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TAXONOMIC STATUS OF *MYOTIS* (CHIROPTERA: VESPERTILIONIDAE) IN PARAGUAY

CELIA LÓPEZ-GONZÁLEZ,* STEVEN J. PRESLEY, ROBERT D. OWEN, AND MICHAEL R. WILLIG

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131 (CLG, RDO)
Program in Ecology, Department of Biological Sciences and Museum of Texas Tech University, Lubbock, TX 79409-3131 (SJP, MRW)
Dirección de Ordenamiento Ambiental, Ministerio de Agricultura y Ganadería, San Lorenzo, Paraguay (RDO)

Qualitative and quantitative variation in morphology was assessed for 6 species of *Myotis* from South America to determine which taxa occur in Paraguay, characteristics that allow for their discrimination, and the degree of geographic and secondary sexual variation that occurs in Paraguayan forms. Secondary sexual dimorphism and geographic variation were evaluated from univariate and multivariate perspectives. Multivariate morphometric differences in cranial morphology among taxa, independent of size, and mensural characters that best separate species were determined using principal components analysis followed by size-adjusted discriminant function analysis. Five species, *M. albescens, M. nigricans, M. riparius, M. ruber,* and *M. simus,* occur in Paraguay and can be distinguished using combinations of cranial and external characteristics. No significant sexual dimorphism or geographic variation was detected in these taxa of *Myotis* in Paraguay. *M. levis* has not been recorded for Paraguay as previously reported, but it may occur in the country. *M. simus,* a species previously considered to be restricted to the Amazon Basin, occurs as far south as Paraguay and northern Argentina. Although *M. simus* varies significantly in size across its range, highly differentiated cranial and external morphology allows for recognition of this species across its range.

Key words: Chiroptera, geographic variation, morphometrics, *Myotis*, Paraguay, sexual dimorphism, taxonomy

Bats of the genus *Myotis* occur in most terrestrial biomes throughout the world. The genus is diverse, with 4 subgenera and 84 species currently recognized (Koopman 1994). Nonetheless, species of *Myotis* rarely have evinced sufficient morphologic differentiation to allow allocation of individuals to taxa in an unambiguous manner. Those inhabiting the South American tropics probably are among the least differentiated (LaVal 1973). No comprehensive work on taxonomic status of *Myotis* in South America has been attempted since the revision by LaVal (1973). He examined most material available in collections and recognized 14 species of *Myotis* for South America. Four (*M. albescens, M. nigricans, M. riparius,* and *M. ruber*) were recorded for Paraguay. *Myotis simus,* a species believed to be confined to the Amazon Basin (LaVal 1973), was reported later from Paraguay (Myers and Wetzel 1979) and Bolivia (Anderson 1997). Baud and Menu (1993) examined a sample of *Myotis* from Paraguay and adjacent countries and concluded that 1 of their Paraguayan specimens represented *M. levis,* a new record for the country, and that *M. simus* did not occur in Paraguay. Also, they referred those specimens considered by Myers and Wetzel

* *Correspondent: celialg@prodigy.net.mx*

(1979) as *M. simus* to *M. ruber*. They further redefined *M. simus,* and again restricted its distribution to the Amazon Basin, but did not discuss status of *M. riparius.* Therefore, according to those authors, only 4 species of *Myotis* occur in Paraguay (*M. albescens, M. levis, M. nigricans,* and *M. ruber*—Baud and Menu 1993).

Recent collecting in Paraguay by personnel of Texas Tech University (López-González et al. 1998; Willig et al. 2000) produced large samples of *Myotis,* including a specimen from Departamento Misiones tentatively identified as *M. simus* (sensu Baud and Menu 1993, except color of pelage) and a number of individuals considered to be *M. riparius* (sensu LaVal 1973). Upon comparison of this new material with specimens of *Myotis* from Paraguay and adjacent countries, a different picture emerged regarding number of species and degree of variation in *Myotis* from Paraguay.

Our objective was to reassess taxonomic status of Paraguayan *Myotis* by reevaluating qualitative characters traditionally used to distinguish species. Additionally, we used a quantitative univariate and multivariate approach to describe and compare cranial variation in size and shape of species occurring in Paraguay and assess validity of morphometric data as taxonomic characters to distinguish taxa. Although our assessment focuses on Paraguayan populations, comparisons with specimens from other regions and inclusion of those specimens in our analyses provided a wider perspective on the degree of morphologic variation of *Myotis* in central and southern South America.

MATERIALS AND METHODS

Specimens examined.—Taxonomy and nomenclature were based on the revision of Neotropical *Myotis* by LaVal (1973). A total of 413 specimens of South American *Myotis* representing the 6 species considered by previous authors to occur in Paraguay (*M. albescens, M. levis, M. nigricans, M. riparius, M. ruber,* and *M. simus*) was examined. Variation in Paraguayan samples was quantified and compared with samples from the Amazon Basin (Brazil, Colombia, Ecuador, and Peru), Argentine Chaco, southern Brazil, Bolivia, and Uruguay; areas hereinafter referred to as localities. Two subspecies of *M. levis* currently are recognized, *M. l. levis* and *M. l. dinellii* (Anderson 1997; LaVal 1973). Specimens of each geographic race were treated as belonging to a single locality in all analyses. Quantitative and qualitative intraspecific differences between eastern and western Paraguayan bats have been reported (López-González 1998; Myers and Wetzel 1983); therefore, when possible, samples from each region were treated separately in analyses. Reference material consisted of standard museum skins and skulls, or specimens in spirits with extracted and cleaned skulls. Only adults (phalanges and basisphenoid suture well ossified) were included in analyses. Specimens (Appendix I) are deposited in the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Museum of Comparative Zoology (MCZ), Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG), Museo Nacional de Historia Natural del Paraguay (MNHNP), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), Museum of Texas Tech University (TTU), Museum of Zoology, University of Michigan (UMMZ), and United States National Museum of Natural History (USNM). Many specimens were not cataloged; those are listed by field number (TK) and are deposited at TTU or MNHNP.

Qualitative data.—A set of qualitative characters was selected to distinguish among taxa. Attributes discussed here are a subset of those deemed important to distinguish among species of *Myotis* by previous authors (Handley 1960; Miller and Allen 1928; Thomas 1901, 1902), and that have been useful in distinguishing Neotropical species in LaVal's revision of *Myotis* (LaVal 1973). The point of insertion of the plagiopatagium was considered as an artifact by LaVal (1973) but was recognized as a useful character in a subsequent analysis of Paraguayan *Myotis* (Baud and Menu 1993); therefore, it also is discussed. Extremes of variation in these characters are given in parentheses; insertion of plagiopatagium (at ankle, at toes), texture of hair (silky, woolly), length of dorsal hair at midline on rump (3 mm, >5 mm), position of P3 (displaced lingually and almost hidden between P2 and P4 when seen laterally, molariform teeth in a row), sagittal crest (present, absent), and fringe of hair at edge of uropatagium (present, absent). Descriptions of fur and membrane color follow LaVal (1973).

Quantitative data.—Fourteen cranial and 2 external characters were measured using a digital caliper: greatest length of skull, including incisors; condylocanine length; condylobasal length, including incisors; mastoidal breadth; zygomatic breadth; breadth of braincase; interorbital constriction, least width of skull at postorbital constriction; breadth across upper canines; breadth across upper molars; length of rostrum, taken as perpendicular distance between breadth across canines and breadth across molars; length of maxillary toothrow; length of upper molariform toothrow; length of mandibular toothrow; length of lower molariform toothrow; length of forearm; length of 3rd metacarpal. Values were rounded to the nearest 0.1 mm. Other standard external measurements (total length, length of tail, length of foot, length of ear, and weight) were not included in analyses because data were missing for several specimens and interpreparator variation may have obscured results. External measurements for Paraguayan specimens of *Myotis* were reported in Myers and Wetzel (1983) and López-González (1998).

Morphometric analysis.—Specimens were assigned to species based on characters described above. For descriptive and comparative purposes, mean, standard deviation, and range of each character were calculated for each species by locality (Appendix II). Ratio of breadth across canines to interorbital constriction was calculated for all specimens and an approximation to the cranial index ((interorbital constriction + breadth of braincase)·greatest length of skull/2) and maxillary index ((breadth across canines + breadth across upper molars)·length of rostrum/2) of Baud and Menu (1993). In subsequent analyses, data were log-transformed to linearize them. Secondary sexual dimorphism, geographic variation in size, and their interactions were tested in a univariate fashion using 2-way analysis of variance when samples were sufficiently large ($>$10 individuals/locality at $>$1 locality). A posteriori univariate comparisons were performed using Tukey's multiple-range tests when interlocality differences were significant. Significance of multiple univariate comparisons was adjusted using the Bonferroni sequential adjustment (Rice 1989) to maintain experiment-wise error rate at 0.05/set of tests, by species.

Analogous multivariate analyses of sexual dimorphism and geographic variation were conducted on cranial characters using multivariate analysis of variance (MANOVA). For multivariate analyses, missing data were estimated using the estimation-maximization algorithm of Little and Rubin (1987). Principal components analysis (PCA) and discriminant function analysis (DFA) were used to facilitate comparisons of species. Although overall size may be an effective taxonomic character to distinguish among taxa, it may obscure other morphologic characters potentially useful in their separation. Therefore, a size-adjusted discriminant function analysis (DFA) was performed to determine how species differ in traits not related to size and to identify which characters were more useful in reflecting those differences. Size-adjusted discriminant functions were calculated using residuals from regressions of each variable separately on the pooled-within-group principal component 1 (PC1). This approach was effective in accounting for differences among populations by eliminating potentially confounding effects of geographic and intrapopulational variation in size (dos Reis et al. 1990). Structure coefficients or vector correlations (i.e., Pearson's correlation between a variable and each discriminant function) were calculated as a measure of how closely a variable and a discriminant function were related. Such correlation reflected relative importance of a variable on each discriminant axis (Bryant 1984; Kleka 1980). Statistical validity of interspecific differences was assessed by a MANOVA among species on size-adjusted residuals. Confidence limits for percentages of explained variance and vector correlations were estimated by bootstrapping (resampling with replacement from the original data set) the DFA 1,000 times to create sampling distributions of parameters.

The sample from Paraguay included the specimen identified by Baud and Menu (1993) as the 1st record of *M. levis* for Paraguay. That individual was identified subsequently as a large *M. albescens* (López-González 1998). The specimen was not included in any analyses but was classified subsequently using the minimum Mahalanobis distance to species centroids. The training set (all observations minus *M. levis* from Paraguay) was bootstrapped 1,000 times to estimate the frequency distribution of classification. Levels of significance for statistical tests

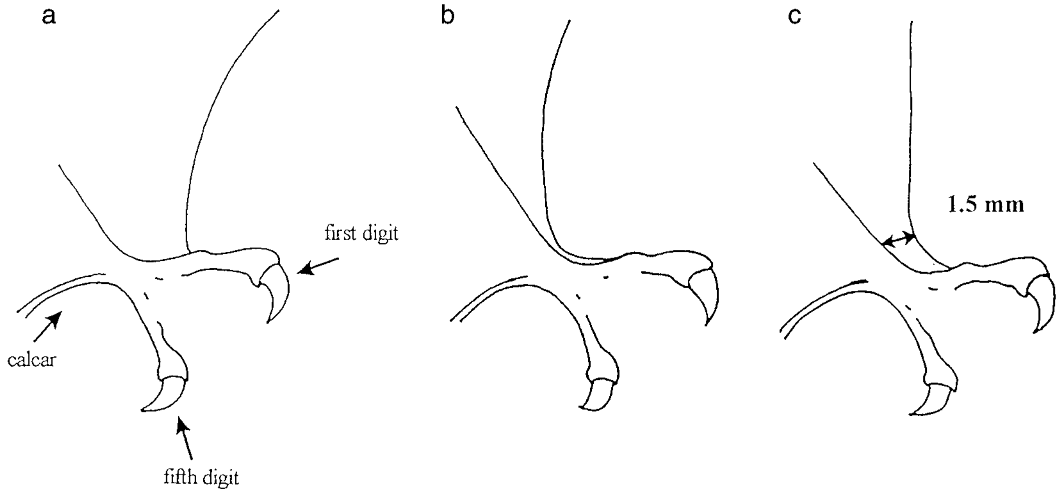

FIG. 1.—Schematic representation of diagnostic variation in width of plagiopatagium at its insertion on the leg of Paraguayan *Myotis*: a) at toes (all South American *Myotis* except *M. simus*); b and c) at the ankle (*M. simus*).

were 0.05. Statistical analyses were performed using SAS statistical software (SAS Institute Inc. 1995) and Matlab for Windows (The MathWorks, Inc. 1994) using functions and script files written by C. López-González or R. E. Strauss. Script files and functions are available upon request from C. López-González and R. E. Strauss.

RESULTS

Qualitative variation.—Myotis simus was described by Thomas (1901) based on 1 specimen from Peru. Wings attached to the ankle was 1 of the distinctive characteristics of the type specimen. Nonetheless, insertion of the plagiopatagium at the ankle in *M. simus* instead of at the toes, as in other species of Neotropical *Myotis*, was considered by Handley (1960) and LaVal (1973) to be an artifact of preparation. In contrast, Baud and Menu (1993) argued that it was not an artifact and emphasized that it represented 1 of the most important features that separated *M. simus* from other Neotropical *Myotis.* We concur with Baud and Menu (1993); insertion of the plagiopatagium at the ankle is not an artifact, although the character varies across the range of the species, with no apparent geographic pattern. Examination of *M. simus* available to us, including specimens from Ecuador, Brazil, Bolivia, Peru, and Paraguay, showed that in most individuals, the membrane narrows as it extends distally, so that at the level of the ankle it is nonexistent or extremely narrow (Fig. 1b). However, in some specimens, the membrane may be as wide as 1.5 mm at the ankle (e.g., AMNH 91473 from Amazonas, Brazil; Fig. 1c). That condition differed from other Paraguayan *Myotis* in which the membrane greatly broadened as it departed from the base of the toes (Fig. 1a; Table 1).

In general, Paraguayan species of *Myotis* correspond in fur characteristics to those described by LaVal (1973; Table 1). The exception was *M. riparius,* which in Paraguay had slightly longer fur than specimens from northern areas, making distinction from *M. nigricans* difficult. Nevertheless, in most cases, the woolly texture of the fur was sufficient to separate *M. riparius* from the silkier *M. nigricans.*

Myotis simus was described by LaVal (1973:31) as ‘‘usually bright orange or somewhat duller, varying from cinnamon-brown to cinnamon; tips not contrasting; below, hairs longer, tips yellow, bases

TABLE 1.—Diagnostic characteristics for 6 species of *Myotis* that occur or may occur in Paraguay. Quantitative characters are given as mean (range). Acronyms of characters as in Table 4.

	Species					
Character	*M. albescens*	*M. levis*	*M. nigricans*	*M. riparius*	*M. ruber*	*M. simus*
Attachment of plagiopatagium	At toes	At toes	At toes	At toes	At toes	At ankle
Length of fur	Long (>4 mm)	Long (4.5–5.5 mm)	Long (>5 mm)	Short (3–5 mm)	Short (~4 mm)	Short (<3 mm)
Texture of hair	Silky	Silky	Silky	Woolly	Silky	Woolly
Color of hair	Pale to dark brown, tips frosted	Dark brown bases, yellow to brown midparts, tips frosted in dark specimens	Black to sandy brown, tips with darker bases	Dull brown, unicolored or bases slightly darker	Bright cinnamon, unicolored or bases slightly darker	Bright orange (fresh), or ochraceous to cinnamon
Fringe of hair on edge of uropatagium	Present	Present	Absent	Absent	Absent	Absent
Position of P3	Usually on toothrow	Usually on toothrow	Usually on toothrow	Often crowded to lingual side	On toothrow	Crowded to lingual side
Sagittal crest	Absent	Absent	Absent	Present	Present	Present
Breadth across upper canines	<1 mm	<1 mm	<1 mm	≥1 mm	≥1 mm	≥1 mm
Interorbital constriction	0.87 (0.81–0.96) mm	0.96 (0.84–1.12) mm	0.96 (0.86–1.03) mm	1.03 (0.93–1.12) mm	1.06 (0.98–1.13) mm	1.03 (0.94–1.14) mm
Cranial index	77.8 (70.3–84.0)	80.9 (71.2–88.6)	68.6 (62.9–76.6)	70.0 (64.6–76.1)	81.8 (78.4–85.0)	79.8 (73.0–88.1)
Maxillary index	25.9 (23.5–28.8)	30.6 (26.0–36.9)	25.6 (23.2–29.4)	28.1 (25.0–31.1)	34.8 (33.5–35.8)	31.1 (27.3–34.6)

somewhat darker.'' In contrast, in their redefinition of the species, Baud and Menu (1993) considered that the ochraceous coloration might be an effect of preservation rather than a natural feature. Specimens they studied were all mummy-brown and never ochraceous. The specimen of *M. simus* collected by us at Ayolas, Misiones, Paraguay, was a bright orange animal when alive. After a year of storage, the dry skin became ochraceous-brown, the same color as in some of the series from the Amazon Basin at AMNH (Appendix I) and specimens from Bolivia. Dark, cinnamon-red individuals also occurred (e.g., TTU 46348 from near Tingo María, Peru), and the red coloration remained after 15 years of storage in a museum. Other specimens (dry skins) from the same areas were dull brown, as described by Baud and Menu (1993). We detected no geographic pattern to color variation, although apparent lack of a pattern may have resulted from change in color of specimens across time.

Fringe of hair at the edge of the uropatagium was a diagnostic feature within species. It separated *M. albescens* and *M. levis,* which have a fringed uropatagium, from all other Paraguayan species. Some Paraguayan specimens of *M. nigricans* and *M. riparius* had a few hairs at the edge of the uropatagium that were sparse and required magnification to be seen.

Presence or absence of a sagittal crest was a useful character to separate species in Paraguay (Table 1). Intraspecific variation in degree of development of crests was minimal. All Paraguayan *M. riparius* had a crest, as did all examined specimens of *M. ruber* and *M. simus.* In a large sample of *M. simus* examined by LaVal (1973), only 8 of 67 specimens lacked a sagittal crest.

The P3 crowded to the lingual side was a diagnostic character for *M. simus* (Thomas 1901); only 1 specimen of *M. simus* examined by us lacked that condition. Although *M. riparius* was described based on specimens with a crowded P3 (Handley 1960), much variation in that trait occurred in that species. In Paraguay, only 16 of 59 specimens examined had P3 crowded to the lingual side, whereas 84 of 86 specimens from Central and South America (excluding Paraguay and Uruguay) had a crowded P3 (LaVal 1973). No geographic pattern in crowding was detected. This condition also occurred sporadically in *M. nigricans.*

No single character sufficiently differentiated species of *Myotis* in Paraguay, except for insertion of the plagiopatagium at the level of the ankle, which separated *M. simus* externally from other species of Neotropical *Myotis*. The remaining species could be separated by a combination of the aforementioned pelage characteristics and cranial features (Table 1). However, combinations of character states considered as diagnostic of species were not present in all specimens, reducing ability to make positive identification using only qualitative characters.

Quantitative variation.—Because of small samples, secondary sexual dimorphism was not examined in *M. ruber.* Sexual differences in cranial morphology were not significant in any remaining species based on univariate or multivariate analyses, but sex by locality interaction was significant for greatest length of skull, condylobasal length, and length of maxillary toothrow in *M. levis* (sequential Bonferroni adjustment, $P < 0.001$). The corresponding effect also was significant in the multivariate test (Table 2). Interlocality differences also were significant in the multivariate test for *M. levis* (Table 2). Significant geographic differences consistently were found for condylocanine length, mastoid breadth, zygomatic breadth, interorbital constriction, and length of maxillary toothrow ($P < 0.001$). *M. riparius* differed significantly across localities according to MANOVA. However, univariate results were significant only for 1 character after adjustment; specimens from the Amazon Basin were larger for breadth across upper molars ($P < 0.001$). The locality effect was highly significant in the MANOVA for *M. simus* (Ta-

TABLE 2.—*P*-values of multivariate analysis of variance (MANOVA) tests for sexual dimorphism, geographic variation, and their interaction in South American *Myotis*. NT, effect not tested.

	MANOVA		
Species of *Myotis*	Sex	Locality	Sex by locality
M. albescens	0.185	0.207	0.483
M. levis	0.386	0.017*	0.015*
M. nigricans	0.483	0.087	0.247
M. riparius	0.664	0.006*	0.139
M. ruber	NT	NT	NT
M. simus	0.754	<0.001*	0.561

* Significant after sequential Bonferroni adjustment by species ($\alpha = 0.05$).

ble 2). Specimens of *M. simus* from the Amazon Basin were significantly smaller than those from outside the Basin in 7 characters, and Bolivian specimens were significantly larger than those from Paraguay in 4 of those characters (Table 3). Neither geographic variation nor sexual dimorphism was detected for *M. nigricans* or *M. albescens.*

The PCA illustrated major trends in cranial morphology for populations examined (Fig. 2a). PC1 accounted for 70% of total variation in the sample and represented a general size axis. Smaller taxa (*M. albescens, M. nigricans,* and *M. riparius*) had low or negative scores, whereas larger species (*M. levis, M. ruber,* and *M. simus*) had high, positive scores on that component. Because within-species variance was large compared with intertaxon differences for most variables, size alone did not discriminate among those species, with the possible exception of *M. ruber*. PC2 and PC3 indicated shape differences among taxa (Fig. 2b). Based on shape, 3 distinct groups of specimens were formed, *M. albescens, M. simus*, and the 4 remaining species (*M. levis, M. nigricans, M. riparius,* and *M. ruber*).

First and 2nd axes in the size-adjusted discriminant function analysis showed about the same relationship among species as did PC2 and PC3, except that, as expected, groups were more distinct (Figs. 2 and 3). The first 3 discriminant axes accounted for 96.7% of total variation among taxa after size adjustment (Table 4). That analysis also allowed recognition of 3 distinct cranial morphologies: *M. albescens, M. simus,* and the remaining species as a group (Fig. 3). Relationships among *M. levis, M. nigricans, M. ruber,* and *M. riparius* were less clear, suggesting little species-specific differentiation in shape among those taxa. A relatively broad interorbital

TABLE 3.—A posteriori comparisons of sample means (Tukey's test) for populations of *Myotis simus* with a significant geographic variation in univariate tests ($\alpha = 0.05$). Values of means are given in millimeters; means sharing an asterisk are not significantly different from each other by locality.

	Locality		
Character	Bolivia	Paraguay	Amazon Basin
Condylocanine length	12.9*	12.8*	12.3
Mastoid breadth	8.2	8.0	7.8
Breadth of braincase	7.4	7.2	7.0
Length of rostrum	6.5	6.3	6.1
Length of maxillary toothrow	5.3*	5.3*	5.0
Length of upper molariform toothrow	4.4	4.3	4.0
Length of mandibular toothrow	5.7*	5.6*	5.4

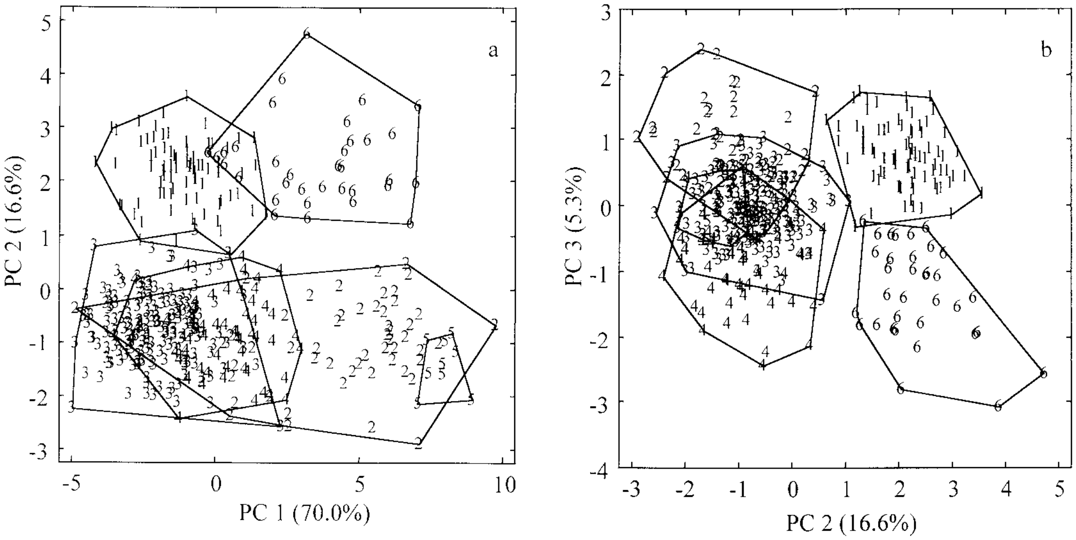

FIG. 2.—Projection of individual scores for samples of 6 species of South American *Myotis* in principal components space: a) PC1 and PC2; b) PC2 and PC3. Species codes are 1, *M. albescens*; 2, *M. levis*; 3, *M. nigricans*; 4, *M. riparius*; 5, *M. ruber*; 6, *M. simus.* Numbers in parentheses indicate percent variation among species explained by each principal component.

constriction and cranial vault and a short rostrum placed *M. albescens* and *M. simus* on the negative side of discriminant function 1 (DF1) and separated them from the remaining species. Large values of greatest length of skull, condylocanine length, condylobasal length (indicative of a long braincase), small zygomatic breadth, and breadth

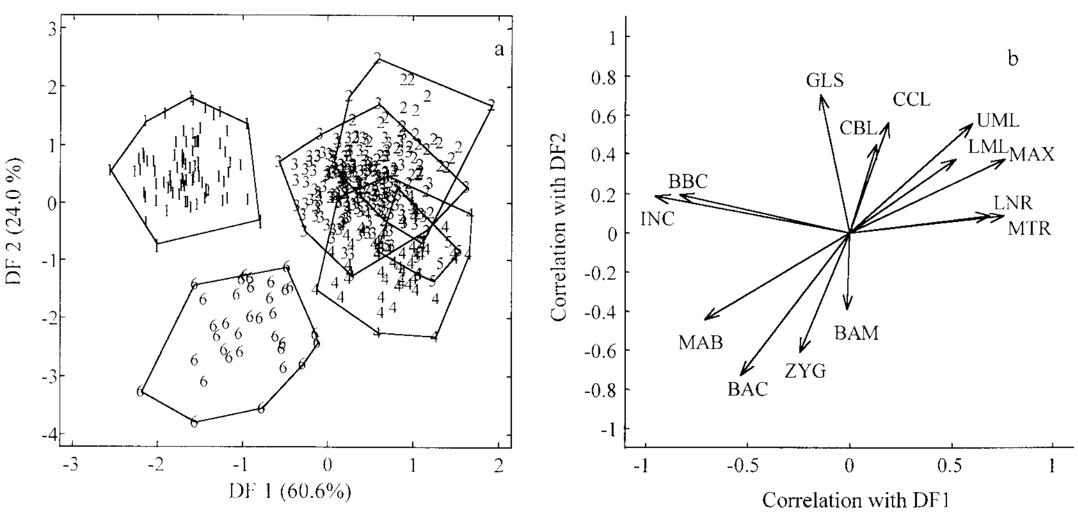

FIG. 3.—Size-adjusted discriminant function analysis of 14 cranial variables from 6 species of South American *Myotis*: a) projection of individual scores on discriminant axes 1 and 2; b) vector correlations of particular characters with discriminant axes. Numbers in parentheses indicate percent variation among taxa explained by each discriminant function; acronyms of variables as in Table 4 and species codes as in Fig. 2.

TABLE 4.—Size-adjusted loadings of cranial characters on each of 3 size-adjusted discriminant functions (DFs) constructed to distinguish among taxa of *Myotis* in Paraguay. Numbers in parentheses correspond to bootstrapped 95% *CI* for the vector correlation between each character and the corresponding DF.

	DF1	DF2	DF3
Greatest length of skill (GLS)	−0.14 (−0.29–0.00)	0.70 (−0.00–0.76)	−0.06 (−0.55–0.64)
Condylocanine length (CCL)	0.19 (0.00–0.36)	0.55 (0.29–0.68)	0.32 (−0.24–0.51)
Condylobasal length (CBL)	0.13 (−0.02–0.29)	0.44 (0.17–0.57)	0.21 (−0.26–0.41)
Mastoid breadth (MAB)	−0.71 (−0.78 to −0.62)	−0.45 (−0.55 to −0.05)	−0.10 (−0.42–0.30)
Zygomatic breadth (ZYG)	−0.24 (−0.40 to −0.08)	−0.61 (−0.72 to −0.25)	−0.27 (−0.54–0.30)
Breadth of braincase (BBC)	−0.83 (−0.87 to −0.77)	0.19 (−0.26 to 0.31)	−0.33 (−0.44–0.37)
Interorbital constriction (INC)	−0.95 (−0.96 to −0.89)	0.18 (−0.06–0.33)	−0.02 (−0.18–0.24)
Breadth across upper canines (BAC)	−0.53 (−0.63 to −0.39)	−0.73 (−0.80–0.06)	0.20 (−0.78–0.68)
Breadth across upper molars (BAM)	0.01 (−0.12–0.15)	−0.39 (−0.48–0.44)	0.10 (−0.55–0.56)
Length of rostrum (LNR)	0.69 (0.56–0.77)	0.08 (−0.28–0.21)	−0.10 (−0.29–0.24)
Length of maxillary toothrow (MAX)	0.77 (0.65–0.83)	0.37 (0.03–0.52)	0.15 (−0.22–0.33)
Length of upper molariform toothrow (UML)	0.60 (0.41–0.75)	0.54 (0.31–0.73)	0.39 (−0.19–0.55)
Length of mandibular toothrow (MTR)	0.76 (0.68–0.80)	0.08 (−0.28–0.21)	−0.09 (−0.27–0.21)
Length of lower molariform toothrow (LML)	0.52 (0.35–0.65)	0.37 (0.10–0.53)	0.24 (−0.18–0.45)
Percent of variance explained	60.63 (46.56–65.12)	23.97 (19.78–34.42)	12.69 (9.41–19.50)

across upper molars separated *M. albescens* from *M. simus*, which also had a wider rostrum and base of skull. *M. nigricans*, *M. riparius*, *M. ruber*, and *M. levis* had long rostrums (large length of rostrum and length of mandibular toothrow) and narrow cranial vaults (small interorbital constriction and breadth of braincase). *M. ruber* and *M. riparius* were indistinguishable in shape of skull; their relatively short braincase (small greatest length of skull, condylocanine length, and condylobasal length) and large breadth across upper molars and zygomatic breadth separated those 2 taxa from the rest of the long-faced *Myotis* (Fig. 3). Based on discriminant functions obtained from the analysis, specimen MHNG 1747.54 from Arroyo Pirayu-i, 40 km N Capitán Meza, Itapua, identified as *M. l. levis* by Baud and Menu (1993), was classified as *M. albescens* in 100% of 1,000 iterations in the bootstrapped DFA.

DISCUSSION

Unlike many vespertilionids, in which females are larger than males (Myers 1978; Ralls 1976; Williams 1978; Williams and Findley 1978), no significant difference in size between sexes was found for any species of *Myotis* from Paraguay. Although Myers and Wetzel (1983) found significant sexual dimorphism in Paraguayan *M. albescens*, they considered differences to be sufficiently small to allow for pooling sexes in morphometric analyses. Similarly, Willig (1983) found no significant sexual dimorphism in *M. riparius* from northeastern Brazil. Significance of the locality by sex interaction in *M. levis* may represent different expressions of sexual dimorphism in each subspecies, but because of small samples available and the high degree of overlap in size between them (Appendix II), these results must be interpreted with caution.

Significant, albeit slight, geographic differences in cranial and external characters have been reported in *M. nigricans* and *M. albescens* from Bolivia, Chaco Boreal, and eastern Paraguay (Myers and Wetzel 1983). Lack of significance for *M. nigricans* and *M. albescens* examined here may be the result of not including Bolivian specimens, which were the most differentiated in samples examined by Myers and Wetzel (1983). In their analysis, differences between east and west were only marginally significant, with Chacoan specimens averaging 1–2% larger than eastern specimens. *M. nigricans* and *M. albescens* show opposite clinal trends in size south of the Amazon Basin (LaVal 1973); *M. nigricans* is smaller to the south, whereas *M. albescens* increases in size with latitude. Geographic variation reported by Myers and Wetzel (1983) may reflect these clinal trends because the specimens used in their analyses were from a sample that largely followed a transect from the Bolivian Chaco south–southeast to eastern Paraguay. No geographic variation in size has been detected in *M. riparius* from Venezuela to eastern Peru to Uruguay (LaVal 1973). Specimens from western Paraguay were smaller than individuals from the eastern region in previous analysis (Myers and Wetzel 1983). However, small samples precluded powerful statistical analysis of geographic variation in *M. riparius.* Our results reflect those of previous authors, although multivariate results were significant, only 1 of the variables examined was significant, and no pattern is apparent in variation of characters examined. Geographic differences may exist among populations of this species across its range, but available evidence is not sufficient to draw incontrovertible conclusions or to determine if a pattern exists. Geographic variation in *M. simus* had not been recorded previously. Specimens from the Southern Cone were larger than those from the Amazon Basin (Appendix II). In turn, Bolivian and Paraguayan specimens differed significantly in cranial measurements. Nonetheless, we believe designation of subspecies in this taxon is not warranted because no matching geographic pattern occurs in differences in coloration or any other external features examined so far. A comprehensive study of the entire range of the species would be necessary to evaluate the extent of interpopulational variation.

Despite variation in size, shape of skull is consistent across populations within species. Neither PCA nor DFA suggested any distinct populations below the specific level. Five species are recognized for Paraguay: *Myotis albescens, M. nigricans, M. riparius, M. ruber,* and *M. simus.* DF1 was correlated highly and positively with characters related to length of rostrum and toothrows and negatively correlated with width of cranial vault and interorbital constriction. *M. albescens* and *M. simus* have a short rostrum, broad cranial vault, and wide interorbital constriction, whereas the remaining species have the opposite characteristics. Scores on DF2 were related to relative length of braincase with respect to total length of skull. DF2 was correlated negatively with characters related to width of rostrum and braincase. *M. albescens* and *M. simus* are essentially indistinguishable along the 1st axis but differed along the 2nd axis; *M. simus* has wider base of skull, wider rostrum, and shorter braincase. *M. albescens* has a comparatively narrow base of skull, which, together with the wider vault, confers the characteristic, globose appearance of its braincase.

We concluded that *M. levis* has not been documented for Paraguay. The only specimen from Paraguay previously identified as *M. levis* (MHNG 1747.54) has the cranial morphology of *M. albescens.* Additionally, dorsal pelage of this individual is long and dark, with frosted tips. Although the specimen is relatively large (Appendix II) and frosted hair-tips occur in *M. l. levis* from São Paulo, Brazil (e.g., FMNH 141600, 145327, 145328), the specimen has a short rostrum, globose braincase, and wide interorbital constriction, which firmly place it within *M. albescens*. Nonetheless, the known distribution of *M. levis* in northern Argentina and southern Brazil (LaVal 1973) suggests that it may occur in Paraguay.

Although different in size and coloration, *M. l. levis* and *M. l. dinellii* are similar in cranial shape. Degree of cranial resemblance is comparable to that between *M. nigricans* and *M. riparius* (Fig. 3), which are considered distinct species. In fact, *M. levis* and *M. dinellii* were described originally as species and subsequently relegated to subspecies of *M. chiloensis* by Miller and Allen (1928), assigned by Cabrera (1958) to *M. ruber*, and referred to as *M. levis* (distinct from *M. ruber*) by LaVal (1973). Under LaVal's definition (followed here), *M. levis* occurs in southeastern Brazil, Uruguay, and Argentina. He recognized 2 major groups, *M. l. levis* from southeastern Brazil to Uruguay and *M. l. dinellii* from northwestern and southern Argentina. LaVal (1973) distinguished the 2 forms by size and color and remarked that differences between them were striking. *M. l. levis* is large with broad color variation across its range (so much so that LaVal [1973] suggested the possibility that his sample represented 2 species). *M. l. dinellii,* conversely, is smaller, with long, silky, strongly bicolored fur (bases black, tips reddish brown to blond). Nonetheless, differentiation of these 2 forms is far from clear. Specimens from Argentina can be separated by size (Barquez et al. 1999). However, specimens from Entre Ríos Province, Argentina, were intermediate between *M. l. levis* and *M. l. dinellii* (LaVal 1973). Our samples, which included specimens from Bolivia, Brazil, Argentina, and Uruguay, were significantly different in size for only 4 of 14 cranial characters. We included specimens from Bolivia not available to LaVal, which extended the range of size measurements for *M. l. dinellii* to overlap with that of the nominate subspecies in most measurements. LaVal (1973) suggested the existence of an intergradation zone between the 2 forms, or else possibility that they represented different species, but no data were available from intermediate areas to draw definitive conclusions. However, externally, the Bolivian material shows the characteristic coloration of *M. l. dinellii* (Anderson 1997). Although more material is available now, sample sizes are still insufficient to assess geographic variation in *M. levis* with statistical reliability. Clearly, populations now included as *M. levis* await thorough examination; additional, nonmorphologic information may help clarify taxonomic boundaries.

Quantitative indices have been used to distinguish among Paraguayan species of *Myotis*. Cranial and maxillary indices (Baud and Menu 1993) describe different aspects of the skull (Table 1). Maxillary index is a measure of size of rostrum; thus, *M. albescens* has smaller maxillary index, whereas *M. levis* would have large values. Cranial index is a measure of breadth of braincase and cranial vault; *M. nigricans* has small cranial indices, whereas *M. albescens* and *M. ruber* have large values. Clearly, these indices reflect overall cranial size. As such, they show a high degree of overlap and by themselves are of little use in separating species. Baud and Menu (1993) used them in combination, creating biplots of maxillary versus cranial index. Such biplots successfully separated *M. ruber* (actually a mixture of *M. ruber* and *M. simus*) from the remaining species. LaVal (1973) used ratio of breadth across canines to interorbital constriction as a taxonomic character to separate species. This ratio is useful to separate *M. albescens* from the remaining species in most cases, although not consistently so (Table 1). This ratio is helpful in distinguishing *M. riparius* and *M. nigricans.* Other species are better identified by a combination of cranial and external characters described previously, and summarized below.

KEY TO PARAGUAYAN SPECIES OF *MYOTIS* PLUS *M. LEVIS*

1. Fur <3 mm long on dorsum, color bright orange or tawny to cinnamon-red on back, length of forearm >37 mm, P3 crowded lingually, so that it is scarcely visible in lateral view, insertion of plagiopatagium at base of tarsals . . . . . *M. simus*
– Dorsal pelage >3 mm, color from cinnamon red to black, tips may be white, giving a frosted appearance, P3 not crowded to lingual side, insertion of plagiopatagium at toes 2
2. Sagittal crest usually present, often well developed, breadth across canines usually greater than interorbital constriction, or if about equal, then interorbital constriction usually >3.7 mm, dorsal pelage silky and reddish-brown to cinnamon, or woolly and dull to dark brown, fur relatively short (<5 mm) . . . 3
– Sagittal crest usually absent, or poorly developed if present, breadth across canines usually less than interorbital constriction, or if not, then interorbital constriction usually <3.7 mm, dorsal pelage silky, color yellow or sandy brown to black, tips of hairs may be white, giving a frosted appearance, fur long (>5 mm) 4
3. Fur silky, color cinnamon-red, hair on dorsum of uropatagium extends to or past the knees, greatest length of skull >14.5 mm, length of forearm >37 mm . . . . *M. ruber*
– Fur woolly, color reddish-brown to dark-brown, hair on dorsum of uropatagium does not extend to or past the knees, greatest length of skull <14.5 mm, length of forearm <37 mm . . . . *M. riparius*
4. Pelage strongly bicolored, color brown to almost black at bases of hairs and silvery on tips, giving a frosted appearance, or dark brown on bases and yellow to brown on midparts with paler tips. A fringe of hair at the posterior edge of uropatagium is present (may need magnification to be observable), breadth of braincase >7 mm, or if smaller, then length of rostrum >5.7 mm 5
– Pelage weakly bicolored, color sandy brown (in specimens from northwestern Chaco), to blackish, uropatagium without a fringe of hair, breadth of braincase <7 mm, length of rostrum usually >5.5 mm . . . . *M. nigricans*
5. Dorsal fur brown to almost black at bases of hairs and silvery on tips, giving a frosted appearance, cranial vault and interorbital constriction relatively broad, giving a globose appearance to skull, rostrum relatively short, breadth between canines >7 mm or if smaller, then length of rostrum <5.7 mm . . . . *M. albescens*
– Dorsal fur with dark bases and silvery tips giving a slightly frosted appearance similar to that of *M. albescens* (in *M. l. levis*), or fur dark brown on bases, yellow to brown on midparts, and paler on tips (in *M. l. dinellii*), cranial vault and interorbital constriction narrow, rostrum relatively long, breadth between canines <7 mm, or if wider, then length of rostrum >6 mm . . . . *M. levis*

SPECIES ACCOUNTS

Paraguayan species of *Myotis* represent 2 subgenera, *Leuconoe*, including *M. albescens*, *M. riparius*, *M. ruber*, and *M. simus*, and *Selysius*, represented by *M. nigricans* (Koopman 1993, 1994). Cabrera (1958) designated a monotypic subgenus, *Hesperomyotis*, to include *M. simus*, based on its high degree of morphologic divergence from congeners. Our results indicate that degree of differentiation of *M. simus* is similar to that in *M. albescens* or *M. ruber*. With the evidence at hand, we see no reason to consider *M. simus* to belong to a different subgenus.

Myotis albescens (É. Geoffroy Saint-Hilaire, 1806)

A small species of *Myotis*, and the most distinctive of those occurring in Paraguay. Dorsal fur ranges from pale to dark brown or almost black, tipped with golden yellow or silvery white, resulting in a frosted appearance. Individual dorsal hairs are long (>4 mm); ventral hairs are dark brown with buffy tips. Coloration of pelage ranges from almost black to sandy brown, always with frosted tips. Some specimens have ≥1 patches of rusty-brown or black hair on the dorsum. No difference in color was detected between specimens from eastern and western Paraguay. The plagiopatagium attaches to the toes (Fig. 1a). A fringe of hairs is present on the posterior border of the uropatagium, although it may be difficult to see without magnification. This character is consistent throughout Paraguay. The skull is of moderate size (Appendix II), with little forehead slope, and a narrow, short rostrum. Cranial vault and interorbital constriction are wide relative to size of skull. These characters separate *M. albescens* from all other species (Fig. 3). External characteristics separate *M. albescens* from all other species of Paraguayan *Myotis* (Table 1), except for *M. levis* (which may occur in Paraguay) and *M. nigricans,* which may have similar coloration. However, its globose cranial vault, short rostrum, and proportionally wider postorbital constriction (ratio breadth across canines to interorbital constriction <1) suffice to separate it.

Distribution.—Myotis albescens occurs throughout Paraguay, although it seems more common in the west (López-González 1998; Willig et al. 2000).

Remarks.—Although clinal variation in size exists for Mato Grosso (Brazil), Paraguay, and Uruguay, no subspecies have been recognized (Koopman 1994; LaVal 1973). Reproductive biology and natural history have been described by Myers (1977). *M. albescens* shares roosts with *M. nigricans* in the Paraguayan Pantanal. Findley (1993) classified this species as a forest and clearing aerial insectivore.

Myotis nigricans (Schinz, 1821)

This is the most common species of *Myotis* in Paraguay and on average the smallest (Appendix II). The dorsal pelage is silky. Coloration ranges from black on bases and tips of hairs in the eastern region, to sandy brown on tips with darker bases in the northwestern Chaco. Wing membranes insert at toes (Fig. 1a). Both rostrum and braincase are narrow, and upper molariform teeth usually are arranged in a row, although in a few specimens (e.g., TK 60156, 60231, 60263), P3 is crowded to the lingual side. *M. nigricans* usually lacks a sagittal crest, although some specimens from Fuerte Olimpo, Departamento Alto Paraguay, have a low, barely perceptible sagittal crest. However, pelage characteristics place these specimens in *M. nigricans.* This species is distinguishable externally from congeners in Paraguay by color, length and texture of hair, and overall size (Table 1). *M. nigricans* can be confused only with *M. riparius*; these 2 species are more similar to each other than to any other Paraguayan species in size or shape of skull. However, *M. nigricans* generally is smaller, the ratio of interorbital constriction to breadth of canines usually is <1 (as opposed to >1 in *M. riparius*), and *M. nigricans* lacks a sagittal crest, which is present in *M. riparius.* In Paraguay, pelage of *M. riparius* is not as distinctive as it is in more northern areas of South America and resembles that of *M. nigricans.* Some Paraguayan specimens reported previously in the literature as *M. nigricans* actually may be referable to *M. riparius.*

Distribution.—Widely distributed throughout Paraguay in eastern and western regions (López-González 1998; Willig et al. 2000).

Remarks.—Four (LaVal 1973; Wilson and LaVal 1974) or 5 (Koopman 1994) subspecies of *M. nigricans* have been recognized. Under either interpretation, Paraguayan populations can be ascribed to the nominate subspecies. *M. nigricans* has been found sharing roosts with *M. albescens* in the Paraguayan Pantanal. Reproductive patterns in Paraguay were described by Myers (1977). Females give birth in spring and summer and probably continue at low frequency during autumn and winter. Males are aseasonal with regard to their testis cycle, no storage of sperm has been found in either males or females. Findley (1993) classified *M. nigricans* as a forest and clearing aerial insectivore.

Myotis riparius (Handley 1960)

Myotis riparius has short and woolly fur, buffy-brown dorsum, and individual hairs slightly burnished at the tips and slightly grayer toward the bases (Handley 1960). Cinnamon-red specimens also may exist (LaVal 1973). The wing membrane attaches to the base of toes (Fig. 1a). The type specimen is large in external measurements (length of forearm, 39.2 mm), but with a comparatively small skull (greatest length, 14.2 including incisors, as measured by C. López-González). The skull is long and narrow, and well-developed sagittal and lambdoidal crests are present. P3 is crowded to the lingual side in the type specimen.

Broad variation in size exists among Paraguayan specimens. Nonetheless, *M. riparius* averages larger than *M. nigricans.* Dorsal pelage may not be as short and markedly woolly as it is in more northern specimens, and P3 is not always crowded to the lingual side in Paraguayan *M. riparius.* Moreover, P3 is crowded in some *M. nigricans,* which may make individuals difficult to identify. However, presence of a sagittal crest (always absent in Paraguayan *M. nigricans* where the 2 species are known to occur in sympatry), the ratio interorbital constriction to breadth across canines <1, and shorter fur, are sufficient to distinguish *M. riparius* from *M. nigricans* when both skin and skull are available. *M. riparius* is distinguished easily from other species of *Myotis* in Paraguay by coloration and skull proportions.

Distribution.—Most Paraguayan specimens have been collected in forested areas of the eastern region, although a few have been caught in the lower Chaco (López-González 1998; Willig et al. 2000). No records are known from the dry Chaco.

Remarks.—Little geographic variation has been detected in this species across its range (LaVal 1973), and no subspecies are recognized. According to LaVal (1973), the holotype of *Myotis guaycuru,* a specimen from Mato Grosso (currently Mato Grosso do Sul), Brazil, may represent a *M. riparius* as understood here. In that case, it would become the senior synonym of *M. riparius.* The original publication by Proença (1943), describes *M. guaycuru* as a relatively large bat (length of forearm 37 mm), with P3 crowded to the lingual side (so much that it is not visible from the lateral side), with fulvous-yellow fur, and with insertion of the uropatagium at the level of the tarsals, a character evident in the original description (Proença 1943:figure 3). However, *M. guaycuru* is described as lacking a sagittal crest, a character used by Proença (1943) to distinguish it from *M. simus.* Despite this purported difference, insertion of the uropatagium at the tarsals and crowding of P3 suggest that the type specimen of *M. guaycuru* actually belongs to *M. simus* as understood here, and, therefore, the name *M. guaycuru* Proença 1943 should be considered a junior synonym of *M. simus* Thomas 1901. *M. riparius* has been considered as a ''water bat'' (Findley 1993:88) associated with gallery forests that forages over water. Nonetheless, LaVal and Fitch (1977) reported 78 individuals of this species in the rainforest of La Selva, Costa Rica, collected well away from riparian environments.

Myotis ruber (É. Geoffroy Saint-Hilaire, 1806)

Myotis ruber is a large distinctive bat. Dorsal pelage is bright cinnamon-red, relatively short, but silky, and monocolored or only slightly bicolored. The dorsal surface of the uropatagium is covered with hair to the level of the knees. The venter is yellowish, with dark brown bases. The plagiopatagium attaches at the toes (Fig. 1a). The skull is robust, large, and wide at its base; the rostrum is long and relatively wide, interorbital constriction is narrow, and sagittal crest is well developed. In Paraguay, *M.*

ruber is distinguishable from other congeners by size and coloration (Table 1). Because of similar size, the cranium can be confused with that of *M. simus,* which, however, differs in the position of P3, in having longer rostrum, narrower cranial vault, and ratio of interorbital constriction to breadth across canines <1.

Distribution.—All known Paraguayan records are from the southeastern corner of the country, Departamento Itapua, and from Sapucai, Departamento Paraguari. *M. ruber* inhabits low semideciduous forests and is a rare bat throughout its distribution (Acosta y Lara 1950; López-González 1998).

Remarks.—Baud and Menu (1993) described *M. ruber* from Paraguay in a manner consistent with characters given by LaVal (1973) and clearly recognized differences between it and *M. simus.* Nevertheless, they assigned 2 clear *M. simus* (MVZ 144483 and 144484), under their own definition and that of LaVal (1973), to *M. ruber.* Skulls of *M. simus* and *M. ruber* are markedly different in shape (Figs. 2 and 3). Both PCA and DFA placed these 2 specimens within *M. simus.* Additionally, both individuals have the characteristic short wooly pelage of *M. simus,* and insertion of the plagiopatagium is not at the toes. No subspecies are recognized (Koopman 1994; LaVal 1973).

Myotis simus (Thomas, 1901)

This is a large *Myotis* with extremely short woolly fur. Dorsal color ranges from a bright orange in fresh specimens (which becomes tawny-brown in dry specimens) to cinnamon-brown, to cinnamon. Tips of hairs do not contrast with bases on dorsal pelage. On the venter, hairs are slightly longer, with yellow tips and slightly darker bases. Membranes are dark brown to black. Unlike other *Myotis* in Paraguay, the plagiopatagium attaches at the level of the tarsals (Figs. 1b and 1c). This combination of characters externally distinguishes Paraguayan *M. simus* from other congeners. Large size, presence of a well-developed sagittal crest, crowding of P3 to the lingual side, relatively short, wide rostrum, wide base of skull, and short toothrow characterize *M. simus* cranially. In Paraguay, *M. simus* can be confused only with *M. ruber* because of their similarity in general and size of braincase (mean cranial index 79.8, as opposed to 81.8 in *M. ruber*), but they differ in shape of rostrum. Other characters useful to distinguish the 2 species are discussed in the account for *M. ruber.*

Distribution.—Scattered records are available from the lower Chaco, the vicinity of Asunción, and Ayolas, Departamento Misiones (López-González 1998; Willig et al. 2000). Argentine records are available from near Clorinda, Formosa, across the Paraguay River from Asunción and from Isla Apipé, Corrientes, across the Parana River from Ayolas (Barquez et al. 1999; Fornes 1972).

Remarks.—*Myotis simus* was originally believed to be confined to the Amazon Basin (Handley 1960; LaVal 1973; Miller and Allen 1928). More recently, it has been caught in Bolivia (Anderson 1997), Paraguay (Myers and Wetzel 1979), and Argentina (Barquez et al. 1999; Fornes 1972). Baud and Menu (1993) redefined the species, arguing that some of the most important characters used to distinguish it, insertion of the plagiopatagium at the tarsal level and a larger canine, had been misinterpreted or disregarded by previous authors. Based on a sample of South American *Myotis,* they concluded that *M. simus* was restricted effectively to the Amazon Basin, and it was never orange or ochraceous. Furthermore, they assigned Paraguayan *M. simus* to *M. ruber.* However, their sample was small (<10 individuals) and, by chance, included specimens with brown-colored fur. Specimens AMNH 71484–71486 (examined by them) for instance, are certainly not orange or cinnamon-red, as are other individuals from the Amazon Basin. Nevertheless, texture (woolly) and length of fur are homogeneous throughout its range and distinguish *M. simus* from all other *Myotis,* with the possible exception of *M. riparius* in northern South America. *M. simus* has been classified as a ''water bat,'' an over-water forager and inhabitant of gallery forests (Findley 1993:88).

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Appendix I

Specimens examined.—Museum and field-catalog acronyms are listed in text. Where listed, latitude and longitude are in degrees and decimal minutes.

Myotis albescens (n = 81).—ARGENTINA: Entre Ríos: Departamento Gualeguachu, Islas del Ibicui, Paranacito (7, TTU 32541–32543, 32546, 32550–32552). PARAGUAY: Alto Paraguay: Estancia Doña Julia, 20°10.98′S, 58°04.42′W, 60 m (25, TK 60986–60992, 60994, 60995, 60997, 60998, 61000, 61054, 61055, 61062–61069, 61133, 61135, 61136); Estancia Parra-cue 21°05.91′S, 57°53.52′W, 85 m (7, TK 60760, 60761, 60764, 60765, 60767–60769); Fuerte Olimpo, 21°02.37′S, 57°52.29′W, 95 m (1, TK 60741); Fuerte Olimpo, 21°02.53′S, 57°52.21′W, 95 m (6, TK 60746–60748, 60751–60753). Boquerón: Base Naval Pedro P. Peña, 22°27.16′S, 62°20.65′W, 240 m (3, TK 62827, 62842, 62843). Itapua: Arroyo Pirayu-i, 40 km N Capitán Meza (1, MHNG 1747.54). Misiones:Arroyo Atinguy, 27°20.67′S, 56°40.52′W, 77 m (2, TK 60869, 60871). Ñeembucu: Estancia Yacare, 26°39.58′S, 58°05.56°W, 60 m (1, TK 61655); Estancia Yacare, 26°37.97′S, 58°07.55′W, 60 m (2, TK 61721, 61766). Presidente Hayes: Estancia La Victoria, 23°39.04′S, 58°34.79′W, 120 m (6, TK 60095–60097, 60106, 60158, 60174); Estancia Loma Pora, 23°27.87′S, 57°36.29′W, 77 m (1, TK 62170); Estancia Samaklay, 23°28.81′S, 59°48.43′W, 120 m (6, TK 62698–62699, 62768, 62782, 62786, 62808); Rincón Charrúa, 275 km NW Villa Hayes by road (13, MVZ 144576, 144580–144582, 144584–144587, 144636–144639, 144641).

Myotis levis dinellii (n = 11).—ARGENTINA: Chaco: General Vedia (1, TTU 32556). Córdoba: Villa Dolores (4, TTU 32524, 32525, 32528, 32529). La Rioja: Chuquis, Departamento Castro Barros (1, TTU 32530). Salta: Capital, Buenavista (1, TTU 32531). Tucumán: La Cocha, Dique San Ignacio (1, AMNH 256987). BOLIVIA: Cochabamba: Carrasco, 6.6 km NW López Mendoza (by road), Quebrada Mojón, 3,300 m (1, AMNH 261119). Santa Cruz: Santa Cruz de la Sierra (1, AMNH 248202); 1 km N, 8 km W Comarapa, 17°55′S, 64°34′W, 2,450 m (1, AMNH 260253).

Myotis levis levis (n = 42).—ARGENTINA: Buenos Aires: Maipu (1, TTU 32555). Entre Ríos: Departamento Gualeguachu, Brazo Largo (2, TTU 32533, 32534); Estancia Médanos (1, TTU 32535); Departamento Gualeguachu, Islas del Ibicui, Paranacito (4, TTU 32537, 32544, 32547, 32549). BOLIVIA: Tarija: Narváez (1, MHNG 1748.89). BRAZIL: Río Grande do Sul: Arroyo das Pedras, en la barra con el Río Camacua (17, AMNH 235863–235877, 235880, 235881). São Paulo: Estação Biologica de Boraceia, 820 m (3, FMNH 141600, 145327, 145328). URUGUAY: Acosta y Lara: San José (2, FMNH 63827, 63828); Riviera (1, FMNH 63829). Lavalleja: 9 km S Piraraja, Cunetary (10, AMNH 205503–205505, 205508–205510, 205512–205515).

Myotis nigricans (n = 175).—ARGENTINA: Formosa: Departamento Pilcomayo, Estancia las Mercedes (1, TTU 32557); Departamento Pilcomayo, Bouvier (2, TTU 32558, 32559); Estanislao del Campo (1, TTU 32560). Salta: Estancia Gurruchaga, Rosario de Lerma (1, TTU 32561). Santiago del Estero, Departamento Pellegrini, Nueva Esperanza (20, TTU 32562–32565, 32568, 32570–32573, 32575, 32577–32582, 32584–32587); Departamento Jiménez, San Pedro (2, TTU 32589, 32590). BOLIVIA: La Paz: Sacramento Alto, 8 km N Chuspipata, 2,775 m (1, TTU 34951); 1 mile W Puerto Linares (5, TTU 34952–34956). PARAGUAY: Alto Paraguay, Estancia Doña Julia, 20°10.98′S, 58°04.42′W, 60 m (2, TK 61001, 61003); Cerro León, 20°26.25′S, 60°19.19′W, 250 m (1, TK 60300); 12 km E Destacamento Militar Gabino Mendoza, 25°05.30′S, 61°47.22W, 390 m (13, TK 63261–63264, 63289–63291, 63326–63329, 63337, 63338); Estancia Parra-cue, 21°05.91′S, 57°53.52′W, 85 m (11, TK 60755, 60757, 60759, 60766, 60771, 60772, 60774, 60788, 60791–60793); Estancia Tres Marías, Laguna Tigre, 21°18.09′S, 59°33.73′W, 70 m (1, TK 62446); Fuerte Olimpo, 21°02.53′S, 57°52.21′W, 95 m (3, TK 60742, 60744, 60750); Hito IV, 20°05.35′S, 61°55.34′W, 390 m (1, TK 63358); Puerto Esperanza, West bank of Río Paraguay, 20°24′S, 58°02′W (1, UMMZ 166560). Amambay: Parque Nacional Cerro Cora (2, USNM 552732, 554538). Boquerón: Base Naval Pedro P. Peña, 22°27.16′S, 62°20.65′W, 240 m (2, TK 62881, 62882); Cañada Elisa, 7 km N, 14 km E by road Mariscal Estigarribia, 21°59.42′S, 60°28.20′W, 80 m (1, TK 60231); Estancia Cañada Mil, 22°22.68′S, 62°15.57′W, 240 m (10, TK 63013–63015, 63070, 63077, 63113–63117); Estancia El 43, 22°02.11′S, 60°19.93′W, 80 m (1, TK 60221); Estancia San Jorge, main house, 22°02.11′S, 60°19.93′W, 80 m (3, TK 60266, 60267, 60284); 49.6 km N Filadelfia by road (4, UMMZ 124399–124402); Parque Nacional Teniente Enciso (4, USNM 555671–555674). Canindeyu: 13.3 km N Curuguaty by road (1, UMMZ 125735). Cordillera: Estancia Sombrero, 25°02.52′S, 56°39.58′W, 90 m (1, TK 60479); Estancia Sombrero, 25°02.67′S, 56°39.45′W, 90 m (1, TK 60495); Estancia Sombrero, 25°04.56′S, 56°39.35′W, 110 m (1, TK 60531); Estancia Sombrero, 25°05.20′S, 56°36.13′W, 110 m (1, TK 64285); Juan de Mena (1, USNM 552733); 1.6 km S Tobati, by road (1, UMMZ 125734). Guaira: Villa Rica (1, MCZ 42224). Misiones: Ayolas, Barrio San Antonio, 27°23.42′S, 56°50.15′W, 71 m (1, TK 60845). Ñeembucu: Estancia Yacare, 26°37.97′S, 58°07.55′W, 60 m (5, TK 61646, 61648, 61658, 61719, 61720). Paraguari: Paraguari (7, USNM 115075–115081); Presidente Hayes: Estancia La Victoria, 23°39.04′S, 58°34.79′W, 120 m (1, TK 60127); Estancia La Victoria, 23°40.28′S, 58°35.29′W, 120 m (8, TK 60151–60157, 60159); Estancia La Victoria, 23°41.22′S, 58°35.23′W, 120 m (1, TK 60168); Estancia Loma Pora, 23°27.87′S, 57°36.29′W, 77 m (25, TK 62169, 62171, 62182, 62189–62191, 62193–62201); Rincón Charrúa, 275 km NW Villa Hayes by road (16, MVZ 144734, 144735, 144738, 144740, 144742–144744, 144747, 144749–144752, 144754, 144758, 144762); 24 km WNW Villa Hayes (9, UMMZ 133777–133785). San Pedro: Yaguarete Forests, administration complex, 23°47.33′S, 56°13.09′W, 200 m (1, TK 61241).

Myotis riparius (n = 60).—ARGENTINA: Corrientes: 25 km E Ituzaingo (1, AMNH 214400). BOLIVIA: Santa Cruz: Estancia Cachuela Esperanza (1, AMNH 260251). BRAZIL: Río Grande do Sul: Candelaria (1, AMNH 235919). COLOMBIA: Amazonas: Leticia (2, TTU 09449, 09450). Caqueta: Caqueta, Río Caqueta, Tres Troncos, 185 m (4, FMNH 72177–72179, 72241). Meta: El Parque La Macarena, Cabaña Duda (1, FMNH 58754). ECUADOR: Río Suno (below Loreto) (1, FMNH 31072). Santa Cecilia: Napo-Pastaza (1, TTU 37482). PANAMA: Darién, Tacaracuna Village Camp (1, USNM 310255, holotype of *M. simus riparius*). PARAGUAY: Amambay: Parque Nacional Cerro Cora (1, USNM 554539); Parque Nacional Cerro Cora, 22°37.90′S, 56°01.43′W, 280 m (1, TK 61412); Parque Nacional Cerro Cora, 22°40.00′S, 55°59.14′W, 280 m (1, TK 61411). Caaguazu: 24 km NNW Carayao, Estancia San Ignacio (1, UMMZ 134272). Concepción: Parque Nacional Serranía San Luis, 22°37.91′S, 57°21.35′W, 270 m (1, TK 61544); Parque Nacional Serranía San Luis, 22°40.34′S, 57°20.96′W, 170 m (2, TK 61614, 61615). Cordillera: Estancia Sombrero, 25°02.19′S, 56°39.04′W, 90 m (1, TK 60488); Estancia Sombrero, 25°02.67′S, 56°39.35′W, 90 m (2, TK 60494, 60496). Itapua: Hotel el Tirol, 19.5 km NNE Encarnación by road (1, MVZ 154725); 2 km NNW San Rafael (1, UMMZ 126242); 8 km N San Rafael (2, UMMZ 125736, 125737); Parque Nacional San Rafael, 26°45.46′S, 55°51.67′W, 170 m (1, TK 60951). Misiones: Puerto Turi, 27°24.99′S, 56°45.74′W (1, TK 60830). Paraguari: Estancia Ypoa, 26°02.48′S, 57°25.94′W (1, TK 60588); Parque Nacional Ybycui (2, UMMZ 133775, 133776); Sapucay (7, USNM 115071–115073, 115086, 115088, 115095, 121477). Presidente Hayes: Estancia La Victoria, 23°39.04′S, 58°34.79′W, 120 m (1, TK 60007); Retiro Mandeyu, 20 km SW km 205 Transchaco Highway (2, MVZ 144671, 144676). San Pedro: Yaguarete Forests, Río Aguaray Guazu, 23°46.22′S, 55°59.26′W, 200 m (1, TK 61275). PERU: Cuzco: Consuelo (1, FMNH 123956); Pillahuata (1, FMNH 123958). Huanuco: Agua Caliente (1, FMNH 55400). URUGUAY: Artigas: 6 km NNW Belén (6, AMNH 205461, 205464, 205467, 205471, 205472, 205476). Tacuarembo: 40 km NW Tacuarembo (9, AMNH 205552–205554, 205557, 205558, 205562–205565).

Myotis ruber (n = 9).—BRAZIL: Minas Gerais: Viçosa (2, USNM 39138, 39139). PARAGUAY: Itapua: 4 km SW Salto Tembey (1, MHNG 1695.27); Arroyo Pirayu-i, 40 km NNW Capitán Meza (1, MHNG 1747.56); Arroyo Pirapo, 50 m SE casa (1, MNHNP 0319); 8 km N San Rafael (3, UMMZ 125729, 125730, 125746). URUGUAY: Arroyo Grande (1, MHNG 1748.47).

Myotis simus (n = 36).—BOLIVIA: Beni: 23 km W San Javier (10, AMNH 211156, 211181, 211182, 211184, 211190, 211192–211196). BRAZIL: Amazonas: Río Negro, Cacau Pereira, Igarape (2, AMNH 91474, 91477); Río Negro, near Manaos (2, AMNH 91476, 91478); Río Madeira, Auara Ygarape (6, AMNH 91886–91891); Río Madeira, Rosarinho (2, AMNH 92701, 92702). ECUADOR: Pastaza: Río Capihuara (1, FMNH 43143); Boca Río Curanay (1, AMNH 71846). PARAGUAY: Central: 17 km E Luque by road, Río Salado (1, UMMZ 125731). Misiones: Ayolas, Barrio San Antonio, 27°23.42′S, 56°50.15′W, 71 m (1, TK 60803). Presidente Hayes: 230 km NW Villa Hayes, by road (4, MVZ 144481–144484). PERU: Huanuco: Leoncia Prado Province, 6 km N Tingo María (1, TTU 46348); Loreto: Ucayali, Yarinacocha (4, FMNH 55463–55465, 62165); Pucallpa, Yarinacocha (1, FMNH 97988).

Appendix II

Descriptive statistics (mm) for selected morphometric characters of South Amerian *Myotis* (sexes pooled). Acronyms of cranial characters are given in Table 4; FAR, length of forearm; MCIII, length of 3rd metacarpal.

Taxon	GLS	CCL	CBL	MAB	ZYG	BBC	INC	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
Myotis albenscens																
Western Paraguay (33♂♂, 35♀♀)																
n	66	66	66	65	51	66	67	68	68	68	68	68	68	68	56	56
$\bar{X}$	14.0	12.0	13.0	7.3	8.5	7.1	4.0	3.5	5.4	5.8	4.9	4.0	5.1	4.6	34.0	32.0
SD	0.3	0.2	0.3	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1.0	1.1
Minimum	13.5	11.4	12.5	7.0	7.9	6.7	3.8	3.3	5.1	5.6	4.6	3.7	4.8	4.3	31.8	30.2
Maximum	14.6	12.5	13.6	7.6	8.9	7.5	4.3	3.8	5.7	6.2	5.3	4.4	5.4	4.9	36.8	34.8
Entre Ríos, Argentina; eastern Paraguay (4♂♂, 8♀♀)																
n	12	12	12	12	4	12	12	12	12	12	12	12	11	10	12	12
$\bar{X}$	14.1	12.0	13.0	7.4	8.4	7.2	4.0	3.5	5.3	5.9	4.9	4.0	5.2	4.7	33.6	31.7
SD	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1.0	0.9
Minimum	13.7	11.7	12.6	7.0	8.4	6.9	3.8	3.4	5.1	5.7	4.8	3.9	4.9	4.5	32.1	30.2
Maximum	14.6	12.5	13.6	7.7	8.6	7.4	4.3	3.6	5.5	6.1	5.0	4.3	5.4	4.8	35.1	33.7
M. levis levis																
Northern Argentina; southern Brazil; Uruguay (10 ♂♂, 30♀♀, 2 unknown sex)																
n	40	41	41	42	31	41	42	42	42	42	42	42	42	40	40	37
$\bar{X}$	15.1	13.1	14.2	7.6	9.3	7.1	3.7	3.6	5.8	6.6	5.5	4.6	5.9	5.1	37.7	35.1
SD	0.4	0.4	0.4	0.2	0.2	0.2	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1.7	1.4
Minimum	14.3	12.2	13.2	6.9	8.8	6.7	3.4	3.3	5.0	5.8	5.2	4.2	5.5	4.3	33.0	31.3
Maximum	15.8	13.6	14.7	7.9	9.6	7.5	4.0	4.2	6.4	7.0	5.9	5.0	6.3	5.6	40.7	37.6
M. levis dinellii																
Northern Argentina; Boliva (3♂♂, 8♀♀)																
n	10	11	10	11	5	11	11	11	11	10	10	10	9	9	9	9
$\bar{X}$	14.6	12.6	13.7	7.2	8.6	6.8	3.5	3.4	5.5	6.5	5.4	4.6	5.8	5.1	35.8	33.7
SD	0.5	0.6	0.5	0.2	0.3	0.2	0.1	0.2	0.3	0.3	0.2	0.2	0.2	0.2	1.6	1.6
Minimum	13.8	11.4	13.2	6.9	8.2	6.5	3.4	3.1	5.0	6.1	5.1	4.3	5.6	4.9	33.8	31.4
Maximum	15.6	13.5	14.5	7.4	8.8	7.2	3.8	3.7	5.9	6.9	5.9	5.0	6.2	5.4	38.3	36.4

APPENDIX II
Continued.

Taxon	GLS	CCL	CBL	MAB	ZYG	BBC	INC	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
M. nigricans																
Argentine Chaco; western Paraguay (63♂♂, 83♀♀)																
n	146	145	145	145	85	144	146	145	146	146	146	146	143	143	108	106
$\bar{X}$	13.7	12.0	12.9	7.0	8.3	6.5	3.5	3.4	5.3	5.9	5.0	4.1	5.2	4.6	32.8	30.6
SD	0.3	0.2	0.3	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1.2	1.0
Minimum	13.1	11.5	12.3	6.6	7.7	5.9	3.2	3.1	4.9	5.4	4.6	3.9	4.9	4.2	29.9	28.6
Maximum	14.4	12.6	13.7	7.5	8.8	7.0	3.8	3.7	5.7	6.4	5.3	4.4	5.6	5.1	35.3	33.2
Eastern Paraguay (12♂♂, 11♀♀)																
n	23	23	23	21	6	20	23	23	23	23	23	23	22	22	21	21
$\bar{X}$	13.6	11.9	12.8	7.0	8.3	6.5	3.5	3.4	5.4	5.9	5.0	4.1	5.2	4.6	32.5	30.4
SD	0.3	0.2	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1.2	1.1
Minimum	13.2	11.5	12.3	6.6	8.1	6.2	3.3	3.2	5.1	5.6	4.8	3.9	4.9	4.4	30.4	28.7
Maximum	14.3	12.4	13.5	7.3	8.6	6.7	3.7	3.5	5.6	6.2	5.2	4.4	5.5	5.0	35.1	32.6
Bolivia (3♂♂, 3♀♀)																
n	6	6	6	6	2	6	6	6	6	6	6	6	6	6	3	3
$\bar{X}$	13.7	12.0	12.9	7.0	8.2	6.4	3.5	3.4	5.4	5.9	5.0	4.1	5.2	4.6	34.1	32.3
SD	0.4	0.4	0.4	0.1	0.1	0.2	0.1	0.1	0.2	0.3	0.2	0.2	0.3	0.2	0.9	0.7
Minimum	13.2	11.6	12.5	6.7	8.1	6.2	3.4	3.2	5.1	5.6	4.7	3.9	5.0	4.4	33.1	31.6
Maximum	14.5	12.6	13.6	7.1	8.2	6.6	3.7	3.5	5.7	6.4	5.4	4.5	5.8	5.0	34.9	33.0
M. riparius																
Amazon Basin: Columbia; Ecuador; Peru (5♂♂, 6♀♀)																
n	10	9	9	8	4	9	11	11	11	11	11	11	11	11	6	5
$\bar{X}$	14.2	12.2	13.3	7.3	8.5	6.5	3.5	3.7	5.8	6.3	5.2	4.2	5.6	4.8	35.9	33.4
SD	0.3	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	2.2	0.7
Minimum	13.7	11.8	12.9	7.0	8.3	6.2	3.2	3.6	5.5	6.1	5.0	4.0	5.4	4.7	32.0	32.9
Maximum	14.6	12.5	13.6	7.5	8.7	6.8	3.6	3.9	6.0	6.5	5.4	4.5	5.8	5.2	37.7	34.6

APPENDIX II
Continued.

Taxon	GLS	CCL	CBL	MAB	ZYG	BBC	INC	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
Argentina; Bolivia; southern Brazil; eastern Paraguay (18♂♂, 11♀♀, 4 unknown sex)																
n	33	32	31	30	20	32	33	32	33	33	33	33	33	33	25	24
$\bar{X}$	13.9	12.1	13.1	7.3	8.6	6.6	3.5	3.6	5.5	6.1	5.1	4.2	5.4	4.7	34.2	32.3
SD	0.3	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.1	1.2	0.9
Minimum	13.2	11.5	12.6	6.8	8.3	6.3	3.3	3.2	5.1	5.9	4.8	3.9	4.8	4.4	31.5	30.3
Maximum	14.3	12.8	13.6	7.6	8.9	7.2	3.8	3.8	5.8	6.3	5.4	4.6	5.8	5.0	36.4	34.1
Uruguay (3♂♂, 10♀♀, 2 unknown sex)																
n	15	15	15	15	11	15	15	15	15	15	15	15	13	12	13	13
$\bar{X}$	14	12.1	13.2	7.2	8.7	6.6	3.5	3.6	5.5	6.1	5.1	4.3	5.6	4.8	35.1	32.5
SD	0.3	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.7	1.1
Minimum	13.4	11.7	12.8	6.9	8.4	6.2	3.2	3.4	5.3	5.9	5.0	4.0	5.2	4.6	33.8	30.4
Maximum	14.4	12.6	13.7	7.5	9.0	7.0	3.7	3.7	5.7	6.4	5.4	5.0	5.9	5.2	36.3	33.8
M. ruber																
Southern Brazil; eastern Paraguay; Uruguay (2♂♂, 7♀♀)																
n	9	9	9	9	5	9	9	9	9	9	9	8	9	8	9	5
$\bar{X}$	15.3	13.4	14.7	7.8	9.53	7.0	3.7	3.9	6.0	7.0	5.8	4.7	6.3	5.4	39.2	36.5
SD	0.2	0.1	0.2	0.1	0.12	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.8	1.0
Minimum	15	13.2	14.4	7.5	9.4	6.8	3.6	3.8	5.8	6.9	5.7	4.6	6.2	5.3	37.9	35.3
Maximum	15.5	13.7	14.9	8	9.7	7.2	4.0	4.1	6.2	7.1	6.0	4.8	6.4	5.5	40.5	37.5
M. simus																
Amazon Basin; Brazil; Ecuador; Peru (6♂♂, 12♀♀)																
n	15	15	15	15	6	15	18	18	17	17	17	17	17	16	17	17
$\bar{X}$	14.3	12.3	13.5	7.8	9.4	7.0	3.9	4.0	5.8	6.1	5.0	4.0	5.4	4.7	38.1	34.6
SD	0.3	0.3	0.3	0.2	0.3	0.1	0.1	0.2	0.3	0.1	0.2	0.2	0.1	0.1	1.2	1.3
Minimum	13.7	11.9	13	7.5	9.0	6.8	3.7	3.7	5.4	5.9	4.7	3.4	5.2	4.4	35.9	32.5
Maximum	14.8	12.8	14.1	8.1	9.8	7.2	4.1	4.4	6.1	6.5	5.3	4.3	5.6	4.9	40.5	36.4

APPENDIX II
Continued.

Taxon	Morphometric characters															
	GLS	CCL	CBL	MAB	ZYG	BBC	INC	BAC	BAM	LNR	MAX	UML	MTR	LML	FAR	MCIII
Bolivia (2♂♂, 7♀♀, 1 unknown sex)																
n	10	10	10	10	6	9	10	10	10	10	10	10	10	10	8	8
$\bar{X}$	14.7	12.9	14.1	8.2	9.8	7.4	4.0	4.2	6.1	6.5	5.3	4.4	5.7	5.0	39.2	35.8
SD	0.2	0.2	0.2	0.1	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.9	0.6
Minimum	14.4	12.6	13.8	8.0	9.3	7.2	3.8	4.0	5.9	6.3	5.2	4.2	5.6	4.8	38.2	34.9
Maximum	15	13.3	14.4	8.5	10.1	7.7	4.1	4.4	6.3	6.6	5.5	4.5	5.9	5.3	40.8	36.5
Eastern and western Paraguay (2♂♂, 4♀♀)																
n	6	6	6	6	5	6	6	6	6	6	6	6	6	6	6	6
$\bar{X}$	14.4	12.8	13.8	8.0	9.2	7.2	3.9	4.0	5.9	6.3	5.3	4.3	5.6	4.8	38.3	35.0
SD	0.2	0.1	0.2	0.1	0.01	0.1	0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.3	0.5
Minimum	14.0	12.6	13.6	7.8	9.2	7.0	3.9	3.9	5.8	6.2	5.3	4.0	5.5	4.7	38.0	34.5
Maximum	14.7	13.0	14.1	8.2	9.3	7.4	4.0	4.2	6.0	6.4	5.4	4.4	5.7	4.9	38.8	35.5
Myotis (MHNG 1747.54)																
Arroyo Pirayu-i, 40 km N Capitán Meza, Itapua, Paraguay (1♂)																
$\bar{X}$	15.1	13.1	14.1	7.6	7.6	7.4	4.0	3.8	5.5	6.4	5.4	4.4	5.7	4.9	35.4	35.4