



## Original Investigation

Geographic variation in South American populations of *Myotis nigricans* (Schinz, 1821) (Chiroptera, Vespertilionidae), with the description of two new speciesRicardo Moratelli<sup>a,\*</sup>, Adriano L. Peracchi<sup>b</sup>, Daniela Dias<sup>c</sup>, João A. de Oliveira<sup>d</sup><sup>a</sup> Campus Fiocruz da Mata Atlântica, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil<sup>b</sup> Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil<sup>c</sup> Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil<sup>d</sup> Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

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## ABSTRACT

The genus *Myotis* (Vespertilionidae, Myotinae) comprises a diverse group of small to large-sized vespertilionid bats that present a worldwide distribution. Twelve South American species are currently recognized. In this paper we evaluate the morphological and morphometric variation observed in South American populations of the most widespread species, *Myotis nigricans*. Against this background, two forms can be morphologically distinguished from *M. nigricans* and other known South American species. We describe these new species, documenting their diagnostic external and cranial characters by comparing them to other sympatric and cryptic species of South American *Myotis*. In addition, we provide an emended diagnosis of *Myotis nigricans*.

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## Introduction

The genus *Myotis* Kaup, 1829 comprises a diverse and widely distributed group of small to large-sized vespertilionid bats, with 103 species currently recognized (Simmons, 2005). Despite the revision of LaVal (1973), which remains the basic reference work on the taxonomy of *Myotis* in the Neotropics, the taxonomy of this genus has been considered the most complex among Neotropical bats, due to inconsistent characters used to distinguish species (Barquez et al., 1999). Based primarily on LaVal's (1973) revisionary work, Wilson (2008) recognized 12 South American species, most of them restricted to subtropical zones, with few forms confined to warm arid or semiarid areas. Only *Myotis nigricans* (Schinz, 1821), the most variable and widespread South American species of the genus, occurs in a great diversity of habitats, ranging from lowland to upland forested and semiarid regions (Wilson, 2008).

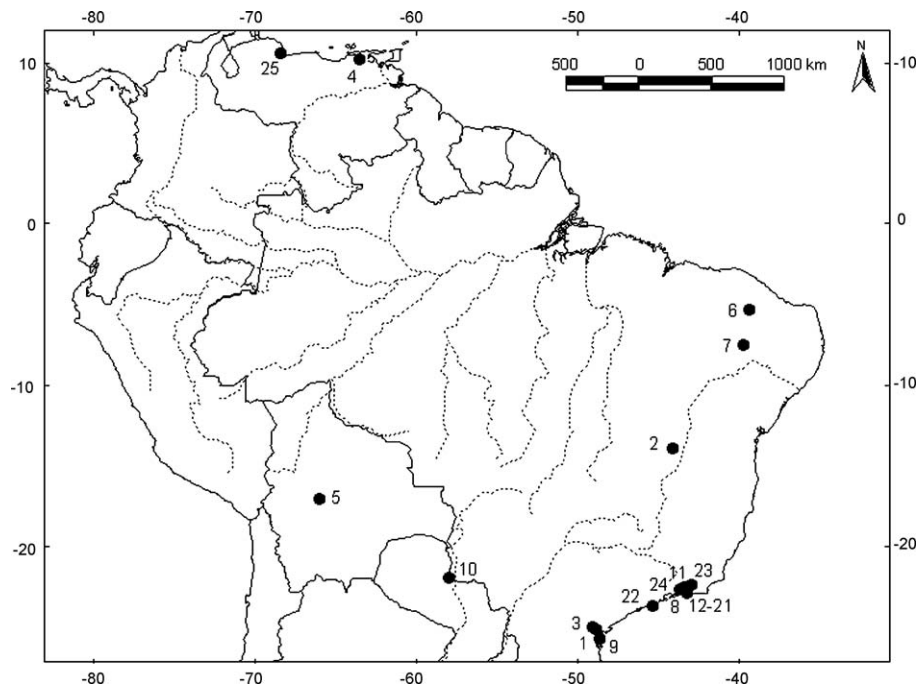
From 1976 to 1978 several specimens of *Myotis* were collected by M. R. Willig and A. L. Gardner, respectively in the states of Pernambuco and Ceará, northeastern Brazil. The former were first assigned to *Myotis nigricans* (Mares et al., 1981; Willig et al., 1983), and, subsequently, to *Myotis riparius* Handley, 1960 (Willig and Mares, 1989), while the specimens caught by A. L. Gardner were

identified as *M. nigricans* according to their tags. Recently, comparing specimens from Ceará and from southern Brazil based on geometric morphometric methods, Bornholdt et al. (2008) found geographical variation in skull size and shape, which suggested the existence of a greater taxonomic diversity for samples assigned to *M. nigricans*.

Recent capture efforts in two adjacent southeastern Brazilian localities revealed a high diversity of *Myotis* in the highlands of Rio de Janeiro Atlantic Forest, with up to four syntopic species (Moratelli and Peracchi, 2007; Dias and Peracchi, 2008). Some individuals from Tinguá Biological Reserve were assigned to *M. levis* (I. Geoffroy, 1824) by Dias and Peracchi (2008), while others from Serra dos Órgãos National Park were assigned to *M. nigricans* by Moratelli and Peracchi (2007). Those highland samples resemble *M. levis* and *M. nigricans* in the shape of skull and in the absence of a sagittal crest, in agreement with LaVal's (1973) and López-González et al.'s (2001) descriptions. However, they differ from *M. levis* by their smaller overall size and by the absence of a fringe of hairs along the trailing edge of the uropatagium, and from *M. nigricans* by their larger overall cranial and external size and by the length and color of fur.

As part of an ongoing systematic and biogeographic review of the South American species of *Myotis*, and in an attempt to evaluate the taxonomic status of the apparently distinct samples from northeastern Brazil and from the uplands of Rio de Janeiro, we herein evaluate the morphological and morphometric variation in available South American samples of *M. nigricans*. Against that background, we then name and describe the two divergent forms

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**Fig. 1.** Geographic mapping of samples analyzed in the present study: (1) Balsa Nova, Paraná, Brazil, 1150 m; (2) Barra, Bahia, Brazil, 393 m; (3) Campinhos, Paraná, Brazil, 890 m; (4) Monagas, Venezuela, 1190 m; (5) Cochabamba, Bolivia, 2000 m; (6) Crato, Ceará, Brazil, 571 m; (7) Exu, Pernambuco, Brazil, 523 m; (8) Tinguá, Rio de Janeiro, Brazil, 760–965 m; (9) Matinhos, Paraná, Brazil, sea level; (10) Mato Grosso do Sul, Brazil, 80 m; (11) Alto da Boa Vista, Rio de Janeiro, Brazil, 300 m; (12–21) Seropédica, Rio de Janeiro, Brazil, 33 m; (22) São Sebastião, São Paulo, Brazil, 10 m; (23) Serra dos Órgãos, Rio de Janeiro, Brazil, 1000 m; (24) Tinguá, Rio de Janeiro, Brazil, 33–100 m; (25) Carabobo, Venezuela, 25 m.

as new species, comparing them to other South American species of *Myotis*.

## Materials and methods

### Specimens selection

To address the variation in qualitative and quantitative characters among South American population samples, 352 specimens were examined (Appendix). These specimens had been formerly assigned to *M. nigricans* based on the following set of traits listed as diagnostic by LaVal (1973) and López-González et al. (2001): small to moderate overall size (forearm generally larger than 33.0 mm; greatest length of skull generally larger than 13.0 mm); silky fur; absence of a fringe of hairs along the trailing edge of the uropatagium; plagiopatagium attached at toes by a broad band of membrane; sagittal crest generally absent or low; rostrum and braincase narrow; and P3 aligned with the other premolars, not displaced to the lingual side.

### Quantitative data

All measurements and observations are from adult individuals with closed epiphyses. Fifteen cranial and six external dimensions were measured using a digital caliper accurate to 0.02 mm. The measurements, reported in millimeters, and their abbreviations are defined as follows (lengths were measured from the anteriormost point of the first structure to the posteriormost point of the second structure mentioned below): *greatest length of skull* (GLS), from the premaxillae, including the incisors, to the occiput; *condylo-canine length* (CCL), from the occipital condyles to the upper canines; *condylo-incisive length* (CIL), from the occipital condyles to the upper incisors; *basal length* (BL), from the foramen magnum to the upper incisors; *zygomatic breadth* (ZB), greatest breadth across the outer edges of the zygomatic arches; *mastoid breadth* (MAB), great-

est cranial breadth across the mastoid region; *braincase breadth* (BCB), greatest breadth of the globular part of the braincase; *interorbital breadth* (IOB), least breadth across orbital bulges; *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; *breadth across molars* (BAM), greatest breadth across outer edges of the crowns of upper molars; *maxillary tooththrow length* (MTL), from the upper canine crown to the crown of M3; *molariform tooththrow length* (M13), from the crown of M1 to the crown of M3; *mandibular length* (MAL), from the dentary, without incisors, to the angular process; *mandibular tooththrow length* (MAN), from the lower canine to m3; *tragus length* (TRL), from the base to the tip of the tragus; *forearm length* (FA), from the elbow to the distal end of the forearm including carpals; *third metacarpal length* (3MC), from the distal end of the forearm to the distal end of the third metacarpal; *thumb length* (THL), from the proximal end of the metacarpal to the tip of the claw; and *length of the dorsal* (LDH) and *ventral hairs* (LVH), from the base to the tip of the hair, measured between scapulas. The weight, reported in grams, and ear length (EL), in millimeters, were obtained from the skin labels.

### Samples analyzed

Specimens were sorted into 25 geographical and altitudinal samples (Fig. 1). To avoid a very unbalanced sampling design for multivariate analyses, each sample was limited to a maximum of 30 randomly selected specimens totaling 290 specimens in the multivariate analyses, as follows: **Group 1** ( $N=10$ ): Balsa Nova, Paraná, Brazil (elevation of 1150 m); **Group 2** ( $N=5$ ): Barra, Bahia, Brazil (393 m); **Group 3** ( $N=26$ ): Campinhos, Paraná, Brazil (890 m); **Group 4** ( $N=7$ ): Monagas, Venezuela (1190 m); **Group 5** ( $N=15$ ): Cochabamba, Bolivia (2000 m); **Group 6** ( $N=8$ ): Crato, Ceará, Brazil (571 m); **Group 7** ( $N=30$ ): Exu, Pernambuco, Brazil (523 m); **Group 8** ( $N=6$ ): Tinguá, Rio de Janeiro, Brazil (760–965 m); **Group 9**

**Table 1**  
*F* and *p* values (ANOVA) for secondary sexual dimorphism in craniometric and external measurements of three samples of *Myotis nigricans*: from Seropédica, Rio de Janeiro, Brazil (type locality) (30 males and 30 females); from Campinhos, Paraná, Brazil (11 males and 15 females); and from Exu, Pernambuco, Brazil (15 males and 15 females). Numbers in bold indicate statistically significant dimorphism ( $p \geq 0.05$ ).

Characters	Rio de Janeiro, Brazil		Paraná, Brazil		Pernambuco, Brazil	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Greatest length of skull (GLS)	2.348	0.131	0.002	0.966	0.256	0.617
Condylar–canine length (CCL)	4.212	<b>0.045</b>	0.001	0.980	0.017	0.897
Condylar–incisive length (CIL)	2.774	0.102	0.078	0.783	0.002	0.968
Mastoid breadth (MAB)	0.094	0.761	1.429	0.244	0.246	0.624
Braincase breadth (BCB)	2.703	0.106	0.323	0.575	0.274	0.605
Postorbital breadth (POB)	1.383	0.244	1.421	0.245	1.017	0.322
Breadth across canines (BAC)	1.104	0.298	0.698	0.412	1.393	0.248
Breadth across molars (BAM)	2.915	0.093	1.427	0.244	0.047	0.831
Maxillary tooththrow length (MTL)	0.399	0.53	0.015	0.903	1.588	0.218
Molariform tooththrow length (M13)	2.276	0.137	0.389	0.538	0.207	0.653
Mandibular length (MAL)	7.852	<b>0.007</b>	0.027	0.870	0.000	0.992
Mandibular tooththrow length (MAN)	2.444	0.124	0.123	0.730	0.466	0.501

( $N=4$ ): Matinhos, Paraná, Brazil (sea level); **Group 10** ( $N=5$ ): Mato Grosso do Sul, Brazil (80 m); **Group 11** ( $N=4$ ): Alto da Boa Vista, Rio de Janeiro, Brazil (300 m); **Groups 12–21** ( $N_{\text{total}}=131$ ): Seropédica, Rio de Janeiro, Brazil (33 m); **Group 22** ( $N=14$ ): São Sebastião, São Paulo, Brazil (10 m); **Group 23** ( $N=4$ ): Serra dos Órgãos, Rio de Janeiro, Brazil (1000 m); **Group 24** ( $N=6$ ): Tinguá, Rio de Janeiro, Brazil (33–100 m); and **Group 25** ( $N=15$ ): Carabobo, Venezuela (25 m) (Fig. 1). The 131 specimens from Seropédica, Rio de Janeiro, comprise a topotypical series of *M. nigricans*. These specimens were randomly sorted into 10 different samples (groups 12–21), nine of which with 13 specimens, and one with 14, to test the strength of the geographic signal captured by morphometric characters in the context of the Discriminant Function Analysis.

#### Secondary sexual dimorphism

To define the characters included in the geographic analyses, secondary sexual dimorphism was evaluated for three samples in single classification analyses of variance (ANOVAs) for 12 of the 15 cranial characters listed above (except BL, ZB and IOB): (1) a topotypical series of *M. nigricans* from Seropédica, Rio de Janeiro, Brazil, composed of 30 males and 30 females; (2) a sample from Campinhos, Paraná, Brazil, composed of 11 males and 15 females; and (3) a sample from Exu, Pernambuco, Brazil, composed of 15 males and 15 females.

#### Analyses of geographic variation

Principal Components (PCA) and Discriminant Function Analyses (DFA) were employed to assess patterns of craniometric geographic variation. PCA was used to summarize the general trends of size and shape variation within the total dataset treated as a unique sample. DFA was used on selected comparisons of *a priori* identified samples to assess craniometric characters that best discriminate among samples (Neff and Marcus, 1980; Manly, 1994; Strauss, 2010). As multivariate procedures require complete data matrices, missing values (2.99% of total dataset) were estimated from the existing data using the expectation-maximization algorithm (Little and Rubin, 1987; Strauss et al., 2003). The statistical significance of differences among samples was assessed by Multivariate Analysis of Variance (MANOVA). Mahalanobis distances between samples were portrayed in an UPGMA (unweighted pair-group method using arithmetic averages) dendrogram. All multivariate analyses were performed in Matlab for Windows, version 4.2c (Mathworks, 1994), using functions written by R. E. Strauss available at <http://www.faculty.biol.ttu.edu/Strauss/Matlab/Matlab.htm> (accessed October 01, 2010).

#### Qualitative characters used in intra and interspecific comparisons

We evaluate the taxonomic status of the distinct samples by comparing them to the currently recognized South American species of *Myotis*, including examination of type specimens, original descriptions and comparative series from different localities, totaling 715 specimens. A list of specimens examined with their localities is in the Appendix. The museum specimens were identified on the basis of a set of qualitative and quantitative characters reported as diagnostic by previous authors (Thomas, 1901, 1902; Miller and Allen, 1928; Handley, 1960; LaVal, 1973; Baud and Menu, 1993; López-González et al., 2001; López-González, 2005; Moratelli, 2008; Wilson, 2008), which was used to characterize and compare taxa, as follows: plagiopatagium attachment (attached at ankles; at toes by a narrow band of membrane; or at toes by a broad band of membrane); occurrence of a fringe of hairs along the trailing edge of the uropatagium (absent or present); position of P3 (aligned with other premolars or displaced to the lingual side, and visible or not visible when observed in lateral view); occurrence and height of sagittal and occipital crests (absent or present, and height: very low, low, medium and high); shape of the braincase roof (parietal inclined forward or straight); shape of the supraoccipital region (supraoccipital and posteriormost part of parietals flattened when observed in lateral view, not projected much beyond the limit of occipital condyles, or supraoccipital and posteriormost part of parietals rounded, projected beyond the limit of occipital condyles). Capitalized colors nomenclature follows Ridgway (1912).

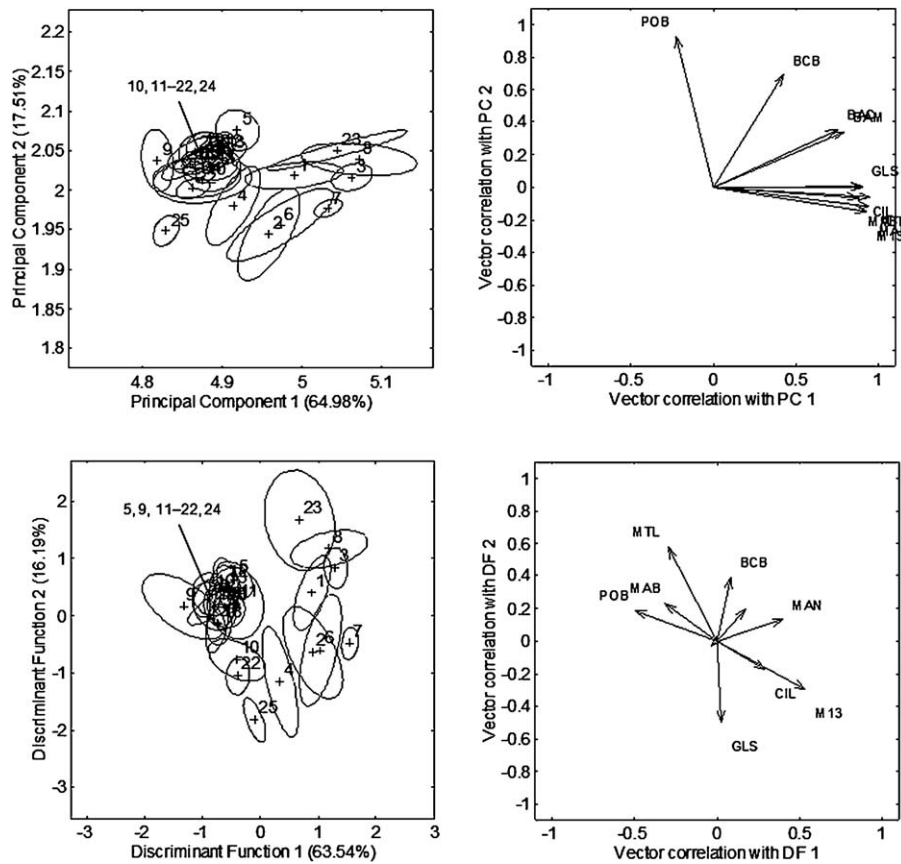
## Results

#### Non-geographic variation

The ANOVAs for secondary sexual dimorphism revealed only two significantly dimorphic characters (CCL and MAL) in the sample from Rio de Janeiro. These characters were therefore not included in geographical analyses, and adult males and females were pooled to enhance sample sizes. Significantly dimorphic characters were not revealed in the other two samples analyzed (Table 1).

#### Geographic analyses

The first principal component (PC1) accounted for 65% of the total sample covariance matrix (Fig. 2; Table 2). PC1 is interpreted here as a general size axis based on the positive sign and high magnitudes of most character loadings, except POB, a constriction that is proportionally smaller in larger individuals in several mammal species. The second principal component (PC2), which accounted for 18%, is interpreted as a general shape axis based on the opposite



**Fig. 2.** Left: 95% confidence ellipses around score centroids of the first two principal components (above) and of the first two discriminant functions (below) obtained from craniometric data of samples: (1) Balsa Nova, Paraná, Brazil, 1150 m; (2) Barra, Bahia, Brazil, 393 m; (3) Campinhos, Paraná, Brazil, 890 m; (4) Monagas, Venezuela, 1190 m; (5) Cochabamba, Bolivia, 2000 m; (6) Crato, Ceará, Brazil, 571 m; (7) Exu, Pernambuco, Brazil, 523 m; (8) Tinguá, Rio de Janeiro, Brazil, 760–965 m; (9) Matinhos, Paraná, Brazil, sea level; (10) Mato Grosso do Sul, Brazil, 80 m; (11) Alto da Boa Vista, Rio de Janeiro, Brazil, 300 m; (12–21) Seropédica, Rio de Janeiro, Brazil, 33 m; (22) São Sebastião, São Paulo, Brazil, 10 m; (23) Serra dos Órgãos, Rio de Janeiro, Brazil, 1000 m; (24) Tinguá, Rio de Janeiro, Brazil, 33–100 m; (25) Carabobo, Venezuela, 25 m. Right: corresponding vector correlations (magnitudes greater than |0.29|) between craniometric characters and the first two eigenvectors of principal component analysis (above) and discriminant analysis (below).

signs of character loadings. Characters associated with the length of skull (GLS, CIL) and rostrum (MTL, M13 and MAN), and width of braincase (MAB and BCB) and rostrum (BAC and BAM) show high correlations with PC1, whereas those related to the width of braincase (BCB) and rostrum (POB, BAC and BAM) show positive and high loadings on PC2 (Table 2).

Along PC1, the most evident result is an unambiguous discontinuity in skull size, with the upland samples from Paraná (groups 1 and 3) and Rio de Janeiro (groups 8 and 23) being larger than the lowland samples from similar latitudes (groups 9, 12–21 and 24). In addition, the northeastern Brazilian samples (groups 2, 6 and 7) have larger skulls than other remaining South American sam-

ples (except groups 1, 3, 8 and 23). PC1 loadings indicate that these series from upland Paraná (groups 1 and 3), upland Rio de Janeiro (groups 8 and 23), Bahia, Ceará and Pernambuco (groups 2, 6 and 7) are composed of individuals with longer rostra (MTL, M13 and MAN). A slight distinction with regard to the breadths of rostrum (BAM and BAC) and braincase (BCB) is observed between the upland samples from Rio de Janeiro and Paraná (groups 1, 3, 8 and 23) and the northeastern Brazilian samples (groups 2, 6 and 7) (Fig. 2).

The first two discriminant functions (DF1 and DF2) accounted for 80% of variation among groups (Fig. 2; Table 2). The interpolation of DF1 scores reveals two main clusters (Fig. 2): specimens from lowland Paraná (group 9), lowland Rio de Janeiro (12–21), São

**Table 2**

Vector correlation coefficients between original variables and principal components (PC1 and PC2) and between original variables and canonical variates (DF1 and DF2) for South American samples of *Myotis nigricans*. Numbers in bold indicate vector correlations with magnitudes greater than |0.29|.

Characters	Loadings of PCA and DFA			
	PC1	PC2	DF1	DF2
Greatest length of skull (GLS)	<b>0.90</b>	0.01	0.03	<b>-0.50</b>
Condylar-incisive length (CIL)	<b>0.90</b>	-0.01	<b>0.30</b>	-0.17
Mastoid breadth (MAB)	<b>0.88</b>	-0.06	<b>-0.31</b>	0.22
Braincase breadth (BCB)	<b>0.42</b>	<b>0.70</b>	0.08	<b>0.39</b>
Postorbital breadth (POB)	-0.22	<b>0.92</b>	<b>-0.50</b>	0.19
Breadth across canines (BAC)	<b>0.75</b>	<b>0.35</b>	0.17	0.20
Breadth across molars (BAM)	<b>0.79</b>	<b>0.34</b>	-0.04	-0.04
Maxillary tooththrow length (MTL)	<b>0.95</b>	-0.06	<b>-0.30</b>	<b>0.58</b>
Molariform tooththrow length (M13)	<b>0.93</b>	-0.15	<b>0.54</b>	<b>-0.30</b>
Mandibular tooththrow length (MAN)	<b>0.94</b>	-0.12	<b>0.40</b>	0.13

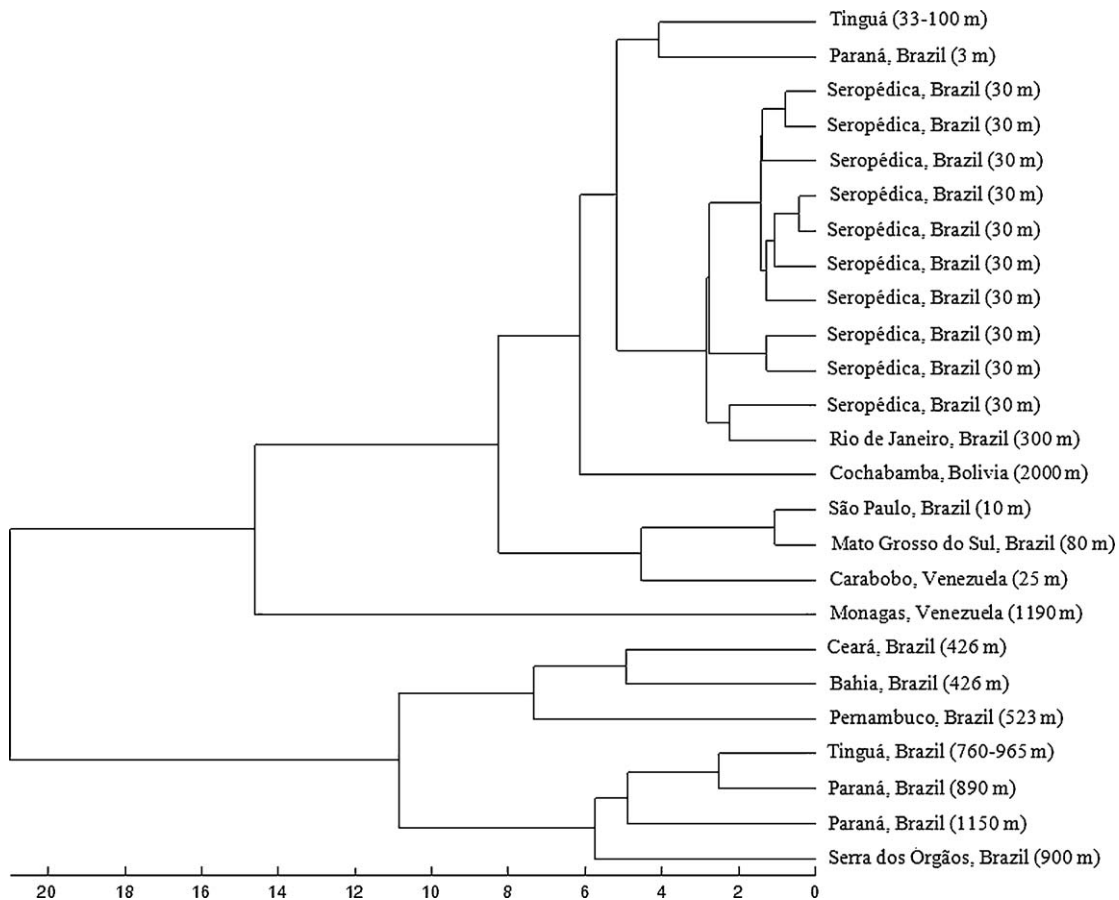


Fig. 3. UPGMA dendrogram of Mahalanobis distances between samples analyzed in the present study.

Paulo (group 22), Mato Grosso do Sul (group 10), highland Bolivia (group 5) and lowland Venezuela (group 25), with negative scores, are spatially separated from the positive scores of specimens from highland Paraná (groups 1 and 3), highland Rio de Janeiro (groups 8 and 23), Bahia (group 2), Ceará (group 6), Pernambuco (group 7) and highland Venezuela (group 4). The characters most associated with DF1 are postorbital breadth (POB) and molariform toothrow length (M13), a contrast which best discriminates the two main groups of samples. Along DF2 two subclusters can be recognized among the groups with positive scores on DF1: specimens from groups 1, 3, 8 and 23 show positive scores, while specimens from groups 2, 4, 6 and 7 show negative scores on this function, with low overlapping. Character loadings in the two discriminant functions reveal that it is the contrasting values of braincase breadth (BCB) and maxillary toothrow length (MTL) with respect to greatest length of skull (GLS) and molariform toothrow length (M13) that best separates these two subclusters.

The UPGMA dendrogram based on Mahalanobis distances also reveals two major clusters (Fig. 3). One of them includes samples from different parts of South America, ranging from northern Venezuela to Bolivia and southern Brazil, among which is the series of topotypes of *M. nigricans* (Seropédica, Rio de Janeiro, Brazil). Two subclusters were revealed inside this cluster, one of them from highland Venezuela (group 4 [1190 m]) and the other from lowland Venezuela, highland Bolivia (group 5 [2000 m]) and lowland Brazil (groups 9–22, 24 and 25). The other cluster includes specimens from mountainous areas in Paraná (groups 1 and 3 [890–1150 m]) and Rio de Janeiro (groups 8 and 23 [760–1000 m]) and from northeastern Brazil (Bahia [group 2], Ceará [group 6] and Pernambuco [group 7]). As observed above, a clear discontinuity is revealed between samples from upland Rio de Janeiro and Paraná, and north-

eastern Brazil on the one hand, and other remaining Brazilian, Bolivian and northern South American samples on the other.

Summarizing, the results of multivariate analyses revealed the existence of two distinct clusters among specimens recognized as *M. nigricans* on the basis of qualitative traits. One of them comprises the samples in the groups 5 (Cochabamba [2000 m]), 9 (Paraná [sea level]), 10 (Mato Grosso do Sul [80 m]), 12–21 (Seropédica [33 m]), 22 (São Paulo [10 m]), 24 (Rio de Janeiro [33–100 m]) and 25 (Carabobo [25 m]). This cluster, which includes the topotypical series of *M. nigricans*, is here regarded as representative of this species. The sample from Venezuelan highlands (Monagas, 1190 m), clustered to this former group by the UPGMA of Mahalanobis distance, is intermediary between the *M. nigricans* cluster and the cluster formed by samples from Eastern Brazil highlands and from Northeastern Brazil (Fig. 3); since it is not presently available for additional comparisons, the confirmation of its taxonomic distinction is hereby postponed. The other major cluster comprises samples in groups 2 (Bahia), 3 (Paraná [890 m]), 6 (Ceará), 7 (Pernambuco), 8 and 23 (Rio de Janeiro [760–965 m]), with groups 1, 3, 8 and 23 and groups 2, 6 and 7 arranged in separate subclusters.

These two subclusters (samples from the mountains of Rio de Janeiro and Paraná, in Southeastern Brazil, and samples from Bahia, Ceará and Pernambuco, in Northeastern Brazil) were significantly distinct from each other and from the remaining samples in the first cluster, including the topotypical series of *M. nigricans*, according to the results of a MANOVA (Wilks' lambda = 0.143;  $F = 13.137$ ;  $p < 0.0001$ ).

The upland samples from Rio de Janeiro and Paraná differ from *M. nigricans* samples by its darker fur coloration and larger general size (except IOB and POB), except for few specimens that overlap in size (Fig. 4; Table 3). The northeastern Brazilian samples (Bahia,

Ceará and Pernambuco) can also be distinguished from *M. nigricans* samples by their larger external and cranial measurements (except BCB, IOB and POB) (Table 3), presence of sagittal crest (Fig. 4) and lighter dorsal fur coloration, with a marked contrast between hair bases and tips. Despite its smaller general measurements, *M. nigricans* has proportionally wider interorbital and postorbital regions than Rio de Janeiro and Paraná upland samples and northeastern Brazilian samples.

Rio de Janeiro and Paraná upland samples are larger on average than samples from Bahia, Ceará and Pernambuco, with the lengths of forearm, thumb and tragus best discriminating these two clusters (Table 3). In qualitative traits, the Rio de Janeiro and Paraná upland samples have almost monochromatic dorsal fur, with black hair bases and dark-brown tips, and lack a sagittal crest in 88% of specimens, while in the northeastern Brazilian specimens the dorsal fur is strongly bicolor, with dark-brown bases and cinnamon-brown tips, and the sagittal crest is generally present (64%). Additionally, in specimens from northeastern Brazil the rostrum is more inclined upwards, a difference not revealed in the morphometric analysis probably because none of the cranial measurements sampled this dimension.

Based on the discontinuities reported above, the Rio de Janeiro and Paraná upland samples (groups 1, 3, 8 and 23), as well as the northeastern Brazilian samples (groups 2, 6 and 9), are regarded as distinct from each other and from *M. nigricans*, and consequently are recognized as different species.

The two new species are herein named, described and compared to other South American species of *Myotis*. Additionally, based on our available series we provide a new diagnosis for *M. nigricans*.

Vespertilionidae Gray, 1825

Myotinae Tate, 1942

*Myotis* Kaup, 1829

*Myotis izecksohni*, sp. nov.

**Holotype:** The holotype of *Myotis izecksohni* (ALP 6675) is an adult male skin and skeleton, including skull and mandible, collected by Daniela Dias (original field number DDT 199) on 25 June 2005. The skin and skeleton, including skull and mandible, are complete, with the exception of a segment missing from the left zygomatic arch (Figs. 5 and 6). The holotype is deposited in the Adriano Lucio Peracchi Mammal Collection (ALP Mammal Collection) at Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, Brazil.

**Type locality:** Fazenda Maria Brandina (22°36'S, 43°27'W), Tinguá Biological Reserve, Rio de Janeiro State, Brazil, 760 m above sea level.

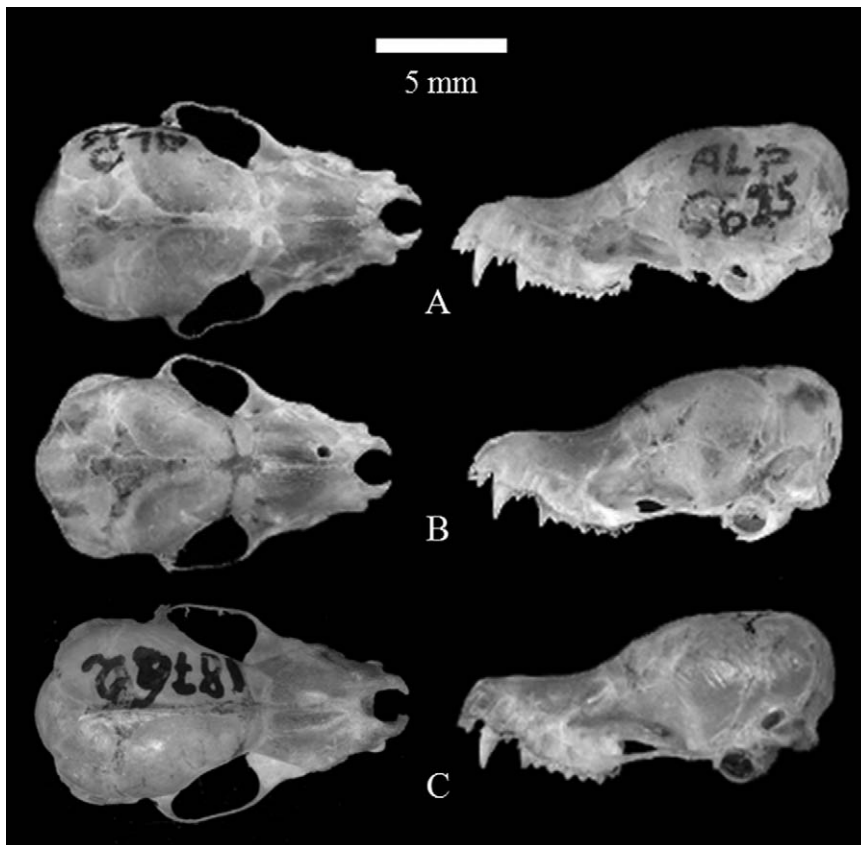
**Paratypes:** The paratypes include five specimens: two adult males (ALP 6676 [25 July 2005], MN 74357 [25 August 2005]), two adult females (ALP 6626 [12 March 2005], MN 74358 [27 August 2005]) and one young female (ALP 6618 [25 March 2005]). They were caught in Tinguá Biological Reserve, between 760 and 864 m, by Daniela Dias, and they are deposited in the ALP Mammal Collection and in the mammal collection at Museu Nacional, Universidade Federal do Rio de Janeiro (MN). Measurements for the type series are provided in Table 4. The holotype and the paratypes had been reported as *M. levis* by Dias and Peracchi (2008).

**Other specimens:** Additional specimens were collected in Rio de Janeiro and Paraná states. In Rio de Janeiro, three females (ALP 6450, 6498, 6513) and one male (ALP 6501) were caught in Serra dos Órgãos National Park, 1000 m above sea level, by R. Moratelli in 2002. These specimens had been reported as *M. nigricans* by Moratelli and Peracchi (2007). In Paraná, 26 specimens were collected in Campinhos State Park, 890 m above sea level; they included 15 females (CCMZ-DZUP 56, 57, 61, 62, 63, 64, 66, 67, 85, 87, 92, 93, 105, 107, 108) and 11 males (CCMZ-DZUP 58, 59,

**Table 3**  
Descriptive statistics of measurements (mm) of three samples assigned to *Myotis nigricans* based on LaVal's (1973) description.

Characters	Rio de Janeiro (33 m; type-locality)			Rio de Janeiro (760–965 m) and Paraná (890 and 1150 m)			Bahia, Ceará and Pernambuco		
	Mean	(Range)	N	Mean	(Range)	N	Mean	(Range)	N
Ear length	10.5	(7.8–12.6)	30	11.5	(8.7–13.2)	25	12.6	(11.0–14.0)	31
Forearm length	33.4	(30.2–35.2)	30	36.2	(33.1–38.3)	32	33.8	(31.5–37.0)	31
Third metacarpal length	30.9	(29.4–32.4)	33	34.2	(31.7–36.0)	32	32.4	(30.0–35.4)	29
Thumb length	4.5	(4.0–5.1)	31	5.3	(4.5–6.0)	32	4.4	(4.11–4.9)	23
Tragus length	5.8	(4.5–6.6)	22	6.2	(5.0–7.4)	25	7.7	(7.0–9.0)	9
Greatest length of skull	13.38	(12.75–13.86)	28	14.11	(12.50–14.62)	32	13.91	(13.43–14.34)	38
Condyllo-canine length	11.90	(11.61–12.21)	27	12.56	(11.70–12.86)	30	12.36	(11.93–12.47)	38
Condyllo-incisive length	12.72	(12.36–12.97)	25	13.45	(12.51–13.79)	31	13.25	(12.82–13.58)	38
Basal length	11.39	(10.88–11.73)	28	12.01	(11.10–12.29)	30	11.85	(11.46–12.24)	38
Mastoid breadth	6.91	(6.69–7.09)	27	7.01	(6.71–7.27)	31	7.00	(6.69–7.20)	37
Braincase breadth	6.51	(6.29–6.76)	28	6.63	(6.25–7.01)	31	6.43	(6.20–6.59)	38
Interorbital breadth	4.66	(4.41–4.97)	29	4.59	(4.35–5.06)	32	4.47	(4.03–4.78)	38
Postorbital breadth	3.57	(3.37–3.76)	30	3.43	(3.20–3.67)	32	3.32	(3.13–3.51)	38
Breadth across canines	3.36	(3.21–3.51)	30	3.57	(3.39–3.74)	31	3.51	(3.24–3.74)	37
Breadth across molars	5.35	(5.01–5.55)	29	5.65	(5.13–5.94)	32	5.49	(5.10–5.74)	38
Maxillary toothrow length	4.95	(4.76–5.11)	30	5.37	(4.87–5.59)	32	5.21	(4.95–5.40)	38
Molariform toothrow length	2.77	(2.66–2.90)	30	3.02	(2.81–3.14)	32	2.99	(2.82–3.11)	38
Mandibular length	9.38	(8.92–9.71)	26	10.04	(9.42–10.70)	27	9.82	(9.44–10.08)	29
Mandibular toothrow length	5.22	(4.77–5.45)	30	5.75	(5.18–5.96)	28	5.60	(5.38–5.79)	36

Summary statistics: SD = standard deviation; N = sample size (adults only, male and females combined). See text for a description of measurement methods.



**Fig. 4.** Dorsal and lateral views of representative skulls from the distinct clusters revealed by morphometric analyses: (A) specimen from upland area in Rio de Janeiro State (ALP 6675, GLS: 14.25 mm); (B) specimen from lowland area in Rio de Janeiro State (ALP 6619, GLS: 13.47 mm); and (C) specimen from northeastern Brazil (MZUSP 18762, GLS: 13.95 mm). All skulls are in the same scale; the picture of the last skull was inverted to allow alignment with remaining skull pictures in the plate.

65, 86, 88, 96, 97, 99, 109, 110, 112). These specimens had been reported as *M. nigricans* by [Arnone and Passos \(2007\)](#). Another 10 specimens were caught in Balsa Nova, 1150 m above sea level; the sample includes four females (CCMZ-DZUP 198, 419, 420, 421) and six males (CCMZ-DZUP 196, 197, 199, 200, 410, 422).

Descriptive statistics of each character for the male and female series from Rio de Janeiro and Paraná states are provided in [Table 5](#).

Distribution: Currently known only from four localities, two of them in Rio de Janeiro State and two in Paraná State. In the former, the specimens were caught in Tingüá Biological Reserve (22°36'S,



**Fig. 5.** Dorsal and ventral views of the skin of *Myotis izecksohni* (ALP 6675). Forearm length 38.3 mm. See [Table 4](#) for other measurements.

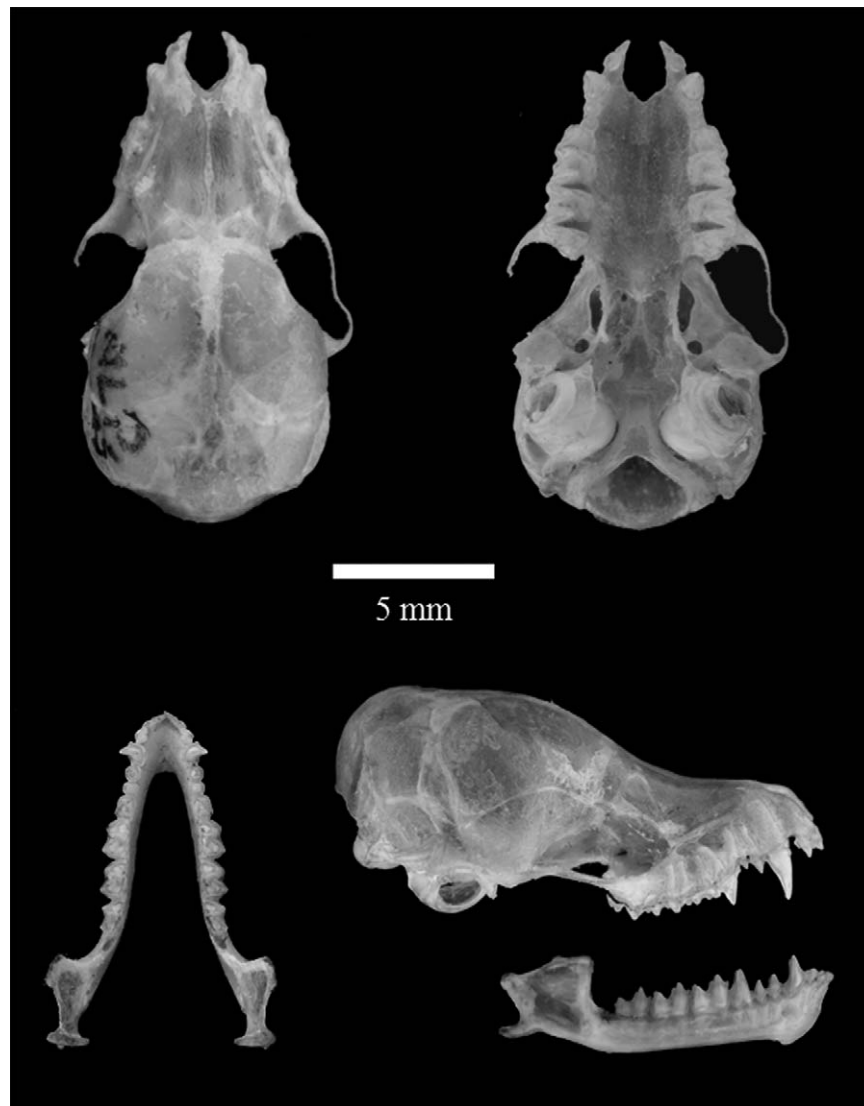


Fig. 6. Dorsal, ventral and lateral views of the skull of the holotype of *Myotis izecksohni* (ALP 6675). Greatest length of skull: 14.25 mm.

**Table 4**

Measurements (mm) of each specimen of the type series (Tinguá, Rio de Janeiro, Brazil) of *Myotis izecksohni*.

	Holotype ALP 6675	Paratype ALP 6618	Paratype ALP 6626	Paratype ALP 6676	Paratype MN 74357	Paratype MN 74358
Sex/age	Adult male	Young female	Adult female	Adult male	Adult male	Adult female
Ear length	12.5	–	12.2	12.4	12.3	12.7
Forearm length	38.3	–	36.2	35.2	37.3	36.3
Third metacarpal length	35.8	–	34.7	34.1	34.9	34.6
Thumb length	4.9	–	4.8	5.5	5.3	4.8
Tragus length	5.9	–	6.3	6.0	6.3	6.3
Greatest length of skull	14.58	14.44	14.46	14.93	14.60	14.64
Condyllo-canine length	12.76	12.65	12.66	–	12.86	12.85
Condyllo-incisive length	13.70	13.52	13.49	13.72	13.77	13.71
Basal length	12.20	12.16	–	12.22	12.25	12.29
Zygomatic breadth	–	–	–	8.72	8.93	–
Mastoid breadth	7.06	6.94	–	7.11	7.07	7.05
Braincase breadth	6.79	6.56	–	6.63	6.69	6.61
Interorbital breadth	4.40	4.40	4.46	4.43	4.82	4.52
Postorbital breadth	3.51	3.38	3.35	3.49	3.52	3.43
Breadth across canines	3.52	3.51	3.62	3.66	3.60	3.74
Breadth across molars	5.60	5.70	5.64	5.70	5.67	5.81
Maxillary tooththrow length	5.47	5.51	5.48	5.47	5.55	5.41
Molariform tooththrow length	3.14	3.13	3.00	3.09	3.11	3.12
Mandibular length	10.13	10.14	–	10.14	10.29	10.21
Mandibular tooththrow length	5.80	5.91	–	5.92	5.96	5.80



**Table 5**  
Descriptive statistics for *Myotis izecksohni* from Rio de Janeiro, Brazil, and Paraná, Brazil.

Character	Females				Males			
	Mean	(Range)	SD	N	Mean	(Range)	SD	N
Ear length	11.5	(8.7–13.2)	1.35	16	11.9	(8.7–12.7)	1.18	17
Tragus length	6.4	(5.6–7.4)	1.22	21	6.1	(5.0–7.2)	1.32	19
Forearm length	36.4	(34.0–38.1)	0.94	21	36.1	(33.1–38.3)	1.01	19
Third metacarpal length	34.4	(32.5–36.0)	0.34	21	34.1	(31.7–35.8)	0.37	19
Thumb	5.2	(4.8–5.9)	0.53	16	5.4	(4.5–6.0)	0.55	17
Dorsal fur	7.9	(7.8–7.9)	0.08	4	8.3	(8.0–8.5)	0.26	6
Ventral fur	6.2	(6.2–6.2)	0	4	6.7	(6.2–7.0)	0.38	6
Greatest length of skull	14.21	(13.19–14.93)	0.33	21	14.18	(13.15–14.62)	0.33	19
Condylar-canine length	12.56	(11.69–12.85)	0.27	20	12.60	(11.70–12.86)	0.29	17
Condylar-incisive length	13.43	(12.52–13.79)	0.28	20	13.50	(12.51–13.77)	0.31	19
Basal length	12.01	(11.17–12.29)	0.29	18	12.02	(11.00–12.25)	0.28	19
Zygomatic breadth	8.67	(8.34–8.85)	0.22	8	8.72	(8.54–8.93)	0.14	13
Mastoid breadth	7.01	(6.71–7.27)	0.15	19	7.02	(6.74–7.16)	0.12	19
Braincase breadth	6.61	(6.34–6.82)	0.13	19	6.64	(6.25–7.01)	0.19	19
Interorbital breadth	4.51	(4.27–4.80)	0.13	21	4.66	(4.37–5.06)	0.22	19
Postorbital breadth	3.40	(3.20–3.64)	0.12	21	3.49	(3.30–3.67)	0.12	19
Breadth across canines	3.57	(3.40–3.74)	0.09	20	3.58	(3.39–3.73)	0.09	19
Breadth across molars	5.68	(5.47–5.90)	0.12	21	5.62	(5.13–5.94)	0.16	19
Maxillary tooththrow length	5.34	(4.87–5.48)	0.13	21	5.41	(4.87–5.59)	0.17	19
Molariform tooththrow length	3.01	(2.83–3.12)	0.07	21	3.03	(2.81–3.14)	0.08	19
Mandibular length	10.03	(9.46–10.24)	0.24	15	10.07	(9.42–10.70)	0.26	19
Mandibular tooththrow length	5.71	(5.11–5.89)	0.18	16	5.79	(5.18–5.96)	0.18	19

Summary statistics: SD = standard deviation; N = sample size (adults only). See text for a description of measurement methods.

43°26'W) and Serra dos Órgãos National Park (22°26'S, 42°59'W), between 760 and 1000 m above sea level. In Paraná State, the specimens were captured in Campinhos State Park (25°03'S, 49°07'W) and in Balsa Nova (25°29'S, 44°49'W). All of these localities are in the Atlantic Rainforest of south and southeastern Brazil (Fig. 1: localities 1, 3, 8 and 23). We expect *M. izecksohni* to occur in other southeastern and southern Brazilian Atlantic Forest localities in the states of São Paulo, Paraná, Santa Catarina and Rio Grande do Sul, as well as in Uruguay.

**Etymology:** *Myotis izecksohni* is named after Dr. Eugenio Izecksohn, in recognition of his outstanding contributions to the knowledge of Rio de Janeiro biodiversity, such as the description of the smallest terrestrial vertebrate of the world, *Brachycephalus didactylus* (Izecksohn, 1971) (Amphibia, Anura, Brachycephalidae), from Tinguá Biological Reserve. This species-group name is a noun in the genitive case formed by adding *-i* to the stem of the name (ICZN, 1999; 31.1.2).

**Common name:** Izecksohn's Myotis

**Diagnosis:** A medium to large species of South American *Myotis* (FA 33.1–38.3 mm); medium ears (EL 8.7–13.2 mm); long and silky fur; dorsal fur bicolor with dark bases (2/3 of total length) and dark-brown to medium-brown tips, with bases and tips contrasting slightly; length of dorsal fur between 7.8 and 8.5 mm; ventral fur bicolor with dark to medium-brown bases (2/3 of total length) and light-brown tips, with bases and tips in the ventral fur contrasting more than in the dorsal fur; length of ventral fur between 6.2 and 7.0 mm (Fig. 5); membranes medium-brown; fringe of hairs along the trailing edge of the uropatagium absent, although some hairs may be present; plagiopatagium attached to feet at the level at toes by a broad band of membrane; skull moderately large (GLS 13.19–14.93 mm); braincase long and flattened; supraoccipital region rounded; sagittal crest generally absent, but one specimen with a very low sagittal crest (ALP 6513); P3 in tooththrow, not crowded to the lingual side, smaller than P2, and visible in lateral view (Fig. 6).

Of the characters above, the following are useful for field identification: length of forearm (range 33.1–38.3 mm; mean 35.9 mm); length of ear (8.7–13.2 mm; mean 11.5 mm); dorsal and ventral color of fur (dorsal fur with dark bases and dark-brown to medium-brown tips; ventral fur with dark to medium-brown bases and

light-brown tips), texture (silky) and length of fur (>7 mm dorsally, >6 mm ventrally); absence of a fringe of hairs along trailing edge of uropatagium.

**Description and Comparisons:** *Myotis izecksohni* has been recorded in South America in sympatry with *M. albescens* (É. Geoffroy, 1806), *M. levis*, *M. nigricans*, *M. riparius* and *M. ruber* (É. Geoffroy, 1806). *Myotis izecksohni* can be distinguished from *M. albescens* by its narrower and longer rostrum, narrower interorbital constriction, more flattened braincase, absence of frosted appearance in the dorsal pelage and absence of a fringe of hairs along the trailing edge of the uropatagium; from *M. levis*, it can be distinguished by a non-inflated interorbital region, absence of a fringe of hairs along the trailing edge of the uropatagium (present in syntopic specimens of *M. levis* from Serra dos Órgãos, Rio de Janeiro, Brazil), shorter forearm and ear, smaller skull and darker tips of dorsal and ventral pelage; from *M. nigricans*, it differs by its larger general size, darker fur coloration and proportionately narrower interorbital and postorbital regions; from *M. riparius*, by its larger size, flattened skull, absence of sagittal crest and longer pelage; from *M. ruber*, by its flattened skull, absence of sagittal crest, and long, dark-brown dorsal fur. Additionally, *M. izecksohni* (GLS: range 13.19–14.93 mm; mean 14.21 mm) is on average larger than *M. albescens* (GLS: range 13.42–14.27; mean 13.94), *M. nigricans* (GLS: range, 12.62–13.90; mean 13.37) and *M. riparius* (GLS: range 12.99–14.59; mean 13.50), but is smaller than *M. levis* (GLS: range 14.21–15.42; mean 14.82) and *M. ruber* (GLS: range 14.17–15.29; mean 14.80). Although slightly different in fur color, *M. levis* and *M. nigricans* can be considered the most cryptic sympatric species with *M. izecksohni*.

Five specimens from Tinguá and Serra dos Órgãos (Rio de Janeiro State) could not be unequivocally identified, since storage in alcohol rendered their pelage color unreliable, and because their dimensions were intermediate between those of *M. izecksohni* and *M. nigricans*. These specimens have been initially excluded from morphometric analyses, but, in the absence of further qualitative diagnostic traits, we probabilistically classified each one *a posteriori* with regard to topotypical samples of *M. izecksohni* and *M. nigricans* based on the frequencies of shortest Mahalanobis distances obtained in a 1000 bootstrap iterations (Table 6). Four specimens were then classified with *M. nigricans* (ALP 6479, 6625, 6679, 6682),

**Table 6**

Frequency distribution of classification of single specimens using the minimum Mahalanobis distances to the centroids of selected samples based on 1000 bootstrap iterations. Bold values correspond to higher classification values and dashes correspond to zero.

Specimens	Groups													Classification
	8	12	13	14	15	16	17	18	19	20	21	23	24	
ALP 6479	–	<b>0.98</b>	–	–	–	–	–	–	0.01	–	–	–	0.01	<i>M. nigricans</i>
ALP 6524	<b>0.90</b>	–	–	–	–	0.01	–	–	–	–	–	0.09	–	<i>M. izecksohni</i>
ALP 6625	–	<b>0.57</b>	0.02	–	–	0.17	–	–	0.03	–	0.06	0.01	0.12	<i>M. nigricans</i>
ALP 6679	–	–	–	–	0.02	0.02	–	–	0.36	–	<b>0.56</b>	–	0.04	<i>M. nigricans</i>
ALP 6682	0.01	<b>0.94</b>	–	–	–	–	–	–	0.02	0.01	–	0.01	–	<i>M. nigricans</i>

Groups: (8) Tinguá, 760–965 m; (12–21) Seropédica, 33 m; (23) Serra dos Órgãos, 1000 m; (24) Tinguá, 33–100 m.

and one with *M. izecksohni* (ALP 6524), indicating that both species can be found in syntopy. Three other specimens from Paraná, Santa Catarina and Rio Grande do Sul were probabilistically tentatively classified with *M. izecksohni* and *M. nigricans*. All of them were classified with *M. izecksohni* (CCMZ-DZUP 338 [84% to Balsa Nova sample and 14% to Serra dos Órgãos National Park sample], CCMZ-DZUP 400 [100% to Balsa Nova] and CCMZ-DZUP 428 [65% to Balsa Nova and 33% to Serra dos Órgãos National Park]), indicating the possible occurrence of this species in Santa Catarina and Rio Grande do Sul, which comprise the southernmost part of Brazil.

When in syntopy, the main quantitative characters that distinguish these species are forearm length, condylo-canine length, condylo-incisive length, basal length, zygomatic breadth, braincase breadth, mandibular length and mandibular tooththrow length (Table 7). *Myotis izecksohni* is intermediate in size between *M. nigricans*, which is smaller, and *M. levis*, which is larger, with little overlap in measurement ranges.

For the purpose of this description, *M. izecksohni* was also compared with the allopatric species and subspecies *M. aelleni* Baud, 1979, *M. atacamensis* (Lataste, 1891), *M. chiloensis* (Waterhouse, 1840), *M. levis dinellii* Thomas, 1902, *M. elegans* Hall, 1962, *M. keaysi* J.A. Allen, 1914, *M. nesopolus larensis* LaVal, 1973, *M. oxyotus* (Peters, 1867) and *M. simus* Thomas, 1901 (Appendix). It can be distinguished from all of these species by the following qualitative and quantitative craniodental and external characters: from *M. simus* by its plagiopatagium attached to the toes by a broad band of membrane; from *M. aelleni*, by its bicolored fur, without white bases on the dorsal hairs; from *M. atacamensis*, *M. elegans* and *M. nesopolus* by its larger general size and by its darker coloration; from *M. keaysi* by the absence of a sagittal crest and by its darker coloration; from *M. l. dinellii* by the absence of a fringe of hairs along the trailing edge of the uropatagium and by its darker coloration; and from

*M. chiloensis* and *M. oxyotus* by its darker coloration. Although *M. chiloensis* and *M. oxyotus* are the most similar species in skull shape and size among the allopatric species that occur in South America, *M. oxyotus* occurs from Costa Rica to Bolivia (Simmons, 2005), with all South American populations restricted to the Andes Mountains (LaVal, 1973; Wilson, 2008), and *M. chiloensis* is restricted to Chile and Northern Argentina (Barquez et al., 1999; Simmons, 2005; Wilson, 2008).

Natural History: Four animals (ALP 6450 [27 March 2001], ALP 6498 [22 January 2002], ALP 6501 [23 January 2002] and ALP 6513 [31 July 2002]) were caught in the first three hours after dusk in ground-level mist nets across a small creek (2 m or less in depth) in late successional secondary forest. Two animals (ALP 6618 [15 January 2005] and ALP 6676 [25 June 2005]) were caught in mist nets placed along trails in secondary forest. One was collected in a clearing surrounded by secondary forest (ALP 6675 [25 June 2005]). Three specimens were caught in roosts, one of which (ALP 6626 [12 March 2005]) was in a rocky crevice, and the others (MN 74357 and 74358 [both on 27 August 2005]) in the ruins of an abandoned church bordered by a late successional secondary forest. All of them were caught in Rio de Janeiro conservation units. The specimens from Campinhos State Park, Paraná, were caught in caves and trails near the entrance of caves. All *M. izecksohni* were captured in mountainous forests between 760 and 1000 m above sea level. A check of southern and southeastern Brazilian collections revealed that no specimens had apparently been collected at lower elevations, being probably restricted to areas of subtropical climate like other Neotropical species of *Myotis* (e.g., *M. levis*, *M. oxyotus*, *M. chiloensis*). Specimens of *Basilisa lindolphoi* Graciolli, 2001 (Diptera, Nycteribiidae) were recorded as ectoparasites on two specimens of *M. izecksohni* from Tinguá Biological Reserve (ALP 6618, 6676).

**Table 7**

Descriptive statistics (mm) for *M. nigricans*, *M. izecksohni* and *M. levis* from the mountains of Rio de Janeiro, Brazil.

Character	<i>M. nigricans</i>				<i>M. izecksohni</i>				<i>M. levis</i>			
	Mean	(Range)	SD	N	Mean	(Range)	SD	N	Mean	(Range)	SD	N
Ear length	–	–	–	–	12.5	(12.2–13.2)	0.35	7	16.1	(14.8–17.0)	0.59	13
Forearm length	33.9	(33.3–35.1)	0.81	5	36.9	(35.2–38.3)	1.10	7	39.7	(38.0–41.4)	0.88	14
Tragus length	6.1	(5.6–6.6)	–	2	6.4	(5.9–7.2)	0.41	7	9.2	(8.2–9.9)	0.49	12
Greatest length of skull	13.44	(13.31–13.59)	0.09	9	14.63	(14.46–14.93)	0.15	7	15.18	(14.38–15.89)	0.33	14
Condylo-canine length	12.01	(11.64–12.21)	0.17	9	12.78	(12.66–12.86)	0.08	7	13.23	(12.54–13.80)	0.29	14
Condylo-incisive length	12.67	(12.36–12.88)	0.15	9	13.66	(13.49–13.77)	0.11	7	14.17	(13.52–14.80)	0.31	14
Basal length	11.52	(11.31–11.69)	0.12	9	12.23	(12.20–12.29)	0.03	6	12.77	(12.16–13.27)	0.28	14
Zygomatic breadth	8.14	(7.89–8.24)	0.15	5	8.67	(8.34–8.93)	0.24	4	9.12	(8.89–9.39)	0.14	9
Mastoid breadth	6.97	(6.81–7.12)	0.11	8	7.05	(6.85–7.16)	0.10	6	7.49	(7.14–7.66)	0.12	14
Braincase breadth	6.50	(6.38–6.63)	0.09	9	6.67	(6.53–6.79)	0.09	6	7.14	(6.82–7.41)	0.14	14
Interorbital breadth	4.57	(4.28–4.86)	0.17	9	4.60	(4.40–5.06)	0.24	7	4.94	(4.74–5.34)	0.16	14
Postorbital breadth	3.53	(3.41–3.63)	0.07	9	3.50	(3.35–3.67)	0.10	7	3.98	(3.75–4.21)	0.14	14
Breadth across canines	3.54	(3.29–3.88)	0.20	8	3.60	(3.51–3.74)	0.08	7	3.71	(3.50–3.85)	0.09	14
Breadth across molars	5.39	(5.15–5.75)	0.25	8	5.65	(5.58–5.81)	0.07	7	5.97	(5.70–6.17)	0.13	14
Maxillary tooththrow length	5.10	(4.90–5.26)	0.12	8	5.46	(5.29–5.59)	0.09	7	5.64	(5.31–5.97)	0.16	14
Molariform tooththrow length	2.87	(2.69–3.06)	0.15	8	3.05	(2.89–3.14)	0.08	7	3.15	(3.02–3.29)	0.08	14
Mandibular length	9.57	(9.22–9.92)	0.24	8	10.20	(10.13–10.29)	0.06	6	10.63	(10.17–11.19)	0.24	13
Mandibular tooththrow length	5.40	(5.16–5.61)	0.16	9	5.85	(5.79–5.96)	0.07	6	6.05	(5.77–6.24)	0.13	13

Summary statistics: SD = standard deviation; N = sample size (adults only). See text for a description of measurement methods.



Fig. 7. Dorsal and ventral views of the skin of *Myotis lavalii* (MZUSP 18762). Forearm length 34.4 mm. See Table 8 for other measurements.

The second form, from northeastern Brazil, also revealed by our analyses, is herein described as

*Myotis lavalii*, sp. nov.

**Holotype:** The holotype of *Myotis lavalii* (MZUSP 18762) is an adult male skin and skull collected by Michael R. Willig. The skin and skull are complete (Figs. 7 and 8), and are deposited in the mammal collection at Museu de Zoologia da Universidade de São Paulo (MZUSP).

**Type locality:** 6 km S of Exu (7°30'S, 39°43'W), Pernambuco State, Brazil, 523 m above sea level.

**Paratypes:** The paratypes include 29 specimens from the same locality of the holotype, all of them collected by M. R. Willig (15 females: MZUSP 18753, 18755, 18783, 18784, 18785, 18792, 18793, 18813, 18823, 18849, 18807, 18753, 18814, 18813, 18755; and 14 males: MZUSP 18759, 18762, 18814, 18815, 18819, 18820, 18821, 18846, 18847, 18848, 18759, 18820, 18815, 18821). These specimens include skin and skull. Descriptive statistics of cranial and external measurements for the type series are provided in Table 8.

**Other specimens:** Other specimens were caught in the Floresta Nacional do Araripe (1 female: USNM 555714; and 1 male: USNM 555713) and Itaitera, Crato, Ceará State (6 males: USNM 555715,

**Table 8**  
Measurements of the holotype and descriptive statistics for the paratype series of *Myotis lavalii* from Exu, Pernambuco, Brazil.

Character	Holotype	Males				Females			
		Mean	(Range)	SD	N	Mean	(Range)	SD	N
Ear length	13.0	12.7	(11.0–14.0)	0.83	18	12.4	(11.0–14.0)	1.05	13
Forearm length	34.4	33.6	(31.5–37.0)	1.30	18	34.0	(32.0–36.0)	1.08	13
Third metacarpal length	32.8	32.1	(30.0–33.8)	1.06	18	32.8	(30.6–35.4)	1.22	11
Tragus length	7.0	7.5	(7.0–8.0)	0.53	8	9.0	–	–	1
Thumb	4.9	4.4	(4.1–4.7)	0.20	11	4.5	(4.2–4.9)	0.20	12
Weight	4.5	4.1	(3.0–5.0)	0.68	18	5.1	(4.0–8.0)	1.14	13
Greatest length of skull	13.98	13.88	(13.58–14.12)	0.16	22	13.95	(13.43–14.34)	0.29	16
Condylar–canine length	12.50	12.33	(11.95–12.61)	0.19	22	12.39	(11.93–12.74)	0.27	16
Condylar–incisive length	13.41	13.23	(12.84–13.54)	0.20	22	13.28	(12.82–13.58)	0.25	16
Basal length	12.07	11.84	(11.50–12.14)	0.20	22	11.87	(11.46–12.24)	0.24	16
Zygomatic breadth	8.46	8.36	(8.07–8.60)	0.18	10	8.63	(8.48–8.73)	–	3
Mastoid breadth	7.04	7.00	(6.77–7.20)	0.12	22	7.00	(6.69–7.19)	0.06	15
Braincase breadth	6.38	6.42	(6.20–6.59)	0.09	22	6.44	(6.20–6.59)	0.12	16
Interorbital breadth	4.61	4.46	(4.03–4.69)	0.17	22	4.49	(4.20–4.78)	0.14	16
Postorbital breadth	3.32	3.31	(3.13–3.51)	0.09	22	3.33	(3.19–3.48)	0.08	16
Breadth across canines	3.49	3.47	(3.28–3.71)	0.12	21	3.56	(3.24–3.74)	0.14	16
Breadth across molars	5.46	5.46	(5.18–5.74)	0.13	22	5.52	(5.10–5.74)	0.17	16
Maxillary tooththrow length	5.30	5.18	(4.95–5.32)	0.11	22	5.24	(5.03–5.40)	0.12	16
Molariform tooththrow length	3.07	2.98	(2.82–3.07)	0.07	22	2.99	(2.87–3.11)	0.08	16
Mandibular length	10.03	9.81	(9.49–10.08)	0.16	16	9.83	(9.44–10.07)	0.31	13
Mandibular tooththrow length	5.73	5.59	(5.39–5.73)	0.10	21	5.63	(5.38–5.79)	0.13	15

Summary statistics: SD = standard deviation; N = sample size (only adults). See text for a description of measurement methods.

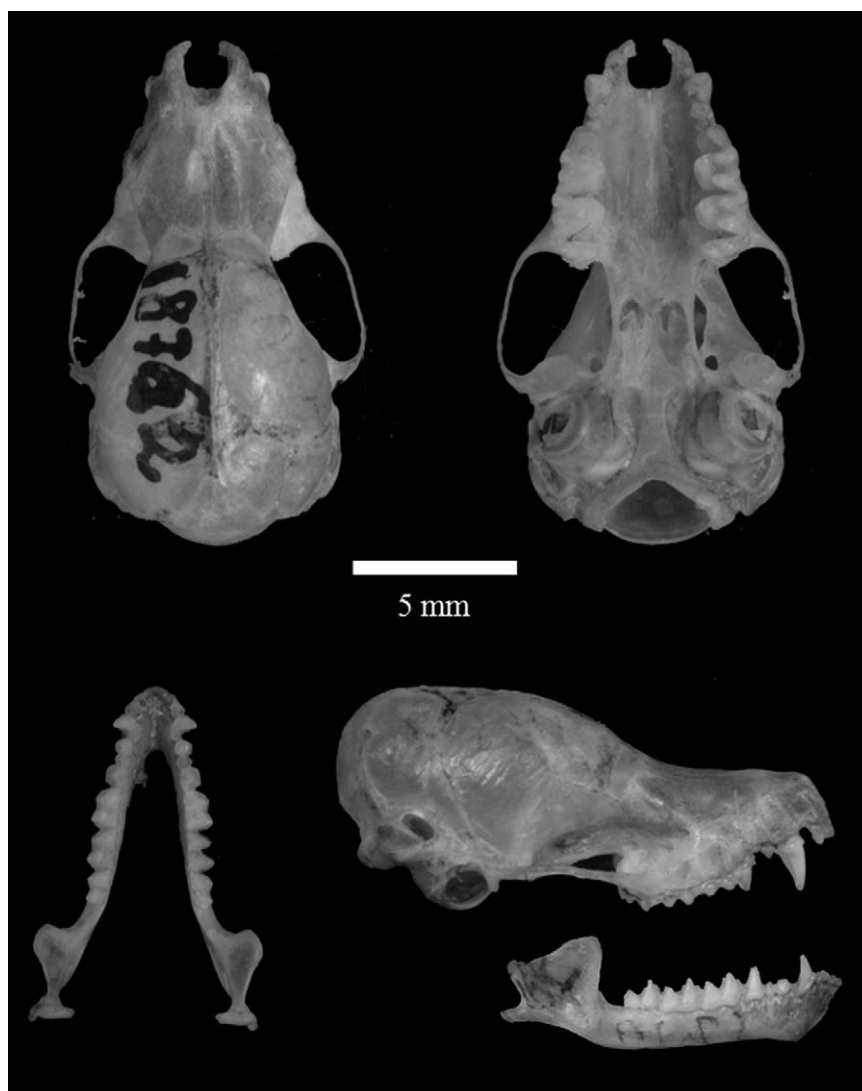


Fig. 8. Dorsal, ventral and lateral views of the skull and mandible of the holotype of *Myotis lavalii* (MZUSP 18762). Greatest length of skull: 13.95 mm.

555717, 555718, 555720, 555721, 555722); Russo, Ceará State (2 males: MN 3422, 3424); and Barra, Bahia State (5 males: MN 3405, 3406, 3410, 3412, 3415). These specimens consist of skin and skull.

Distribution: Known from Exu, Pernambuco State (7°30'S, 39°43'W [523 m]); Crato, Ceará State (7°13'S, 39°22'W [426 m] and 7°27'S, 39°17'W [900 m]); Russo, Ceará State (5°19'S, 39°22'W [15 m]); and Barra, Bahia State (13°54'S, 44°08'W [393 m]). Although these localities are situated in the northeastern Brazilian Caatinga ecosystem (Fig. 1: localities 2, 6 and 9), with the exception of Russo, they are sub humid and deciduous forest formations, with distinctive lower temperatures compared with other adjacent localities in lower altitudes.

Etymology: *Myotis lavalii* is named to honour Dr. Richard K. LaVal, in recognition of his important contribution to the systematics of *Myotis*. His revision of Neotropical *Myotis* remains the main reference for the taxonomy of the genus in South and Central America. This species-group name is a noun in the genitive case formed by adding *-i* to the stem of the name (ICZN, 1999; 31.1.2).

Common name: LaVal's Myotis

Diagnosis: A small to medium species of South American *Myotis* (FA 31.5–37.0 mm); medium ears (EL 11.0–14.0 mm); long and silky fur; dorsal fur strongly bicolor with medium-brown hair bases (2/3 of total length) and light-brown tips; length of dorsal fur ca. 7.0 mm; ventral fur strongly bicolor, with dark-brown bases (2/3 of total

length) and Cinnamon-buff tips; length of ventral fur ca. 6.0 mm (Fig. 7); fringe of hairs along the trailing edge of the uropatagium absent, although some hairs may be present in few specimens (MZUSP 18755, 18762, 18815, 18820); plagiopatagium attached to the toes by a broad band of membrane; skull of small to moderate dimensions (GLS 13.43–14.34 mm); postorbital constriction narrow; forehead steeply sloping with regard to the skull; supraoccipital region rounded; sagittal crest (64%) and lambdoid crests (92%) generally present and low; P3 generally in tooththrow (93%) (Fig. 8), although displaced to the lingual side in few specimens (MZUSP 18785, USNM 555713).

For field identification the most relevant characters are the color of the fur, with dark-brown bases and Cinnamon-buff tips, and the absence of a fringe of hairs along the trailing edge of the uropatagium.

Description and Comparisons: *Myotis lavalii* can be distinguished from other South American species of *Myotis* on the basis of both craniodental and external characters. *Myotis lavalii* can be distinguished from *M. simus* by its plagiopatagium attached to the toes by a broad band of membrane, and by its longer and silkier fur; from *M. aelleni*, by its bicolor fur, without white bases on the dorsal hairs; from *M. atacamensis*, by its larger general size and sagittal crest generally present; from *M. chiloensis* by its paler dorsal fur and sagittal crest generally present; from *M. keaysi* by

its longer, and paler dorsal fur; from *M. izecksohni* by its paler fur coloration, with a strong contrast between the hair bases and tips in the dorsal fur; from *M. levis* and *M. albescens* by the absence of a fringe of hairs along the trailing edge of the uropatagium and sagittal crest generally present; from *M. nesopolus larensis* by its paler dorsal fur and by its skull shape, with a higher rostrum; from *M. oxyotus* by its smaller general size; from *M. riparius* and *M. ruber* by its longer and bicolor dorsal fur and supraoccipital region rounded; and from *M. nigricans*, by its longer and upwardly inclined rostrum and by its paler dorsal fur coloration.

*Myotis nigricans* (Schinz), emended diagnosis

Common name: Black Myotis

Neotype: The holotype was not originally specified. Maximilian Alexander Philipp zu Wied-Neuwied described *Vespertilio nigricans* in Schinz (1821) based on specimens collected by himself in the State of Espírito Santo, Brazil, during an expedition to the coast of Brazil between 1815 and 1817. Those specimens have not been located in European collections or in the Wied's collection acquired by the American Museum of Natural History, USA, after his death (LaVal, 1973). LaVal (1973) designed as neotype an adult pregnant female (LACM 36877), skin and skull, collected in 14 October 1968 by A. L. Peracchi.

Type locality: Seropédica (ca. 22°45'S, 43°41'W), Rio de Janeiro State, Brazil, elevation of 33 m.

Description: Based on the available samples here assigned to *M. nigricans*, it can be described as follows: a small species (mean of FA 33.9 mm), with a wide range of body-size variation (FA 30.5–38.9 mm); small to medium ears (8–15 mm; mean 11.4 mm); silky pelage; length of dorsal hairs ranging from 6.2 to 8.1 mm; dorsal fur without contrast between bases and tips or slightly bicolor, with black bases and Mummy-brown tips; length of ventral hairs ranging from 5.0 to 5.8 mm; ventral fur slightly lighter than the dorsal fur, with Mummy-brown bases and Cinnamon-brown tips; membranes medium-brown; lacking a fringe of hairs along the trailing edge of the uropatagium, although some hairs are present in few specimens; plagiopatagium attached at feet by a broad band of membrane; skull small to moderate (GLS 12.62–14.14); sagittal crest generally absent (88%); P3 generally in tooththrow and visible in lateral view (97%), although in some specimens is displaced to the lingual side and not visible, or aligned and not visible. In lateral view, the parietal is generally inclined forward (96%) and the region formed by the supraoccipital region is generally projected much beyond the posterior limit of the occipital condyles (69%).

## Discussion

Phylogenetic analyses for the New World *Myotis* (Ruedi et al., 2001; Stadelmann et al., 2007) indicate *M. nigricans* and *M. levis* as sister taxa, and *M. oxyotus* closely related with them. The divergence between *M. nigricans* and *M. levis* was found to be one of the most recent among New World *Myotis*, dating from ca. 1.5 MYA. Despite its relatively recent origin, *M. nigricans* has the largest geographic and altitudinal range among Neotropical *Myotis*, while *M. levis* and *M. oxyotus* are currently restricted either to subtropical or upland habitats (Wilson, 2008).

The two new species here described also inhabit restricted portions of the geographic range of *M. nigricans*. *Myotis izecksohni* is currently restricted to select mountainous localities in the Serra do Mar of Eastern Brazil, whereas *M. lavalii* has been recorded so far from select localities in northeastern Brazil. Notwithstanding, the geographic range of *M. nigricans* possibly includes these ranges, since records of the new species are so far restricted to specific localities and at least with respect to *M. izecksohni*, *M. nigricans* has been documented in syntopy.

Our analyses suggest that *M. nigricans*, as here recognized, may still comprise a species complex. Further studies will benefit from a more comprehensive sampling of localities and character systems, particularly DNA sequence data, as long as previous karyological analyses have resulted taxonomically uninformative. Such improvements will eventually allow an objective evaluation of the taxonomic diversity of this widespread form, which has been so far only recognized on a morphological basis.

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## Appendix

Specimens examined: Abbreviations of institutions are as follows: Museu Nacional, Rio de Janeiro, Brazil (MN); Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil (ALP); Museu de Zoologia, São Paulo, Brazil (MZUSP); Universidade do Estado de São Paulo, São José do Rio Preto, Brazil (DZSJRP); Museu de História Natural Capão da Imbuia, Curitiba, Brazil (MHNCI); Universidade Federal do Paraná, Curitiba, Brazil (CCMZ-DZUP); American Museum of Natural History, New York, USA (AMNH); and National Museum of Natural History, Washington, DC, USA (USNM). The abbreviation JAO corresponds to field numbers of João Alves de Oliveira, and those specimens will be deposited in mammal collection at Museu Nacional. The coordinates were obtained from the skin tags, from the Gazetteer of Marginal Localities of Gardner (2008) and from the Google Earth Program. Individuals marked with an asterisk were used in the morphometric analyses.

***Myotis albescens*:** BRAZIL: Paraná: Paiçandu (23°27'S, 52°03'W; DZSJRP 10458, 10459, 10460, 10524, 10525, 10550, 10551, 10552, 10553, 10554, 10555, 10556, 10557, 10558, 10559, 10560, 10561, 10562, 10563, 10564, 10565, 10566, 10567, 10568, 10569, 10570, 10571, 10572, 10573, 10574, 10575, 10576). Rio de Janeiro: Piraí: Estação Ecológica de Piraí (22°38'S, 43°54'W; ALP 4659, 5165). São Paulo: Avandava (21°27'S, 49°56'W; MZUSP 1292, 22691). São Paulo: Fernando Prestes (21°15'S, 48°41'W; DZSJRP 13609, 13612, 13617). São Paulo: Itatiba (23°00'S, 46°50'W; DZSJRP

12590). São Paulo: Vale do Ribeira (24°29'S, 47°50'W; DZSJRP 12554). PARAGUAY: Paraguairí: Yaguarón (25°34'S, 57°16'W; AMNH 205195).

***Myotis chilensis***: CHILE: Coastal Town N of Valparaíso: Zapallar (32°23'S, 71°27'W; USNM 391785).

***Myotis izecksohni***: BRAZIL: Rio de Janeiro: Tinguá: Reserva Biológica do Tinguá (22°36'S, 43°26'W; ALP 6618\*, 6626\*, 6675\*, 6676\*, MN 74357\*, 74358\*). Rio de Janeiro: Teresópolis: Parque Nacional da Serra dos Órgãos (22°26'S, 42°59'W; ALP 6450\*, 6498\*, 6501\*, 6513\*, 6524). Paraná: Balsa Nova: São Luis do Purunã (25°29'S, 44°49'W; CCMZ-DZUP 196\*, 197\*, 198\*, 199\*, 200\*, 410\*, 419\*, 420\*, 421\*, 422\*). Paraná: Campinhos (25°03'S, 49°07'W; CCMZ-DZUP 56\*, 57\*, 58\*, 59\*, 61\*, 62\*, 63\*, 64\*, 65\*, 66\*, 67\*, 85\*, 86\*, 87\*, 88\*, 92\*, 93\*, 96\*, 97\*, 99\*, 105\*, 107\*, 108\*, 109\*, 110\*, 112\*).

***Myotis keaysi keaysi***: BOLIVIA: Santa Cruz: Vallegrande (18°29'S, 64°06'W; AMNH 260880, 262647). PERU: Cuzco: Cordillera Vilcabamba (12°36'S, 73°29'W; AMNH 214371, 233850, 233851, 233853, 233854, 233857, 236134). Huánuco (8°42'S, 71°53'W; AMNH 216117). Puno: Inca Mines (13°30'S, 70°70'W; AMNH 15814). VENEZUELA: Aragua: Rancho Grande Biological Station (10°21'N, 67°40'W; USNM 370901). Bolívar: Gran Sabana (6°01'N, 63°50'W; AMNH 130625, 130626).

***Myotis keaysi pilosatibialis***: VENEZUELA: Aragua: Rancho Grande Biological Station (10°21'N, 67°40'W; USNM 370929, 562920, 562921). Carabobo: Montalbán (10°15'N, 68°21'W; USNM 441741, 441742). Miranda: Curupao (10°31'N, 66°38'W; USNM 387714, 387715, 387716, 387718).

***Myotis lavalii***: BRAZIL: Ceará: Crato: Floresta Nacional do Araripe (7°27'S, 39°17'W; USNM 555713\*, 555714\*). Ceará: Crato: Itaiteira (7°13'S, 39°22'W; USNM 555715\*, 555716, 555717\*, 555718\*, 555720\*, 555721\*, 555722\*). Ceará: Russo (5°19'S, 39°22'W; MN 3422, 3424). Pernambuco: 6 km of Exu (7°30'S, 39°43'W; MZUSP 18753\*, 18755\*, 18759\*, 18762\*, 18783\*, 18784\*, 18785\*, 18792\*, 18793\*, 18813\*, 18814\*, 18815\*, 18819\*, 18820\*, 18821\*, 18823\*, 18846\*, 18847\*, 18848\*, 18849\*, 18807\*, 18753\*, 18814\*, 18813\*, 18755\*, 18759\*, 18762\*, 18820\*, 18815\*, 18821\*). Bahia: Barra (13°54'S, 44°08'W; MN 3405\*, 3406\*, 3410\*, 3412\*, 3415\*).

***Myotis levis dinellii***: ARGENTINA: Córdoba (31°23'S, 64°10'W; USNM 142560, 142561, 142562). Chuquisaca: Tomina (19°10'S, 64°29'W; AMNH 263629). Tucumán: La Rocha (27°47'S, 65°34'W; AMNH 256987). BOLIVIA: Cochabamba (17°12'S, 64°04'W; AMNH 261119). Potosí: Unknown locality (AMNH 39003). Santa Cruz: Caballero (17°55'S, 64°34'W; AMNH 260253).

***Myotis levis levis***: ARGENTINA: Buenos Aires: LaValle (34°36'S, 58°24'W; USNM 236236, 236237). Córdoba (31°23'S, 64°10'W; USNM 252766). Tucumán: Los Vásquez (27°02'S, 65°19'W; MZUSP 2055). Entre Ríos: Puerto Constanza (32°07'S, 58°46'W; USNM 582461). BRAZIL: Minas Gerais: Mariana (20°22'S, 43°25'W; MZUSP 1748). Minas Gerais: Ouro Preto (20°17'S, 43°29'W; MZUSP 15344, 15345). Paraná: Palmas (26°29'S, 51°59'W; CCMZ-DZUP 380). Paraná: Porto Rico (22°46'S, 53°15'W; CCMZ-DZUP 216, 217, 218, 369, 371, 372, 373, 376, 377, 381, 382, 384, 385, 386, 387, 388, 389, 391, 392, 393, 394, 395, 396). Rio de Janeiro: Jacarandá (22°26'S, 42°54'W; JAO 1812, 1814, 1816, 1817, 1818, 1819, 1820, 1822, 1826, 1848). Rio de Janeiro: Macaé de Cima: Parque Estadual dos Três Picos (22°23'S, 42°29'W; JAO 1761, 1762, 1763, 1765, 1766, 1767, 1768, 1769, 1770, 1771, 1772). Rio de Janeiro: Nova Friburgo (22°17'S, 42°32'W; MZUSP 2799). Rio de Janeiro: Teresópolis: Parque Nacional da Serra dos Órgãos (22°26'S, 42°59'W; ALP 6481, 6523). Rio Grande do Sul: Camaquã (30°51'S, 51°48'W; AMNH 235863, 235864, 235865, 235866, 235867, 235868, 235869, 235870, 235871, 235872, 235873, 235874, 235875, 235876, 235877, 235878, 235879, 235880, 235881). Rio Grande do Sul: Harmonia (31°19'S, 52°17'W; AMNH 235892).

Rio Grande do Sul: São Leopoldo (29°45'S, 51°09'W; DZSJRP 10393). Rio Grande do Sul: Taim (32°33'S, 52°34'W; DZSJRP 14548, 14549, 14550, 14552, 14553, 14554, 14555). Santa Catarina: Passos Maia (26°47'S, 52°02'W; CCMZ-DZUP 333, 334, 335, 336). São Paulo: Boracéia: Estação Biológica de Boracéia (22°10'S, 48°44'W; MZUSP 15224, 15225, 15273, 15274, 15304, 15305, 15306, 15307, 15308, 15309, 15358, 27491). São Paulo: Cacequá (23°30'S, 46°29'W; MZUSP 3167). São Paulo: Cananéia: Ilha do Cardoso (25°00'S, 47°57'W; MZUSP 27680, 27976). São Paulo: Casa Grande (23°42'S, 46°35'W; MZUSP 16473, 16474, 16475, 16476, 16477, 16478, 16479, 16480, 16481, 16482, 16483, 16484, 16485, 16486, 16487, 16488, 16489, 16490, 16491, 16492, 16493, 16494, 16495, 16496, 16497, 16498, 16499, 16500, 16501, 16502, 16503, 16504, 16505, 16506, 16507, 16508, 16509, 16510, 16477). São Paulo: Itapeva (23°58'S, 48°53'W; DZSJRP 11364, 11365). URUGUAY: Lavalleja: Piraraja (31°49'S, 55°58'W; AMNH 205477, 205478, 205503, 205504, 205505, 205508, 205509, 205510, 205511, 205512, 205513, 205514, 205515). Colón (34°48'S, 36°14'W; USNM 252599). Tacuarembó: Arroyo Yaguari (31°52'S, 55°13'W; MZUSP 28979, 28981). Unknown locality (MZUSP 10084, USNM 102588, 102589, 102590).

***Myotis nesopolus***: VENEZUELA: Falcón: Capatárida (11°10'N, 70°37'W; USNM 441711, 441728, 441735, 441736, 441737, 441740). Lara: Rio Tucuyo (10°07'N, 69°51'W; USNM 441710). Zulia: Cojoro (11°38'N, 71°50'W; USNM 441721).

***Myotis nigricans***: BOLIVIA: Cochabamba: Chapare (17°05'S, 65°59'W; AMNH 211214\*, 211215\*, 211216\*, 211217\*, 211218\*, 211219\*, 211220\*, 211221\*, 211222\*, 211223\*, 211226\*, 211227\*, 211228, 211229, 211243\*, 211244\*, 211245\*, 211246). Santa Cruz: El Refugio: Parque Nacional Kempff Mercado (14°45'S, 61°02'W; USNM 584500, 584501). BRAZIL: Amazonas (03°46'S, 66°25'W; MZUSP 6091). Mato Grosso do Sul: Pantanal (21°58'S, 57°55'W; CCMZ-DZUP 170, 172, 174, 176, 177). Mato Grosso do Sul: Rio Brilhante (21°47'S, 54°42'W; DZSJRP 12220). Mato Grosso do Sul: Unknown locality (CCMZ-DZUP 170\*, 172\*, 174\*, 176\*, 177\*). Minas Gerais: Caxambu (21°58'S; 44°56'W; ALP 2182). Minas Gerais: Pains (20°22'S, 45°39'W; USNM 391131). Minas Gerais: Sete Lagoas (19°28'S, 44°14'W; USNM 391129). Minas Gerais: Viçosa (20°45'S, 43°19'W; USNM 391132, 391133, 391135). Paraná: Matinhos (25°48'S, 48°32'W; CCMZ-DZUP 141\*, 142\*, 144\*, 148\*). Paraná: São José dos Pinhais (25°32'S, 49°45'W; CCMZ-DZUP 428). Rio de Janeiro: Seropédica: Serra do Caçador (22°51'S, 43°46'W; ALP 2284, 2290). Rio de Janeiro: Piraí: Estação Ecológica de Piraí (22°38'S, 43°54'W; ALP 4587, 4783). Rio de Janeiro: Rio de Janeiro: Alto da Boa Vista (22°58'S, 43°15'W; ALP 3047\*, 3048\*, 3049\*, 3050\*). Rio de Janeiro: Seropédica: Universidade Federal Rural do Rio de Janeiro (22°45'S, 43°41'W; ALP 585\*, 588\*, 589\*, 625\*, 626\*, 627\*, 628\*, 629\*, 630\*, 631\*, 636\*, 639\*, 640\*, 655\*, 658\*, 904\*, 1396\*, 1826\*, 2862\*, 3427\*, 3428\*, 3498\*, 3499\*, 3581\*, 3697\*, 3703\*, 3705\*, 3715\*, 3716\*, 3718\*, 3723\*, 3740\*, 3741\*, 3742\*, 3744\*, 4815\*, 4816\*, 4817\*, 4819\*, 4825\*, 4827\*, 4839\*, 4844\*, 4906\*, 4930\*, 4931\*, 4938\*, 4939\*, 4940\*, 4943\*, 4944\*, 4947\*, 4949\*, 4950\*, 5012\*, 5017\*, 5020\*, 5032\*, 5033\*, 5034\*, 5036\*, 5037\*, 5040\*, 5043\*, 5044\*, 5045\*, 5068\*, 5074\*, 5075\*, 5089\*, 5090\*, 5092\*, 5094\*, 5095\*, 5097\*, 5098\*, 5102\*, 5103\*, 5105\*, 5130\*, 5131\*, 5132\*, 5134\*, 5171\*, 5172\*, 5173\*, 5174\*, 5175\*, 5176\*, 5179\*, 5180\*, 5181\*, 5185\*, 5186\*, 5187\*, 5188\*, 5235\*, 5327\*, 5331\*, 5332\*, 5338\*, 5340\*, 5341\*, 5342\*, 5344\*, 5346\*, 5347\*, 5348\*, 5349\*, 5350\*, 5499\*, 5501\*, 5504\*, 5510\*, 5511\*, 5520\*, 5521\*, 5523\*, 5525\*, 5543\*, 5592\*, 5593\*, 5594\*). Rio de Janeiro: Teresópolis: Parque Nacional da Serra dos Órgãos (22°26'S, 42°59'W; ALP 6479). Rio de Janeiro: Tinguá: Reserva Biológica do Tinguá (22°36'S, 43°26'W; ALP 2505\*, 2870\*, 6262\*, 6619\*, 6620\*, 6624\*, 6625, 6679, 6682). Rio Grande do Sul: Frederico Westphalen (27°21'S, 53°23'W; CCMZ-DZUP 338). Santa Catarina: Passos Maia (26°47'S, 52°02'W; CCMZ-DZUP 400). São Paulo: Botu-

catu: Edgardia (22°53'S, 48°27'W; ALP 2270, 2271). São Paulo: Fernando Prestes (21°15'S, 48°41'W; DZSJRP 13616, 13619). São Paulo: São José do Rio Preto (20°46'S, 49°23'W; DZSJRP 14979). São Paulo: São Sebastião (23°45'S, 45°24'W; USNM 141395\*, 141396\*, 141398\*, 141400\*, 141401\*, 141403\*, 141405\*, 141406\*, 141408\*, 141409\*, 141411\*, 141412\*, 141413\*, 141414\*). COLOMBIA: Magdalena: Bonda (10°08'N, 74°17'W; AMNH 14587). Nariño: Guayacona (USNM 309021, 309023). Nariño: Riquarte (USNM 309020). ECUADOR: Esmeraldas: Esmeraldas (00°56'N, 79°39'W; AMNH 33239). Esmeraldas: San Javier (01°04'N, 78°46'W; USNM 113343). Pichincha: Santo Domingo; 47 km S, Rio Palenque Science Center (00°10'S, 78°43'W; USNM 528566). Zamora-Chinchipe: Cumbaratza (03°59'S, 78°52'W; USNM 513488, 513489). Zamora-Chinchipe: Los Encuentros (03°45'S, 78°38'W; USNM 513490). Pambilar (USNM 113345, 113346). Paramba (USNM 113349). GUIANA: Upper Demerara-Berbice (05°40'N, 57°51'W; USNM 582351, 582352). PANAMÁ: Canal Zone: Barro Colorado Island (09°00'N, 79°31'W; USNM 296266, 296270, 296271, 296272, 296273). Darién: Boca de Cupe (USNM 306796). Darién: Jaque (08°09'N, 77°50'W; USNM 306796, 363085, 363086, 363087, 363088). Unknown locality (AMNH 18736). PARAGUAY: Boquerón: Parque Nacional Teniente Enciso (26°25'S, 56°11'W; USNM 555673, 555674). Paraguairí (USNM 115078, 115080). Paraguairí: Sapucay (26°05'S, 55°38'W; USNM 115073, 115089, 121477). Paraguairí: Ibcuy National Park (26°01'S, 56°49'W; USNM 531197). PERU: Amazonas: Cordillera Del Condor: Valle Rio Comaina (04°06'S, 78°24'W; USNM 581966, 581967). VENEZUELA: Amazonas: Boca Mavaca: 84 km SE Esmeralda (02°30'N, 65°14'W; USNM 405801). Amazonas: San Juan: Ayacucho, 25 km S (05°27'N, 67°38'W; USNM 409424, 409455). Apure: Nulita, 29 km SW Santo Domingo (07°19'N, 71°57'W; USNM 441722). Bolívar: Maripa (07°26'N, 65°09'W; USNM 17069). Carabobo: 10 km NW Urama (10°32'N, 68°23'W; USNM 373921\*, 373922\*, 373923\*, 373924\*, 373926\*, 373929\*, 373932\*, 373933\*, 373935\*, 373936\*, 373942\*, 373943\*, 373946\*, 373948\*, 373950\*). Monagas: San Agustín, 3 km NW Caripe (10°12'N, 63°32'W; USNM 409391\*, 409429, 409430\*, 409431\*, 409433\*, 409435\*, 409437\*, 409438\*). Trujillo (USNM 387708).

**Myotis oxyotus:** COLOMBIA: Nariño: El Guabo (01°10'N, 77°55'W; USNM 309019). ECUADOR: Chimborazo: Pallatanga (01°57'S, 78°55'W; USNM 513480). Pastaza: Mera (01°28'S, 78°08'W; USNM 548337, 548339). Pastaza: Mirador (USNM 513491, 513492, 513493, 513494). PERU: Cuzco: Iquente (USNM 195196). Cuzco: Santa Ana (12°52'S, 72°43'W; USNM 194452, 194453, 195141, 195147, 195149). Junín: Río Palca (11°08'S, 75°20'W; USNM 507204). VENEZUELA: Amazonas: Cerro Neblina: Camp VII (00°50'N, 65°58'W; USNM 560809, 560810, 560811). Mérida: Tabay, 4 km E (=La Mucuy) (08°36'N, 71°01'W; USNM 373919). 85 Km SE Bolívar: El Dorado (05°59'N, 61°26'W; USNM 387712).

**Myotis riparius:** BRAZIL: Mato Grosso: Cachoeira São Simão (12°42'S, 55°56'W; MN 3757). Mato Grosso do Sul: Paranaíba (19°41'S, 51°11'W; DZSJRP 12022). Pará: Altamira, 52 km SW (03°39'S, 52°22'W; USNM 549517, 549518). Pará: Belém: Utinga (01°27'S, 48°30'W; USNM 361782, 361786, 361788, 361789, 361790, 361791, 460139). Pará: Mocambo: Área de Pesquisas Ecológicas do Guamá (00°42'S, 55°54'W; ALP 1915, 2002, 2003, 2004, 2554, 2557, 2562, 2568, 2587, 2610, 2710). Rio de Janeiro: Macaé de Cima: Parque Estadual dos Três Picos (22°25'S, 42°31'W; JAO 1757). Rio de Janeiro: Piraí: Estação Ecológica de Piraí (22°38'S, 43°54'W; ALP 4573). Rio de Janeiro: Tinguá: Reserva Biológica do Tinguá (22°36'S, 43°25'W; ALP 4356, 4357, 5421, 6622, 6680, 6681). São Paulo: Buri (23°49'S, 48°36'W; MZUSP 32968, 32969, 32970). São Paulo: Juquitiba (23°56'S, 47°04'W; MZUSP 32963, 32964, 32966). São Paulo: São Paulo: Parque Estadual da Cantareira (23°26'S, 46°38'W; MZUSP 31466).

**Myotis ruber:** BRAZIL: Minas Gerais: Viçosa (20°45'S, 43°19'W; USNM 391138, 391139, 391140). Rio de Janeiro: Macaé de Cima: Parque Estadual dos Três Picos (22°23'S, 42°29'W; JAO 1751, 1756, 1773). Rio de Janeiro: Teresópolis: Parque Estadual da Serra dos Órgãos (22°26'S, 42°59'W; ALP 6452, 6457, 6458, 6497, 6499, 6506, 6512). Rio de Janeiro: Teresópolis (MN 3400). Rio de Janeiro: Tinguá: Reserva Biológica do Tinguá (22°36'S, 43°25'W; ALP 6621, 6623, 6683). Rio Grande do Sul: São Lourenço do Sul (22°26'S, 42°59'W; MZUSP 1298, 1988). São Paulo: Boracéia: Estação Biológica de Boracéia (22°10'S, 48°44'W; MZUSP 28359, 28367, 28368). São Paulo: Buri (23°49'S, 48°36'W; MZUSP 32971, 32972, 32973, 32975). São Paulo: Cananéia: Ilha do Cardoso (25°00'S, 47°57'W; MZUSP 27595). São Paulo: São Paulo: Ipirangua (23°35'S, 46°36'W; MZUSP 15254, 31470, 31471, 31472, 31473, 31971). Unknown locality (DZSJRP 17014).

**Myotis simus:** BOLÍVIA: Beni: Cercado: Rio Mamoré, ca. 23 km W San Javier (14°39'S, 64°39'W; AMNH 211155, 211156, 211167, 211168, 211169, 211170, 211171, 211172, 211173, 211174, 211178, 211179, 211180, 211181, 211182, 211183, 211190, 211192, 211193, 211194, 211195, 211196, 211197, 211198). Santa Cruz: El Refugio: Parque Nacional Kempff Mercado (14°45'S, 61°02'W; USNM 584502). BRAZIL: Amazonas: Borba: Madeira River (6°53'S, 52°02'W; AMNH 91886, 91887, 91888, 91889, 91890, 91891, 91892, 94224, 94225, 94227, 94230, 94231, 94232, 94233, 94234). Amazonas: Itacoatiara (03°08'S, 58°26'W; MZUSP 3472). Amazonas: Manaus: Negro River (01°04'S, 63°36'W; AMNH 79534, 91472, 91473, 91474, 91475, 91476, 91477, 91478, 91500). Amazonas: Parintins: Serra do Parintins (02°38'S, 56°44'W; AMNH 92983, 93489, 93490, 93491, 93492, 93493, 93494, 93495, 93496, 93497, 93922, 93923, 93924, 93925). Amazonas: Rio Juruá (04°48'S, 68°67'W; MZUSP 638, 1074). Mato Grosso: Taiaimã (16°48'S, 57°28'W; MZUSP 13815). Mato Grosso do Sul: Salobra (20°09'S, 56°31'W; ALP 9277). PERU: Loreto: Maynas: Apayacu, Amazon River (03°19'S, 72°07'W; AMNH 71483, 71485, 71486, 71487, 71488, 71490, 71491, 71492, 71493, 71494, 74105, 74109, 74110, 74378, 74379, 74380, 74381). Loreto: Ucayali: Sarayacu, Ucayali River (06°44'S, 75°06'W; AMNH 76240, 76241, 76242, 76243, 76244, 76245, 76246, 76247, 76248, 76249, 76252, 76253). Pasco: San Juan (10°30'S, 74°53'W; USNM 364481, 364482).

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