adults: 6 females; young: 3 females, 1 male): *Valle del Cauca*, Cauca river, 1067 m (AMNH 32787* [holotype of *M. caucensis*]); *Valle del Cauca*, Candelaria, Ingenio Mayanguez, 975 m (USNM 461858*, 461859*, 461860*, 461861*, 461862, 461863*, 461864, 461865*, 461866, 461867).

Myotis handleyi (*N* = 27): VENEZUELA (adults: 15 females, 11 males; young: 1 female): *Aragua*, Rancho Grande Biological Station, 13 km NW Maracay, 1050 m (USNM 517503); *Aragua*, Rancho Grande, 1100 m (USNM 562923*, 562924, 562925*, 562926*, 562927*, 562928*, 562929*, 562930, 562931*, 562932, 562933*, 562934*, 562935*, 562936, 562937*); *Distrito Federal*, Pico Ávila, 5 km NE Caracas, near Hotel Humboldt, 2150 m (USNM 370932* [holotype]); *Distrito Federal*, Pico Ávila, 5 km NE Caracas, near Hotel Humboldt, 2092 m (USNM 370891* [paratype]); *Miranda*, Curupao, 5 km NW Guarenas, 1180 m (USNM 387723*); *Monagas*, 3 km NW Caripe, near San Agustín, 1190 m (USNM 409391*, 409429*, 409430*, 409431*, 409433*, 409435*, 409437*, 409438*).

Myotis keaysi (*N* = 45): VENEZUELA: (adults: 12 females, 11 males; young: 11 female, 11): *Aragua*, Rancho Grande Biological Station, 13 km NW Maracay, 1081 m (USNM 370893–370895, 370898–370902, 370911–370913, 370915–370922, 370924, 370926, 370929); *Aragua*, Rancho Grande Biological Station, 13 km NW Maracay, 1100 m (USNM 370927, 370928, 370930, 370931); *Aragua*, Pico Guayamayo, 13 km NW Maracay, 1800 m (USNM 521564); *Aragua*, Rancho Grande, Portachuelo, 1100 m (USNM 562920, 563005, 563006); *Aragua*, Rancho Grande, 1100 m (USNM 562921); *Bolívar*, Gran Sabana (USNM 130625, 130626); *Carabobo*, Montalban, 4 km NW Montalban, La Copa, 1810 m (USNM 441741, 441742); *Distrito Federal*, Los Venados, 4 km NW Caracas, 1400 m (USNM 370889); *Dis-*

trito Federal, Pico Ávila, 5 km NNE Caracas, near Hotel Humboldt, 2092 m (USNM 370890); *Distrito Federal*, junction Puerto Cruz Highway and Colonia Tovar Highway, 0.5 km W, 2150 m (USNM 562984); *Guarico*, Hacienda El Vira, 10 km NE Altagracia, 630 m (USNM 387707); *Miranda*, San Andres, 16 km SE Caracas, 950 m (USNM 373920); *Miranda*, Curupao, 5 km NW Guarenas, 1160 m (USNM 387714–387716, 387718); *Monagas*, Caripe (USNM 534265);

Myotis nesopolus (*N* = 9): CURAÇAO, Punda area, Willemstad (USNM 101849 [holotype of *M. nesopolus*]).VENEZUELA (adults: 5 females, 4 males); *Falcón*, Capatarida, 40 m (USNM 441710, 441735–441737, 441740); *Falcón*, 6 km SW Capatarida, 50 m (USNM 441711); *Falcón*, Capatarida, 55 m (USNM 441728); *Lara*, Río Tucuyo, 500 m (AMNH 130709 [holotype of *M. larensis*]); *Zulia*, Near Cojoro, 35 km NNE Paraguaipoa, 5 m (USNM 441721).

Myotis nigricans (*N* = 136): BOLIVIA (adults: 10 females, 5 males): *Cochabamba*, Chapare, 2000 m (AMNH 211214*, 211215*, 211216*, 211217*, 211218*, 211219*, 211220*, 211221*, 211222*, 211223*, 211226*, 211227*, 211243*, 211244*, 211245*). BRAZIL (adults: 30 females, 14 males): *Mato Grosso do Sul*, sea level (CCMZ-DZUP 170*, 172*, 174*, 176*, 177*); *Paraná*, Matinhos, sea level (CCMZ-DZUP 141*, 142*, 144*, 148*); *Rio de Janeiro*, Seropédica, 33 m (ALP 585*, 588*, 589*, 625*, 626*, 627*, 628*, 629*, 630*, 631*, 636*, 639*, 640*, 655*, 658*); *Rio de Janeiro*, Tinguá, 33–100 m (ALP 2505*, 6262*, 6619*, 6620*, 6622*, 6624*); *São Paulo*, São Sebastião, sea level (USNM 141395*, 141396*, 141398*, 141400*, 141401*, 141403*, 141405*, 141406*, 141408*, 141409*, 141411*, 141412*, 141413*, 141414*). COLOMBIA (adults: 1 females, 2 males, 1 undetermined): *Magdalena*, Bonda, 50 m (AMNH 14587* [holotype of *M. bondae*]; *Nariño*, Ricuarte, 1500 m (USNM 309020*†); *Nariño*, La Guayacana, 250 m (USNM 309021*†, 309023*†). ECUADOR (adults: 4 females, 3 males): *Esmeraldas*, Esmeraldas, 18 m (USNM 113343*†, 113345*, 113346*†); *Esmeraldas*, Esmeraldas, sea level (AMNH 33239* [holotype of *M. esmeraldae*]); *Zamora-Chinchipe*, 3 km NE Cumbaratza, ca. 850–914 m (USNM 513488*, 513489*); *Zamora-Chinchipe*, 4 km ENE Los Encuentros, 914 m (USNM 513490*). PERU (adults: 2 females): *Amazonas*, Valle del Rio Comaina (USNM 581966*, 581967*). VENEZUELA (adults: 36 females, 9 males; young: 9 females, 10 males): *Amazonas*, Boca Mavaca, 84 km SE Esmeralda, 7 km up Río Mavaca, 138 m (USNM 405801); *Amazonas*, Paria, 25 km S Puerto Ayacucho, 114 m (USNM 409424*, 409455*); *Apure*, Nulita, 29 km SW Santo Domingo, Selvas de San Camilo, 24 m (USNM 441722*); *Aragua*, 3 km S Ocumare de La Costa, sea level (USNM 517504, 517505); *Bolívar*, Maripa, 100 m (AMNH 17069* [holotype of *M. maripensis*]); *Carabobo*, 10 km NW Urama, El Central, 25 m (USNM 373921*, 373922*, 373923*, 373924*, 373925, 373926*, 373927, 373928, 373929*, 373930, 373931, 373932*, 373933*, 373934, 373935*, 373936*, 373937–373941, 373942*, 373943*, 373944, 373945, 373946*, 373947, 373948*, 373949, 373950*, 373951–373959, 373989–374004); *Carabobo*, 6 km N Urama, 60 m (USNM 374012); *Trujillo*, 11 km NW Urama, El Central, 25 m (USNM 387708).

Myotis oxyotus (*N* = 10): COLOMBIA (adult: 1 female): *Nariño*, El Guabo, 2150 m (USNM 309019). VENEZUELA (adult: 2 females, 7 males): *Amazonas*, Cerro Duida, Cano Culebra,

50 km NW Esmeralda, 800 m (USNM 405799); *Amazonas*, Cerro Neblina, Camp VII, 1800 m (USNM 560809–56081); *Bolívar*, Km. 125, 85 km SE El Dorado, 1032 m (USNM 387712); *Bolívar*, El Pauji, 21 km NE Icabaru, El Pauji, 851 m (USNM 441750); *Distrito Federal*, Alto Ño León, 33 km SW Caracas, 1665 m (USNM 409427); *Merida*, La Mucuy, 4 km E Tabay, 2107 m (USNM 373919, 387705).

Myotis riparius (*N* = 15): COLOMBIA (adults: 2 females, 1 male): *Valle del Cauca*, Hormiguero, 20 km SE Cali, 1000 m (USNM 483949, 483951); *Valle del Cauca*, Río Arroyohonda, 16 km N Cali (USNM 483950). VENEZUELA (adults: 3 females, 9 males): *Amazonas*, Boca Mavaca, 84 km SSE Esmeralda, 7 km up Río Mavaca, 138 m (USNM 405803, 405804); *Amazonas*, Capibara, 106 km SW Esmeralda, Brazo Casiquiare, 130 m (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, 24 m (USNM 416584, 441746, 441748); *Aragua*, Rancho Grande, 1100 m (USNM 562940); *Barinas*, 7 km NE Altamira, 1070 m (USNM 441743); *Bolívar*, Río Supamo, 50 km SE El Manteco, 150 m (USNM 387721); *Bolívar*, San Ignacio de Yhuruani, 850 m (USNM 448544).

Myotis simus (*N* = 73): BRAZIL (adults: 23 females, 11 males, 1 undetermined; subadults: 3 females, 4 males): *Amazonas*, Borba, 25 m (AMNH 91886–91892, 94224, 94225, 94227, 94230–94234); *Amazonas*, Itacoatiara, 28 m (MZUSP 4372); *Amazonas*, Manaus (AMNH 79534, 91472–91478, 91500); *Amazonas*, Parintins (AMNH 92983, 93489–93497, 93922–93925); *Amazonas*, Rio Juruá (MZUSP 638, 1074); unknown locality (MZUSP 1062). ECUADOR (adults: 3 males; subadults: 5 females, 2 males): *Pastaza*, unknown locality (AMNH 71483, 71485–71488, 71490–71494). PERU (adults: 8 females, 5 males; subadults: 4 females, 4 males): *Loreto*, Maynas (AMNH 74105, 74109, 74110, 74378–74381); *Loreto*, Ucayali (AMNH 76240–76249, 76252, 76253); *Pasco*, Oxapampa, 274 m (USNM 364481, 364482).

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