

A new species of *Myotis* (Chiroptera, Vespertilionidae) from Uruguay

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Abstract

The genus *Myotis* comprises a diverse group of vesper bats with worldwide distribution. Twenty-eight neotropical species are currently recognized. Based on a morphological approach, we describe a new species of *Myotis* from the Uruguayan Pampas grasslands, an ecoregion under high anthropogenic pressure with a largely unknown bat fauna. Qualitative and quantitative morphological analyses support the recognition of the new species and we present a set of external and cranial diagnostic characters by comparing them with other neotropical *Myotis* species. The new species reassembles *Myotis riparius*, but can be distinguished by a set of qualitative and quantitative morphological traits, including its clearly bicolored dorsal fur, tricolored ventral fur, a pelage on the dorsal surface of uropatagium, sagittal crest lower, braincase lower in lateral view and overall smaller size.

Keywords

Morphology, Myotinae, pampa grassland, South America, taxonomy

Introduction

Myotis Kaup, 1829 comprises a diverse and worldwide distributed genus of vesper bats with ca. 140 species recognized (Moratelli et al. 2019a, b; MDD 2021). Despite the high diversity, species have reduced phenotypic variation and conspicuously conserved morphology compared to most of the other genera of vesper bats (Gunnell et al. 2012; Moratelli et al. 2019a). Therefore, *Myotis* is among the most difficult genera of bats to delimit species based on morphology only. However, several neotropical species whose evidence was based solely on morphology have

been confirmed by subsequent molecular assessments, such as the cases of *Myotis lavalii* Moratelli, Peracchi, Dias & Oliveira, 2011 from the South American dry Diagonal, and *Myotis larensis* LaVal, 1973 from Venezuela (Moratelli et al. 2017; Novaes et al. 2021). Even *Myotis diminutus* Moratelli & Wilson, 2011, whose description was based on one subadult individual, was confirmed as a distinct lineage based on molecular evidence (Platt et al. 2018).

New World *Myotis* form a monophyletic group divided into two clades with strong biogeographic associa-

tions, one Nearctic and the other predominantly Neotropical (Stadelmann et al. 2007). Based on the congruence between molecular and morphological data, Moratelli et al. (2019a) recognized four groups of species. Among them, the lucifugus and vivesi groups are restricted to the Nearctic region; the albescens-group is predominantly neotropical, but with a few nearctic species; and the ruber-group is restricted to the Neotropics.

Currently, 28 species of *Myotis* are recognized from the Neotropics (Moratelli et al. 2019a, 2019b; Carrión-Bonilla and Cook 2020; Novaes et al. 2021). However, phylogenetic studies have identified at least 35 independent evolutionary lineages and paraphyletic species, showing that at least 20% of the diversity of neotropical *Myotis* comprise undescribed species (Clare et al. 2007; Larsen et al. 2012; Chaverri et al. 2016), which is also supported by systematic reviews based on morphological data (e.g., Moratelli et al. 2011; Moratelli and Wilson 2014; Novaes et al. 2018, 2021).

Currently, the ruber-group is composed of eight species restricted to the Neotropics: *M. ruber* (É. Geoffroy, 1806), *M. simus* Thomas, 1901, *M. keaysi* J.A. Allen, 1914, *M. riparius* Handley, 1960, *M. elegans* Hall, 1962, *M. pilosatibialis* LaVal, 1973, *M. midastactus* Moratelli & Wilson 2014, and *M. armiensis* Carrión-Bonilla & Cook, 2020 (Moratelli et al. 2013, 2019a; Carrión-Bonilla and Cook 2020). However, morphological and molecular evidence indicate that the species diversity in the ruber-group may be underestimated (Clare et al. 2011; Moratelli and Wilson 2014; Novaes et al. 2017; Carrión-Bonilla and Cook 2020).

During a taxonomic revision of neotropical *Myotis*, we identified a sample of 15 specimens from the Uruguayan Pampa grasslands with a unique set of qualitative and quantitative characters that distinguish them from all South American congeners currently recognized. Based on the morphological discontinuity, we hypothesize that this sample comprises a new species, which we describe and compare with neotropical congeners.

Methods

This research is part of a critical review of neotropical *Myotis*, and material examined comprises more than 7,500 specimens covering all neotropical species currently recognized, including their primary types, and comparative series from different localities. The 15 specimens from the Uruguayan Pampa grasslands that represent the putative new species were collected in 1963, and are deposited at the American Museum of Natural History, USA. Due to the absence of fresh tissue samples or DNA sequences available in biological collections and DNA libraries, respectively, we restricted our analyses to qualitative and quantitative morphological comparisons.

Comparative analyses were based on 15 specimens of the putative new species of *Myotis* from Uruguay, and other 720 specimens from 15 neotropical *Myotis* species

deposited in 19 scientific collections from Argentina, Brazil, Canada, France, Switzerland, and United States (Appendix 1). Species selected for comparisons include all species in the ruber-group (*M. armiensis*, *M. elegans*, *M. keaysi*, *M. midastactus*, *M. pilosatibialis*, *M. riparius*, *M. ruber*, *M. simus*), and those representing the albescens-group that occur in the Southern Cone (*M. albescens*, *M. chiloensis*, *M. dinellii*, *M. izecksohni*, *M. lavalii*, *M. levis*, and *M. nigricans*).

The intra and interspecific morphological variation was evaluated from qualitative and quantitative analyses based on adults (classified as such based on closed epiphyses; see Brunet-Rossini and Wilkinson 2009). Qualitative traits employed here to characterize and distinguish species follow Moratelli et al. (2013) and Novaes et al. (2021). Capitalized color nomenclature follows Ridgway (1912).

External measurements, including the total length (TL), tail length (TL), hind foot length (HF), ear length (EL), and body mass (BM), were recorded from skin labels, and reported to the nearest millimeter and to the nearest gram. Cranial and other external dimensions were taken using digital calipers accurate to 0.01 mm, including: forearm length (FA), length of dorsal fur (LDF), length of ventral fur (LVF), greatest length of skull (GLS), condylo-canine length (CCL), condylobasal length (CBL), condylo-incisive length (CIL), basal length (BAL), zygomatic breadth (ZB), mastoid breadth (MAB), braincase breadth (BCB), interorbital breadth (IOB), postorbital breadth (POB), breadth across canines (BAC), breadth across molars (BAM), maxillary toothrow length (MTL), length of the upper molars (M1–3), mandibular length (MAL), and mandibular toothrow length (MAN). These measurements are described in Table 1.

Discriminant Function Analysis (DFA), performed in the R software (R Development Core Team 2008), with the Mass (Venable and Ripley 2002) and Lattice (Sarkar 2008) packages, was used in order to characterize and discriminate samples. We selected a subset of the cranial dimensions (GLS, CIL, MAB, BCB, POB, IOB, BAC, BAM, MTL, M1-3, MAN, MAL) representing different axes of length and width of skull, rostrum, and mandible. Multivariate analyses require complete datasets, thus, the missing values (< 5% of total dataset) were estimated from the existing raw data using the Amelia II package (Honaker et al. 2011) implemented in R software. Measurements were transformed to natural logs and covariance matrices were computed considering all variables. DFA was run with 15 selected individuals of *M. riparius*, *M. ruber*, and *Myotis* sp. nov. from Uruguay, considering that these species have similar morphology and occurs in the Southern Cone.

Results

The sample from Uruguay that represents the putative new species (hereafter referred as *Myotis* sp. nov. from Uruguay) can be distinguished from all South American congeners,

Table 1. External and craniodental measurements taken from *Myotis* specimens.

Measurement and acronym	Description
Forearm length (FA)	From the elbow to the distal end of the forearm including carpal
Third metacarpal length (3MC)	From the proximal to the distal extremity of the third metacarpal
Ear length (Ear)	From the base to the apex of the ear
Length of dorsal fur (LDF)	Measured at the midpoint of the scapulae
Length of ventral fur (LVF)	Measured at the midpoint of the sternum
Greatest length of skull (GLS)	From the apex of the upper internal incisors, to the occiput
Condylo-canine length (CCL)	From the anterior surface of the upper canines to the occipital condyles limit
Condylo-basal length (CBL)	From the premaxillae to a line connecting the occipital condyles
Condylo-incisive length (CIL)	From the apex of upper internal incisors to the occipital condyles limit
Basal length (BAL)	Least distance from the apex of upper internal incisors to the ventral margin of the foramen magnum
Zygomatic breadth (ZYG)	Zygomatic breadth
Mastoid breadth (MAB)	Greatest breadth across the mastoid region
Braincase breadth (BCB)	Greatest breadth of the globular part of the braincase
Postorbital breadth (POB)	Least breadth across frontals posterior to the postorbital bulges
Interorbital breadth (IOB)	Least breadth between the orbits
Breadth across canines (BAC)	Greatest breadth across outer edges of the crowns of upper canines, including cingulate
Breadth across molars (BAM)	Greatest breadth across outer edges of the crowns of upper molars
Maxillary toothrow length (MTL)	From the upper canine to M3
Molariform toothrow length (M1-3)	From M1 to M3
Mandibular length (MAL)	From the mandibular symphysis to the condyloid process
Mandibular toothrow length (MAN)	From the lower canine to m3

Table 2. External and craniodental measurements of *Myotis* sp. nov. from Uruguay (including holotype abd paratypes), *M. riparius* and *M. ruber* including morphometric variation and sample size (*N*). The measurements are in millimeters. Acronyms and descriptions are available in Table 1.

Meas.	<i>M. sp. nov.</i> AMNH 205471 (holotype)	<i>M. sp. nov.</i>	<i>M. riparius</i>	<i>M. ruber</i>
		Uruguay (paratypes) mean (max–min) <i>N</i>	Panama + Amazon mean (max–min) <i>N</i>	Brazil + Southern Cone mean (max–min) <i>N</i>
FA	35.7	35.1 (33.8–36.3) 15	36.3 (34.0–39.2) 38	39.8 (37.3–42.0) 42
3MC	34.3	32.8 (31.0–34.3) 15	33.5 (31.5–36.1) 38	36.5 (34.7–39.0) 42
EL	13.0	13.0 (12.0–14.0) 15	12.9 (11.6–14.0) 38	14.4 (13.0–15.5) 35
LDF	7.3	7.8 (7.2–8.8) 14	6.8 (5.8–7.7) 21	7.6 (7.0–8.0) 20
LVF	5.9	6.1 (5.1–7.4) 14	5.3 (4.6–6.5) 21	6.0 (4.0–6.5) 20
GLS	13.8	13.9 (13.4–14.4) 15	13.8 (12.8–14.5) 38	14.9 (14.2–15.3) 40
CCL	12.2	12.2 (11.8–12.8) 15	12.4 (11.3–13.1) 38	13.4 (12.9–13.7) 40
CBL	12.9	12.8 (12.4–13.3) 15	13.0 (11.8–13.8) 38	14.1 (13.3–14.5) 40
CIL	13.1	13.1 (12.7–13.5) 13	13.3 (12.1–14.0) 38	14.9 (14.2–15.3) 40
BAL	11.6	11.6 (11.2–11.9) 13	11.9 (10.8–12.5) 38	12.9 (12.3–13.3) 40
ZYG	8.8	8.7 (8.6–9.0) 8	9.0 (8.5–9.5) 13	9.3 (8.0–9.9) 26
MAB	7.1	7.2 (7.0–7.5) 12	7.2 (6.7–7.6) 38	7.7 (7.0–8.2) 40
BCB	6.5	6.6 (6.3–6.8) 15	6.4 (6.1–6.8) 38	6.9 (6.6–7.2) 40
POB	3.6	3.5 (3.3–3.7) 15	3.5 (3.1–3.8) 38	3.8 (3.5–4.0) 40
IOB	4.7	4.6 (4.3–4.8) 15	4.6 (4.3–5.1) 38	5.1 (4.6–5.4) 40
BAC	3.6	3.7 (3.6–3.8) 15	3.8 (3.5–4.1) 38	4.2 (3.9–4.6) 40
BAM	5.5	5.5 (5.4–5.7) 15	5.7 (5.3–6.0) 38	6.1 (5.8–6.3) 40
MTL	5.2	5.2 (4.9–5.4) 14	5.3 (4.7–5.6) 38	5.9 (5.5–6.2) 40
M1–3	2.9	2.9 (2.8–3.0) 14	3.0 (2.7–3.2) 38	3.3 (3.1–3.4) 40
MAL	10.1	10.0 (9.6–10.3) 9	10.2 (9.3–10.8) 35	11.0 (10.3–11.3) 40
MAN	5.6	5.5 (5.3–5.7) 9	5.6 (5.0–6.0) 35	6.4 (5.9–6.0) 40

except *M. riparius* and *M. ruber*, by the following set of traits: small to medium sized species (FA 33.8–36.3 mm; GLS 13.4–14.6 mm); comparatively long wooly dorsal fur subtly bicolored; skull with very low sagittal crest and

braincase roof not inclined forward. Although *M. ruber* has a overall larger size than *Myotis* sp. nov from Uruguay (Table 2), the smallest specimens of *M. ruber* may resemble the largest specimens of *Myotis* sp. nov.



Figure 1. Lateral, dorsal and ventral views of skulls of *Myotis* sp. nov. from Uruguay (AMNH 205471 [holotype]), *Myotis riparius* from Panama (USNM 310255 [holotype]), and *Myotis ruber* from Paraguay (USNM 115097 [neotype]). The images of the mandibles of *M. riparius* and *M. ruber* are inverted.

Myotis sp. nov. from Uruguay can be confused with *M. riparius* and *M. ruber*. However, it can be distinguished by the presence of a fur formed of scattered hairs on the dorsal surface of uropatagium that does not extend beyond the level of the knees; narrower and elongated skull, with less robust appearance; sagittal crest lower; mastoid processes comparatively narrower and practically not visible in dorsal view; braincase lower in lateral view; and posterior region of the braincase more rounded and well projected beyond the posterior limit of the occipital condyles (Fig. 1). *Myotis* sp. nov. from Uruguay has bicolored dorsal fur, with a grayish-brown base and reddish tip, with a burned aspect (Fig. 2). The ventral fur is tricolored, which is unique among neotropical *Myotis*, with medium-brown base, middle portion light gray, and yellowish tip. Analyzing the type series of *Myotis riparius*, the dorsal fur is unicolored medium or reddish-brown, whereas the ventral fur is bicolored, with dark-brown bases and pale-yellow tips (Fig. 2). *Myotis ruber* has a reddish dorsal fur with a slightly darker base, while

the venter is bicolored, with medium-brown base and bright-yellow tip (Fig. 2).

In the DFA, the 1st discriminant function, more related with the skull size, represented 93% of the total variation, whereas the 2nd discriminant function, more related with the skull shape, represented 7% (Fig. 3). Along the 1st axis, *M. riparius* and *M. sp. nov.* overlapped, indicating similar skull sizes, and both do not overlap with *M. ruber* (Fig. 3). *Myotis* sp. nov. from Uruguay and *M. riparius* were retrieved with full overlap along the first axis (related to skull size), but there was a partial segregation of these taxa along the second axis (more related to skull shape). This analysis relied mainly on measurements related to skull and mandibular length, and braincase breadth (Figure 3). Linear measurements reveal that *Myotis* sp. nov. is slightly smaller than *M. riparius* in relation to both skull and external measurements and consistently smaller than *M. ruber* (Table 2).

The set of qualitative morphological characters and the partial distinction of the skull shape evidenced by the



Figure 2. Dorsal and ventral views of the skins of *Myotis* sp. nov. from Uruguay (AMNH 205471 [holotype]), *Myotis riparius* from Panama (USNM 310255 [holotype]), and *Myotis ruber* from Paraguay (USNM 115097 [neotype]).

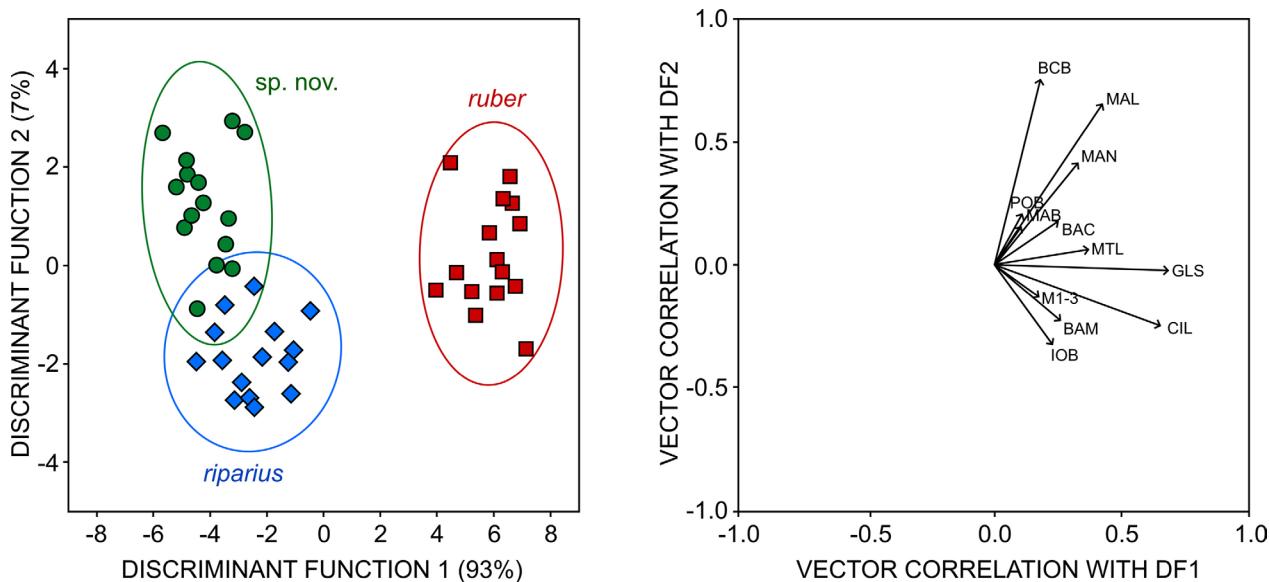


Figure 3. Plots of multivariate individual scores in the 1st 2 discriminant axes (left). Corresponding vector correlations of cranio-metric characters with the 1st 2 eigenvectors (right). Samples: *Myotis* sp. nov. from Uruguay (green dots), *M. riparius* from Panama and Colombia (blue diamonds), and *M. ruber* from Brazil and Paraguay (red squares).



Figure 4. Dorsal (upper left), ventral (upper right), and lateral (lower) views of the skull and mandible of *Myotis pampa* holotype (AMNH 205471) from the Uruguayan Pampas.

DFA support the full distinction of *Myotis* sp. nov. from Uruguay compared to their more similar congeners and other South American *Myotis*. We present here the description of the new species from the Uruguayan Pampas, including a morphological diagnosis and comparisons with the other neotropical *Myotis* species.

Family Vespertilionidae Gray, 1821

Subfamily Myotinae Tate, 1942

Genus *Myotis* Kaup, 1829[†]

Subgenus *Pizonyx* Miller, 1906

Myotis pampa, sp. nov.

<http://zoobank.org/625C3200-0AA6-4611-868A-3C21A628C71F>

Holotype. The holotype (AMNH 205471) comprises the skin and skull of an adult female (Figs. 4–5), collected by M. D. Tuttle in January, 1963. The specimen is deposited in the mammal collection at the American Museum of Natural History (New York, USA).

Type locality. Ca. 6 km NW from Belén, Artigas, Uruguay (30°37'S; 57°50'W; 32 m elevation).

Paratypes. Five individuals from ca. 6 km NW from Belén, Artigas, Uruguay (30°37'S; 57°50'W, 32 m of elevation; AMNH 205461 ♀, AMNH 205464 ♀, AMNH 205467 ♀, AMNH 205472 ♀, AMNH 205476 ♀); and nine individuals from 40 km NW to Tacuarembó city, Tacuarambó, Uruguay (31°38'S; 56°19'W, 240 m of elevation; AMNH 205541 ♀, AMNH 205545 ♀, AMNH 205546 ♂, AMNH 205552 ♂, AMNH 205553 ♀, AMNH 205562 ♀, AMNH 205563 ♂, AMNH 205564 ♀, AMNH 205565 ♂).

Distribution and habitat. Known from only two localities in the provinces of Artigas and Tacuarembó, Uruguay (Fig. 6). The records come from the Uruguayan Pampas, between 30 and 240 m in altitude. The region is characterized by grassland plains with shrubby vegetation patches typical of subtropical landscapes. However, the margins of rivers can present denser riparian forests, with arborescent ferns, orchids, lianas and several trees with more than 10 m in height (Sganga 1994; Panario et al. 2011). According to information available on museum labels, most individuals were captured with mist-nets near watercourses.

Etymology. We name *Myotis pampa* after the Pampas ecoregion, the main habitat occurrence for the species. Pampa is a Quechua word for “plain”, and in Latin languages it is used in the masculine gender, which agrees with the generic name *Myotis*, also masculine (ICZN 1958; Pritchard 1994).

Diagnosis. The tricolored ventral fur, with a Drab basal band, Smoke Gray middle band, and yellowish (generally Naples Yellow) tip is unique among South American *Myotis*. In addition, the following set of traits distinguishes *Myotis pampa* from all its South American congeners: small to medium sized species (FA 33.8–36.3 mm; sagittal crest absent or very low; elongated skull (GLS 13.4–14.4 mm); braincase not inflated and low in profile; braincase roof formed by the parietal bone strongly straight and not inclined forward; frontal bone steeply sloped towards the rostrum; posterior region of the braincase rounded and projected beyond the limit of the occipital condyles; mastoid processes narrower and practically not visible in dorsal view; dorsal fur notably long (7–9 mm), woolly and bicolored, with tips Dresden Brown or paler Ochraceous-Tawny, and bases brownish-gray (giving a fuliginous aspect); ventral fur moderately long (6–7 mm); legs and dorsal surface of the uropatagium covered by scattered fur that extends up to the knees; plagiopatagium inserted into the foot by a broad band of membrane.

Morphological description and comparisons. *Myotis pampa* is a small to medium species of *Myotis* (FA 33.8–36.3 mm; other measurements in Table 2) and the fur texture (woolly) and cranial morphology (broad skull with sagittal and lambdoidal crests presents) resembles species allocated to the ruber-group (q.v., Moratelli et al. 2013, 2019a). Ears are Mummy Brown and comparatively medium sized (EL 11–14 mm), reaching the portion of the rostrum between the eyes and nostrils when extended forward. Tragus is long and slender, with a wide base and



Figure 5. Skin in dorsal (left) and ventral (right) views of the holotype of *Myotis pampa* (AMNH 205471) from the Uruguayan Pampas.

a narrower spear-shaped terminal half, almost straight anterior edge, and rounded tip. Membranes are Mummy Brown; the dorsal surface of tibia, and uropatagium has scattered hairs extending to the level of the knees. The uropatagium lacks the fringe of hairs along the trailing edge. The plagiopatagium is attached to the foot at the level of the toes by a broad band of membrane.

Dorsal and ventral fur are wooly and long (LDF 7–9 mm, LVF 6–7 mm). The dorsal pelage is bicolored with brownish-gray bases (3/4 of the total fur length) and reddish tips (1/4 of the total fur length), ranging from Dresden Brown to paler Ochraceous-Tawny. The dorsal fur has a coloration that looks like the bat is partially covered by soot and with the tip of the hairs burned. The ventral fur is tricolored, with Drab bases (1/4 of the total fur length) progressively turning Smoke Gray in the middle band (2/4 length) and light-yellow tips (1/4 [ranging from Naples Yellow to Cream-Buff]). The tricolored ventral fur is unique among all South American *Myotis* species (Fig. 2). However, this pattern may be less evident in some lighter specimens, where the coloration of the middle band may be confused with the tip band of the hairs.

Dental formula is I 2/3, C 1/1, PM 3/3, M 3/3 = 38, typical of all New World species of *Myotis*. Skull delicate and medium-sized in length (GLS 13.1–14.1 mm), resembling *Myotis* of the ruber-group species. The 2nd upper premolar (P3) is in the toothrow, not displaced to the

lingual side and smaller than first upper premolar (P2). The 1st lower molar (m1) is myotodont, with the postcristid connecting hypoconid and entoconid. Braincase delicate and elongated; sagittal crest and lambdoidal crests are absent or very low; the occipital region is rounded and projects beyond the posterior limits of the occipital condyles; mastoid processes weakly developed. Frontal bone slightly sloping; rostrum comparatively short and narrow.

Considering species from the ruber-group (*armiensis*, *elegans*, *keaysi*, *midastactus*, *moratellii*, *pilosatibialis*, *riparius*, *ruber*, *simus*), and species from the albescens-group in the South American southern cone (*albescens*, *chiloensis*, *dinellii*, *izecksohni*, *lavalii*, *levis*, *nigricans*), *M. pampa* can be distinguished from all by the set of diagnostic traits reported above.

These specimens of *M. pampa* were originally identified as *M. riparius* and this identification was maintained by LaVal (1973) and López-González et al. (2001). In fact, *M. pampa* resembles *M. riparius*, but it can be distinguished by its smaller skull (GLS < 14.4 in *pampa* and generally > 14.5 mm in *riparius*), braincase lower in lateral view, sagittal crest lower (Fig. 1), longer and bicolored dorsal fur with grayish base, tricolored ventral fur (Fig. 2), and presence of scattered hairs along the leg and dorsal surface of the uropatagium. *Myotis riparius* have a higher braincase in lateral view, sagittal crest well-developed, shorter and unicolored dorsal fur, bicolored ventral

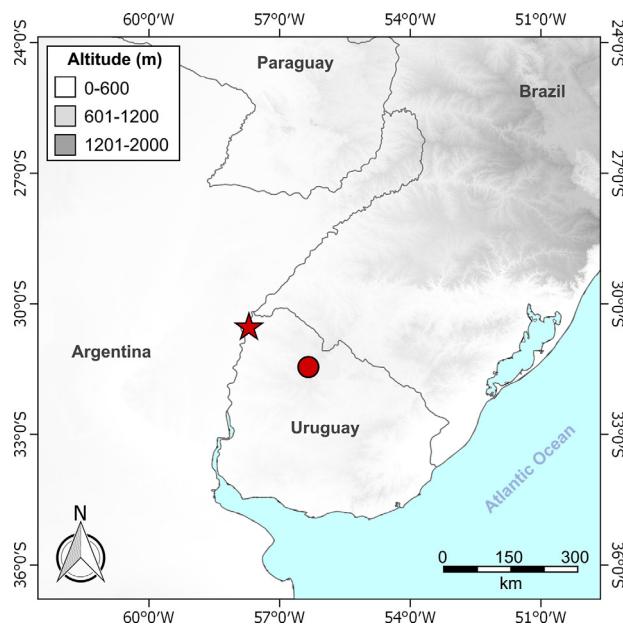


Figure 6. Map with localities of occurrence for *Myotis pampa*, including the type locality (red star).

fur and absence of scattered hairs along the leg and dorsal surface of the uropatagium.

Myotis pampa can also be confused with *M. ruber*, but it can be easily distinguished by its smaller size (both external and cranial; FA > 37.5 mm and GLS > 14.0 mm in *M. ruber*), skull more delicate, braincase lower in lateral view, mastoid processes less developed, dorsal fur longer and clearly bicolored with grayish base (unicolored in *ruber*), tricolored ventral fur (bicolored in *ruber*), and presence of scattered hairs along the leg and dorsal surface of the uropatagium (absent in *ruber*).

Myotis pampa differs from *M. armiensis*, *M. keaysi*, and *M. pilosatibialis* by its external smaller size (FA > 36 mm in *M. armiensis* and *M. keaysi*), more delicate skull, braincase lower in lateral view, sagittal crest lower, mastoid processes less developed, dorsal fur longer and clearly bicolored with grayish base, tricolored ventral fur, and pelage on the dorsal surface of the uropatagium composed of scattered hairs not extending beyond the knees. It differs from *M. elegans* by larger size in general (both external and cranial; FA < 34.5 mm, GLS < 13.0 mm, and BCB < 6.3 mm in *elegans*), skull more robust in general, parietal bone not inclined forward, rostrum longer, dorsal fur clearly bicolored with grayish base, ventral fur tricolored. *Myotis pampa* can be easily distinguished from *M. simus* and *M. midastactus* by its smaller size (generally FA > 36 mm and GLS > 13.5 mm in *M. simus* and *M. midastactus*), more delicate and narrower skull (BCB < 6.8 in *pampa* and > 6.8 in *simus* and *midastactus*), dorsal fur longer and clearly bicolored, ventral fur tricolored, dorsal surface of the uropatagium covered by scattered hairs that extend up to the knees; plagiopatagium inserted into the foot by a broad band of membrane.

In comparison to species from the albescens-group, *M. pampa* can be distinguished from *M. albescens*, *M. dinellii* and *M. levis* by the absence of a fringe of hairs on the posterior margin of the uropatagium, reddish dorsal fur

bicolored with grayish base, and braincase less inflated. In addition, *M. pampa* differs from *M. dinellii* and *M. levis* by its generally smaller size and comparatively shorter ears. It differs from *M. izecksohni* and *M. nigricans* by the braincase less inflated and reddish dorsal fur clearly bicolored with grayish base. *Myotis pampa* can be distinguished from *M. chiloensis* from its smaller size in general, skull lower in lateral view, braincase less inflated, dorsal fur shorter and bicolored, with grayish bases and reddish tips. It differs from *M. lavalii* by its second upper premolar (P3) smaller than first upper premolar (P2), and by its reddish fur with grayish bases (being blackish bases in *M. lavalii*). In addition, *M. pampa* can be distinguished of all species from the albescens-group by its wooly fur (silky in albescens-group species), ventral fur tricolored, and fur composed of scattered hairs on dorsal surface of the uropatagium.

Discussion

The specimens used for the description of *M. pampa* were collected in 1963 during two expeditions in the Uruguayan Pampas, remaining identified as *M. riparius* for more than half a century. This highlights the importance of taxonomic studies based on the review of specimens in museums for the knowledge of the species diversity on Earth.

Myotis pampa occurs near the boundaries of Uruguay with Brazil (Rio Grande do Sul) and Argentina (Entre Ríos) and although individuals from grasslands of these two countries have not been examined, it is likely that the occurrence of *M. pampa* will extend to outside the political boundaries of Uruguay. We believe that *M. pampa* is endemic to the Pampa ecoregion, inasmuch as our taxonomic review of *Myotis*—which comprises more than 7,500 specimens examined—did not find evidence of the species in other South American ecoregions. If our hypothesis is correct, it is possible that *M. riparius* (sensu Novaes et al. 2017), does not occur in the Pampa grassland plain.

The localities where *M. pampa* occur are within the Pampas biome, an ecoregion with high biological diversity, with more than 3,000 species of plants, ca. 90 species of amphibians, 160 species of reptiles, 100 species of mammals, and more than 100 species of birds, including a very high rate of endemism (Pillar et al. 2016). However, it remains as one of the least studied ecoregions in relation to the bat fauna (Bernard et al. 2011). Currently, the Pampas has suffered from the intensification of agricultural production, such that at least 30% of the entire biome has been converted into pastures and agricultural areas and there are very few protected areas (Overbeck et al. 2007; Pillar et al. 2016; Achka 2017; Botto-Nuñez et al. 2019; Souza et al. 2020). Although it is premature to determine the conservation status of *M. pampa*, this possibly endemic species should be monitored due to the anthropogenic pressure.

The present taxonomic revision indicates the unequivocal occurrence of three *Myotis* species for Uruguay: *M. albescens*, *M. levis*, and *M. pampa*. All specimens of *M.*

riparius from Uruguay analyzed in the present study were re-identified as *M. pampa* and, therefore, there is no evidence of the occurrence of this species in the Uruguayan Pampas. Recent literature points to the occurrence of *M. nigricans* in Uruguay (Achaval et al. 2007; González and Martínez-Lanfranco 2010; Botto-Nuñez et al. 2019). *Myotis nigricans* has been considered a species complex with a taxonomic puzzle far from being solved (e.g., Larsen et al. 2012; Moratelli et al. 2011, 2013, 2017, 2019a). In the present review, we did not identify any specimen that fit morphologically into what is known as the *M. nigricans* complex from southern Brazil and Southern Cone (sensu Moratelli et al. 2011). Likewise, we found no evidence of the occurrence of *M. ruber* in Uruguay and previous records (e.g., Acosta y Lara 1950) are due to misidentified specimens of *M. levis*, as also suggested by Botto-Nuñez et al. (2019). However, we do not rule out the possibility of the occurrence of other *Myotis* species in Uruguay, considering that (i) we did not have the opportunity to examine specimens deposited in Uruguayan collections (e.g., Museo Nacional de Historia Natural del Uruguay), and (ii) a large part of the territory does not have satisfactory samples for bats (González and Lessa 2014).

With the description of *M. pampa*, we recognized 23 *Myotis* species occurring in South America, including *M. albescens* (É. Geoffroy, 1806), *M. ruber* (É. Geoffroy, 1806), *M. nigricans* (Schinz, 1821), *M. levis* (I. Geoffroy, 1824), *M. chiloensis* (Waterhouse, 1840), *M. oxyotus* (Peters, 1866), *M. atacamensis* (Lataste, 1892), *M. simus* Thomas, 1901, *M. dinellii* Thomas, 1902, *M. caucensis* Allen, 1914, *M. keaysi* J.A. Allen, 1914, *M. riparius* Handley, 1960, *M. larensis* LaVal, 1973, *M. diminutus* Moratelli & Wilson, 2011, *M. lavalii* Moratelli et al., 2011, *M. izecksohni* Moratelli et al., 2011, *M. handleyi* Moratelli et al., 2013, *M. midastactus* Moratelli & Wilson, 2014, *M. clydejonesi* Moratelli et al., 2016, *M. attenboroughi* Moratelli et al., 2017, *M. bakeri* Moratelli et al., 2019, and *M. armiensis* Carrión & Cook, 2020.

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Appendix 1

Specimens examined in biological collections, as follows: Colección de Mamíferos Miguel Lillo, Universidad Nacional de Tucumán (CML, Tucumán, Argentina), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina), Coleção Adriano Lucio Peracchi da Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Brazil), Museu Nacional da Universidade Federal do Rio de Janeiro (MN, Rio de Janeiro, Brazil), Coleção Científica de Mastozoologia da Universidade Federal do Paraná (CCMZ-DZUP, Curitiba, Brazil), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil), Muséum National d'Histoire Naturelle (MNHN-Paris, France), Muséum d'Histoire Naturelle de la Ville de Genève (MHNG, Geneve, Switzerland), Royal Ontario Museum (ROM, Toronto, Canada), Amer-

Janeiro (MN, Rio de Janeiro, Brazil), Coleção Científica de Mastozoologia da Universidade Federal do Paraná (CCMZ-DZUP, Curitiba, Brazil), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil), Muséum National d'Histoire Naturelle (MNHN-Paris, France), Muséum d'Histoire Naturelle de la Ville de Genève (MHNG, Geneve, Switzerland), Royal Ontario Museum (ROM, Toronto, Canada), Amer-

ican Museum of Natural History (AMNH, New York, USA), Carnegie Museum (CM, Pittsburgh, USA), Field Museum of Natural History (FMNH, Chicago, USA), Museum of Natural History of the Kansas University (KU, Lawrence, USA), Los Angeles County Museum of Natural History (LACM, Los Angeles, USA), Museum of Zoology of the Louisiana State University (LSUMZ, Baton Rouge, USA), Museum of Vertebrate Zoology of the University of California (MVZ, Berkeley, USA), Museum of Texas Tech University (TTU, Lubbock, USA), Sam Noble Oklahoma Museum of Natural History (OMNH, Norman, USA), Smithsonian National Museum of Natural History (USNM, Washington D.C., USA). Asterisks indicate specimens used in the Discriminant Function Analysis.

Myotis albescens (N=79): Argentina: Corrientes, San Martín, La Higuera Cué (MACN 26850, 26856); Entre Ríos, Gualeguaychú (TTU 32543); Formosa, Pilcomayo (TTU 32521, 32522); Jujuy, Doctor Manuel Belgrano, Río Las Capillas, 15 km N Las Capillas, Ruta Provincial No. 20 (OMNH 27930); Jujuy, Santa Bárbara, Aguas Calientes (OMNH 34543); Salta, 6 km SW Santa Victoria (CM 42931, 42932); Salta, San Martín, 12 km W Piquirenda Viejo (CML 5108); Salta, Iyuya, Angosto del Río Pescado, apr. 3 km (MACN 26322); Santiago del Estero, Pellegrini, Santo Domingo (OMNH 23772, 23773, 23774; CML 3240); Tucumán, Sierras de Medina, Aguas Chiquitas (CM 42933); Tucumán, Alberdi, Escaba de abajo, casa abandonada a 300 m de hostería Eskay Apú (CML 10839); Tucumán, Granero (TTU 32523); Tucumán, La Cocha, Dique San Ignacio (OMNH 18877); Tucumán, Leales, 4 km N Bella Vista, Las Talas (OMNH 18878); Tucumán, Cola de Cadillal (OMNH 18879); Tucumán, Ticucho (OMNH 18880). Paraguay: Asunción (MZUSP 2024); Boquerón, Parque Nacional Teniente Enciso (USNM 555671); Canindeyú, Curuguaty (AMNH 234317, 234318, 234319, 234320, 234323, 234324, 234326, 234328, 234329, 234330, 234332, 234333, 234334, 234336); Cordillera, Tacuaral (USNM 105562, 105563, 105564, 105565, 105566, 105567, 105568, 105569, 105570, 105571, 105572, 105575, 105576, 105577, 105578, 105579, 105580, 105581, 105582, 105583, 105584, 105585, 105661, 105662, 105664); Paraguarí, Yaguarón (AMNH 205195). Uruguay: Artigas, ca. 6 km NW to Belén (AMNH 205454, 205456, 205458, 205459, 205460, 205462, 205463, 205465, 205466, 205468, 205469, 205470, 205473, 205474, 205475).

Myotis armiensis (N=14): Ecuador: Tungurahua, Baños (TTU 85060, FMNH 47593). Panama: Chiriquí, Cerro Punta (USNM 323599, 323600); El Volcán, 15.5 Km NW, Osta Clara (USNM 331919, 331922, 331942, 331943, 539888); Cuesta de Piedra (USNM 331953).

Myotis chiloensis (N=31): Argentina: Chubut, El Hoyo [de Epuyén] (CML 5218, MACN 16522–16527, MVZ 150842, 150847–150858); Chubut, El Bolsón, Río Negro (MHNG 1276-46, 1276-47, 1276-48, 1276-49, 1276-50); Neuquén, 19 km N Villa La Angostura along highway 234 (CML 3242); Neuquén, Estancia Chacabuco, 62 km SE San Martín de los Andes (MVZ 150868, 150869, 150883, 150884, 150892); Río Negro, Bariloche, Isla Victoria, 10 km al E de Piedras Blancas (CML 5219).

Myotis dinellii (N=73): Argentina: Buenos Aires, General Guido, Canal 2 y Ruta 2 (MACN 15740); Catamarca (CM 42934–42937); Catamarca, Trancas, 50 km NO Catamarca Ciudad, Las Juntas, Estancia de los Figueira (OMNH 18977–18979); Catamarca, Capayán, 6 km NW Chumbicha, Balneario El Caolin (OMNH 19366, 19367); Catamarca, Capayán, 1 km NW of Balneario by road, Chumbicha

(OMNH 23777–23782); Catamarca, Ambato, Estancia Narvaez, 5.5 km N Las Chacritas on Ruta Provincial No. 1 (OMNH 27931); Catamarca, Ambato, 21.4 km S Humaya (OMNH 36211); Catamarca, Tinogasta, 36.7 km W Fiambalá by road (OMNH 34545); Catamarca, Tinogasta, 57 km W Fiambalá by road (OMNH 34547); Catamarca, El Alto, Bella Vista (OMNH 36208); Catamarca, Capayán, 5.2 km NW Chumbicha (OMNH 36209, 36210); Catamarca, Andalgalá, Pucará (OMNH 36212, 36213); Córdoba (USNM 142560–142562); Córdoba, San Javier (TTU 32524, 32525, 32528, 32529); Córdoba, Calamuchita (TTU 64334); Córdoba, Cruz del Eje (TTU 64335, 64336); Córdoba, Río Cuarto (TTU 64337–64345, 66489, 66490, 66491); Córdoba, Pocho (TTU 66483–6488); Mendoza (MVZ 150861); La Pampa, Pampa Central, Caleu (MACN 49.163, 49.165); La Rioja, San Blas de los Sauces, 4 km SE de San Blas (CML 5439, 5444, 5448, 5449); Mendoza, Lavalle, Reserva Telteca (OMNH 23783); Salta, Guachipas, 25 km SE La Viña (OMNH 36214, 36217); Salta, San Carlos, Los Sauces (OMNH 36215); San Juan, Sarmiento, Pedernal (OMNH 23786); San Luis, Ayacucho, Quebrada de López, San Francisco del Monte de Oro (OMNH 23787); Tucumán (CM 42938–42942); Tucumán, La Cocha, Dique San Ignacio (AMNH 256987); Tucumán, Tafí Viejo, 5 km SW Simbón (OMNH 36216).

Myotis elegans (N=25): Costa Rica (KU 158651). El Salvador (ROM 101293, 101319). Honduras: Olanco (TTU 13299, 13345, 47926); Santa Barbara (TTU 13348); Atlántida (TTU 84138, 84380). Belize: Belize City (AMNH 256848); Mussel Creek (FMNH 58503, 121112). Mexico: Campeche, Escarcega (KU 93534), San Luis Potosí (TTU 8164); Chiapas, Carretera Arriaga-Tapachula (TTU 36157, 41147, 41148, AMNH 254674); Veracruz, Sontecomapan (KU 88398 [holotype], KU 93534, MVZ 167666, 167667). Guatemala: El Petén, Tikal National Park (FMNH 58585–58588), El Petén (ROM 99515, 99433).

Myotis izecksohni (N=48): Argentina: Misiones, San José, Apostoles, Parque Provincial de la Sierra, Chia. Toranco (CML 10200). Brazil: Rio de Janeiro, Tinguá, Reserva Biológica do Tinguá (ALP 6618, 6626, 6675, 6676, MN 74357, 74358); Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos (ALP 6450, 6498, 6501, 6513, 6524); Paraná, Balsa Nova, São Luis do Purunã (CCMZ-DZUP 196, 197, 198, 199, 200, 410, 419, 420, 421, 422); Paraná, Campinhos (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 (N=43): Argentina: Tucumán, Burruyacú (CML 6177, CML 7600, CML 8938, CML 9839, MACN 16795, MACN 16855, MACN 16857, OMNH 23499, 36207, TTU 32588). Bolivia: Cochabamba, Incachaca (CM 5256); La Paz (TTU 23951). Ecuador: Tungurahua, Pillaro, San Antonio (AMNH 67607). Perú: Puno, Inca Mines (AMNH 15814 [holotype]), Ocaneque (MVZ 116050); Cuzco, Cordillera Vilcabamba (AMNH 214371, 233850, 233851, 233853, 233854, 233857, 236134), Hacienda Cadena (FMNH 78686); Huánuco, 7 km por estrada NW Carpish Pass (AMNH 216117); Huánuco, Cordillera Carpish on Carretera Central (LSUMZ 12578, 12580, 14280, 14281, 14284, 14285, 14287, 14288); Pasco, Santa Cruz (LSUMZ 25907); Piura, 15 road km E Canchaque (LSUMZ 19213); Ayacucho, Puncu (LSUMZ 15688); Amazonas, ca. 20 km of La Peca by trail (LSUMZ 21488); Lambayeque, 16 km N and 25 km E Olmos (MVZ 135620, 135621); Junín, Chanchamayo (FMNH 65751). Venezuela: Mérida, Montes de Milla (MNHN-Paris 1984-685, 1984-686, 1984-689).

Myotis lavalii (N=55): Argentina: Salta, San Martín, 13 km al W de Piquirenda Viejo (CML 5051); Salta, 1 km al E de Tonono sobre río

Itiyuro (CML 5324); Santiago del Estero, Pellegrini, Santo Domingo (OMNH 23768, 23769, 23770, CML 5404, 5469, 5470, 5472). Brazil: Ceará, Crato, Floresta Nacional do Araripe (USNM 555713, 555714). Ceará, Crato, Itaitera (USNM 555715, 555716, 555717, 555718, 555720, 555721, 555722). Ceará, Russo (MN 3422, 3424); Pernambuco, 6 km of Exu (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 (MN 3405, 3406, 3410, 3412, 3415).

Myotis levis (N=47): Argentina: Buenos Aires, Lavalle (USNM 236236, 236237); Buenos Aires, Maipú (TTU 32555); Córdoba (USNM 252766); Entre Ríos, Puerto Constanza, Estancia El Tara (USNM 582461). Brazil: Minas Gerais, Mariana (MZUSP 1748). Minas Gerais, Ouro Preto (MZUSP 15344, 15345). Paraná, Palmas (CCMZ-DZUP 380); Rio de Janeiro, Nova Friburgo (MZUSP 2799); Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos (ALP 6481, 6523); Rio Grande do Sul: Camaquá (AMNH 235863, 235864, 235865, 235866, 235867, 235868, 235869, 235870, 235871, 235872, 235873, 235874, 235875, 235876, 235877, 235878, 235879, 235880, 235881). Uruguay: Lavalleja, Pirarajá (AMNH 205477, 205478, 205503, 205504, 205505, 205508, 205509, 205510, 205511, 205512, 205513, 205514, 205515); Colón (USNM 252599); Tacuarembó, Arroyo Yaguarí (MZUSP 28979, 28981); Río Negro, Arroyo Grande (MHNG 1748-47).

Myotis midastactus (N=30): Bolivia: Beni, Cercado (AMNH 211156 [holotype], 211167–211169, 211171–211176, 211178–211184, 211190, 211192–211198); Santa Cruz, Parque Nacional Kempff Mercado, El Refugio (USNM 584502). Paraguay: Presidente Hayes (MVZ 144481–144484).

Myotis nigricans (N=72): Argentina: Chaco, Sargento Cabral, La Forrestal, Capitan Solari (OMNH 18885, 18886); Chaco, Almirante Brown, 20 km NW by road, and 11 km NE by road Pampa El Mangrullo (OMNH 23767); Corrientes, Capital, Laguna Brava (OMNH 18887, 18888); Misiones, Capital, Posadas (MACN 18019); Misiones, Iguazú, Libertad (MACN 18487, 18489). Brazil: Rio de Janeiro, Seropédica, UFRRJ campus (ALP 588, 589, 625–631, 635). Paraguay: Presidente Hayes, 227 km NW Villa Hayes by road (MVZ 144707, 144708, 144710, 144711, 144713–144717, 144719, 144720, 144722, 144726–144732, 144735, 144738, 144739, 144741, 144743, 144744, 144746–144750, 144752, 144753, 144755–144757, 144761–144764, 144766–144780).

Myotis pampa (N=15): Uruguay: Artigas, ca. 6 km NW from Belén (AMNH 205471* [holotype]); Artigas, ca. 6 km NW from Belén (AMNH 205461*, AMNH 205464*, AMNH 205467*, AMNH 205472*, AMNH 205476*); Tacuarembó, ca. 40 km NW to Tacuarembó city (AMNH 205541*, AMNH 205545*, AMNH 205546*, AMNH 205552*, AMNH 205553*, AMNH 205562*, AMNH 205563*, AMNH 205564*, AMNH 205565*).

Myotis pilosatibialis (N=32): El Salvador: Ahuachapán, El Imposible, San Francisco Menéndez (ROM 101273), Santa Ana, Parque Nacional Montecristo (ROM 101352, 101353, 101356, 101357, 101430, 101433, 101465–101467, 101524). Honduras: Francisco Morazán, 1 km W Talanga (LACM 36879 [holotype]), Cortes (CM 112905, 118614, 118615). Guatemala: Chimaltenango, Chocoyos (FMNH 41653, 41840, 41841, 41843, 41844, 41845, 41846, 73365, 73366, 73367); El Petén, Chinajá (KU 82109, CM 118920, 18921). México: Oaxaca (KU 99731, LACM 14244, 14245, 26159,

26127, 26128); Tamaulipas, Ocampo (AMNH 164969, 164945, 164967, 164971, 164972, 164939, 144988); Veracruz, Coatepec, Ojo de Agua (AMNH 254676, 254677).

Myotis riparius (N=61): Argentina: Corrientes, Capital, Laguna Paivas, Barrio Las Lomas (CML 2994); Formosa, Río Porteña, km 64, a 5 km al Sur de Estancia Sta. Catalina (OMHN 18889); Formosa, Río Bermejo, 10 millas al S de Colonia km 503 (CML 5412); Formosa, Parque Nacional Pilcomayo (MACN 20881, 20895); Formosa, Jecc. Cassinera, R. Teuco (MACN 20938); Jujuy, Santa Bárbara, Laguna “La Brea”, 25 km antes de Palma Sola, sobre Ruta 1 (OMNH 18890, 18891); Salta, San Martín, 6 km al W de Piquirenda Viejo (CML 3157); Tucumán, Burruyacú, Balneario Piedra Tendida, 6 km al O del El Cajón (CML 3155); Tucumán, Reserva Provincial Santa Ana (El Saltón), Río Chico (CML 3158). Brazil: Pará, Mocambo (ALP 1915, 2002, 2003, 2554, 2557, 2562, 2587, 2610); Pará, Belém (USNM 361782, 361788–361791); Pará, Altamira (USNM 549517, 549518). Colombia: Valle del Cauca, Hormiguero (USNM 483949*, 483951*); Valle del Cauca, Río Arroyohonda (USNM 483950*); Tolima, Carmen de Apicalá (MVZ 104945, 104946); Caquetá, Río Caquetá (FMNH 72178); Meta, Parque Natural Sierra de La Macarena (FMNH 58754). COSTA RICA: Puntarenas, Parque Nacional Carara (FMNH 180728); Limón, Cariari (LSUMZ 12974); San José, Fila la Maquina (LSUMZ 12928). Panamá: Bocas del Toro, Isla Popa (USNM 464368*, 575586*); Chiriquí, Cotito Near (USNM 331916*); Panamá, Cerro Azul (ROM 99936*); Panamá, Cerro Campana (USNM 306795*); Panamá, San Blas (USNM 335410*); Darién, Tacarcuna Village Camp (USNM 306798*, 310254*, 310255* [holotype], 310256*, 310257*, 338097*). Peru: Loreto, Río Curaray (KU 158162, AMNH 71645); Madre de Dios, Río Tambopata (USNM 530919); Madre de Dios, Lago Sandoval (MVZ 157782); Madre de Dios, Manu (FMNH 174933); Ucayali, Balta (LSUMZ 12268, 12269, 12271). Suriname: Para (CM 68443); Brokopondo (ROM 113879, 114007, 114142).

Myotis ruber (N=42): Brazil: Minas Gerais, Viçosa (USNM 391140, ROM 70911, 78803–78805, 91211); Rio de Janeiro, Teresópolis (ALP 6452*, 6457*, 6458*, 6497*, 6499*, 6506*, 6512*, MN 3400*), Reserva Biológica do Tinguá (ALP 6621*, 6683*), São Paulo, Cananéia (MZUSP 27595*), Boracéia (MZUSP 28359*, 28367, 28368), São Paulo (MZUSP 31470–31473), Buri (MZUSP 32971–32973, 32975), Salesópolis (MVZ 185692); Santa Catarina, Nova Teotonia (MHNG 1916-71); Rio Grande do Sul, São Lourenço da Mata (MZUSP 1988*). Paraguay: Sapucay, Sapucay (USNM 115097* [holotype], 121478*); Itapúa, Arroyo Pirayu (MHNG 1747-56), Santo Temembey, 4 km amont (MHNG 1695-27); Misiones, Iguazu (OMNH 18882).

Myotis simus (N=68): Brazil: Amazonas, Manaus (AMNH 91475–91478, 91500); Amazonas, Borba (AMNH 91886, 91888–91891, AMNH 94224, 94225, 94227, 94230–94234); Amazonas, Parintins (AMNH 92983, 93490, 93492–93496, 93922, 93923); Amazonas, Río Juruá (MZUSP 638, 1062, 1074); Amazonas, Itacoatiara (MZUSP 4372). Colombia: Amazonas (TTU 9073, 9076–9078). Ecuador, Pastaza, Río Capahuari (FMNH 43143). Perú: Pasco, Oxapampa (USNM 364481, 364482); Loreto, Maynas (AMNH 74110); Loreto, Río Curanja (LSUMZ 12251, 14264); Loreto (AMNH 76244, 76252, 76253, MHNG 1694-41, 1694-42); Huánuco (LSUMZ 14262); Ucayali, Balta (LSUMZ 12249, 12250); Ucayali, Yarinacocha (FMNH 62615, 97988).